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Changes in climate drive recent monarch butterfly dynamics

Erin R. Zylstra[1]✉, Leslie Ries[2], Naresh Neupane[2], Sarah P. Saunders[1,3], M. Isabel Ramírez[4], Eduardo Rendón-Salinas[5], Karen S. Oberhauser[6], Matthew T. Farr[1] and Elise F. Zipkin[1]

Declines in the abundance and diversity of insects pose a substantial threat to terrestrial ecosystems worldwide. Yet, identifying the causes of these declines has proved difficult, even for well-studied species like monarch butterflies, whose eastern North American population has decreased markedly over the last three decades. Three hypotheses have been proposed to explain the changes observed in the eastern monarch population: loss of milkweed host plants from increased herbicide use, mortality during autumn migration and/or early-winter resettlement and changes in breeding-season climate. Here, we use a hierarchical modelling approach, combining data from >18,000 systematic surveys to evaluate support for each of these hypotheses over a 25-yr period. Between 2004 and 2018, breeding-season weather was nearly seven times more important than other factors in explaining variation in summer population size, which was positively associated with the size of the subsequent overwintering population. Although data limitations prevent definitive evaluation of the factors governing population size between 1994 and 2003 (the period of the steepest monarch decline coinciding with a widespread increase in herbicide use), breeding-season weather was similarly identified as an important driver of monarch population size. If observed changes in spring and summer climate continue, portions of the current breeding range may become inhospitable for monarchs. Our results highlight the increasingly important contribution of a changing climate to insect declines.

Insect populations are declining at alarming rates with notable losses across ecosystems and lineages[1–5]. Insects provide essential services including pollination, decomposition and food for higher trophic levels[4]. Consequently, the loss of insects has the potential to fundamentally disrupt biological communities and impair ecosystem functions locally, regionally and even globally[5,6]. Identifying factors that govern population dynamics, especially those that contribute to declines of migratory species, is challenging as it requires disentangling the effects of multiple, interrelated stressors that may operate across seasons and spatial scales[2,7]. However, characterizing the proximate, and potentially shifting, drivers of population change is critical to avert this rapidly evolving crisis[7].

One of the most striking examples of insect declines is that of monarch butterflies (*Danaus plexippus*) in North America, with substantial losses in both the eastern and western migratory populations[8–10]. The larger of the two populations occurs east of the Rocky Mountains and has declined sharply since the mid-1990s (Fig. 1a). Each year, the eastern population migrates thousands of kilometres over multiple generations, complicating efforts to identify the relative importance of seasonal stressors in its decline. In late winter and early spring (late February through March), monarchs leave their overwintering sites in central Mexico and migrate to breeding grounds in the southeastern United States, centred in and around eastern Texas, where they produce the first generation of the year. That first generation then migrates to summer breeding grounds in the northern United States and southern Canada, arriving in May and June, where two to three more generations are produced. Starting in late August, individuals in the final generation migrate south to the same overwintering sites in central Mexico.

Although monarchs are one of the most well-studied insects, the pattern and causes of their decline have been intensely debated[9,11], in part because previous assessments have been based on a subset of the annual migratory cycle or a single data source. Three hypotheses regarding the drivers of eastern monarch population dynamics have garnered substantial support. The most prominent is the milkweed limitation hypothesis, which attributes changes in the monarch population, particularly the steep decline observed in the late 1990s, to widespread loss of milkweed (*Asclepias* spp.), the host plant and sole food source for larval monarchs. Many species of milkweed thrive in environments with occasional to frequent disturbance and were common in agricultural areas throughout the Midwestern United States for most of the twentieth century[12,13]. These agricultural regions could support >70 times as many monarchs as non-agricultural environments[14]. However, milkweed in agricultural areas began to decline in the 1990s with the introduction of genetically modified, herbicide-tolerant crops and subsequent increases in glyphosate use (Fig. 1b)[15]. This surge in herbicide use coincided with the steepest drop in the monarch population (Fig. 1). In contrast, the migration survival hypothesis attributes changes in the monarch population to failed autumn migration and/or re-establishment at overwintering sites. Focus on this portion of the annual migratory cycle stems from work illustrating a disconnect between overwintering population declines and counts of adult monarchs from the longest-running monitoring programme on the summer breeding grounds, which appeared to be relatively stable during the same time period[16,17]. This disconnect has spurred investigations into whether nectar availability along the autumn migratory corridor, disease-related migration mortality and/or reductions in habitat at overwintering sites may be

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[1]Department of Integrative Biology, Ecology, Evolution, and Behavior Program, Michigan State University, East Lansing, MI, USA. [2]Department of Biology, Georgetown University, Washington, DC, USA. [3]National Audubon Society, New York, NY, USA. [4]Centro de Investigaciones en Geografía Ambiental, Universidad Nacional Autónoma de México, Morelia, Mexico. [5]World Wildlife Fund-México, Terrestrial Ecosystems Program, Zitácuaro, Mexico. [6]University of Wisconsin Arboretum, University of Wisconsin–Madison, Madison, WI, USA. ✉e-mail: zylstr91@msu.edu

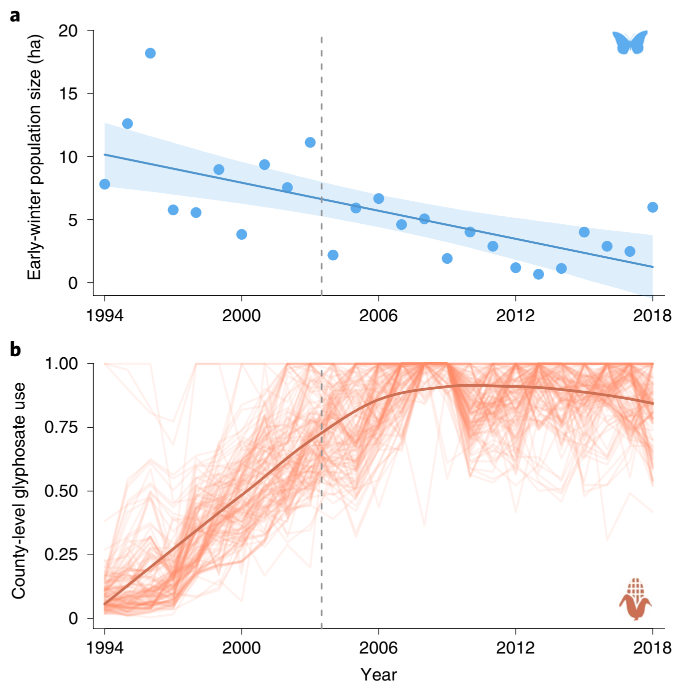

Fig. 1 | Overwintering monarch population size in Mexico and summer glyphosate use in the Midwestern United States. a, Total area occupied, in hectares, at overwintering colonies in late December with linear trend (blue line) and 95% CI (shaded area; slope = −0.37 ha yr^{-1}, 95% CI: −0.55, −0.19). **b**, Proportion of corn and soybean fields treated with glyphosate herbicide in 149 US counties that were surveyed for monarchs and had at least 10% agricultural cover (thin orange lines; thick line shows loess fit). Vertical dashed lines denote the break between our 1994–2003 and 2004–2018 analyses.

driving changes in the monarch population[11,18]. Finally, the climate change hypothesis posits that changes in spring and/or summer climate are negatively impacting monarch population recruitment. Breeding-season temperatures and precipitation influence rates of larval development and survival[19] and may also have indirect effects on the monarch population by altering the distribution, phenology and abundance of milkweed resources. The size of the summer population has been linked to weather conditions[20,21], which are becoming increasingly unsuitable for monarchs and native milkweeds at the southern end of the monarch spring and summer breeding ranges[22,23].

To determine the extent to which each of these hypotheses explain recent dynamics of the eastern monarch butterfly population, we collated available data on adult monarchs and seasonal stressors throughout the annual migratory cycle starting in 1994, when systematic monitoring of the overwintering population began. Each year, researchers comprehensively survey areas in central Mexico where the entire eastern population of monarchs form a limited number of dense aggregations (hereafter, colonies) in high-elevation forests[24]. Because overwintering behaviour prevents precise estimation of monarch abundance within colonies[24,25], researchers measure the area occupied by butterflies (in hectares) and use this as an index of population abundance. Starting in 2004, monitoring agencies reported the area occupied in early winter (late December) at each of 19 overwintering colonies (Supplementary Table 1); only a sum of the total area occupied across all colonies is available in each of the 10 years prior[24].

On the summer breeding grounds, butterfly surveys began in 1975. However, the amount of available data increased substantially in the mid-2000s with the expansion of volunteer-based monitoring programmes throughout the Midwestern United States. Between 2004 and 2018, five independent butterfly monitoring programmes provided systematic counts of adult monarchs from >14,500 surveys at 773 locations in eight US states and southern Ontario, Canada. In contrast, summer count data were available from 4,004 surveys at only 301 locations between 1994 and 2003 (Extended Data Fig. 1 and Supplementary Table 2). Because summer survey locations were not selected randomly, agricultural areas were underrepresented, particularly in the 1990s and early 2000s. This sampling bias could result in underestimates of summer population sizes, especially before 2004, when milkweed—and monarchs—were comparatively more abundant in agricultural areas[15].

For pragmatic reasons, we thus partitioned the data and performed analyses separately for 1994–2003 and 2004–2018, with somewhat limited ability to make inferences before 2004 when data on the summer breeding population were comparatively sparse and estimates of the area occupied by overwintering monarchs were aggregated among colonies. We further expected that the relative importance of various drivers may have shifted between the two time periods, given that average glyphosate use increased from <10% to ~75% between 1994 and 2003 (causing severe declines in milkweed densities)[15] but plateaued at ~75–90% between 2004 and 2018 (presumably maintaining milkweed at lower, but stable, densities; Fig. 1b).

We developed a Bayesian, hierarchical model to estimate seasonal monarch population sizes between 2004 and 2018. The model was composed of two components: the first describes the monarch population from the time at which individuals leave the overwintering grounds through the spring and summer breeding periods (February–August; Fig. 2a–b) and the second describes the final generation as it leaves the summer breeding grounds and arrives on the overwintering grounds (August–December; Fig. 2a,c). We relied on the extensive monarch literature to determine which environmental variables to include in our analysis and excluded factors (Supplementary Information) when evidence from previous studies suggested minimal population-level effects (autumn temperatures and infection with protozoan parasites) or when data were insufficient (parasitism by tachinid flies and insecticide use)[11,15,17,18,20,21,26–28]. In the first seasonal component, we modelled variation in summer count data (from butterfly surveys conducted between 14 June and 15 August) as a function of late-winter population size (measured as the total area occupied by monarchs in late February), spring temperature (measured in growing degree days [GDD]) and precipitation (mm) in eastern Texas (where much of the first generation is produced), as well as temperature (GDD), precipitation, land cover and glyphosate use in counties throughout the summer breeding range (where subsequent generations are produced). In the second component, we modelled variation in the area occupied in early winter (from surveys conducted in late December) as a function of peak-summer population size, autumn nectar availability and forest cover at overwintering sites. We linked the two model components through our index of peak-summer population size, a derived parameter in the first component of the model that we used as a covariate in the second part of the model. We constructed a similar but reduced version of the model to describe population dynamics between 1994 and 2003, when fewer monarch and covariate data were available. Although the structure of our models precludes estimation of the total amount of variance explained by environmental factors, we used hierarchical partitioning to estimate the relative importance of (or the amount of explained variance attributable to) factors in our model during each time period[29]. Finally, to evaluate linkages across the monarch's annual cycle, we calculated the extent to which population size in one season was associated with population size in the previous season via post-hoc regression analyses.

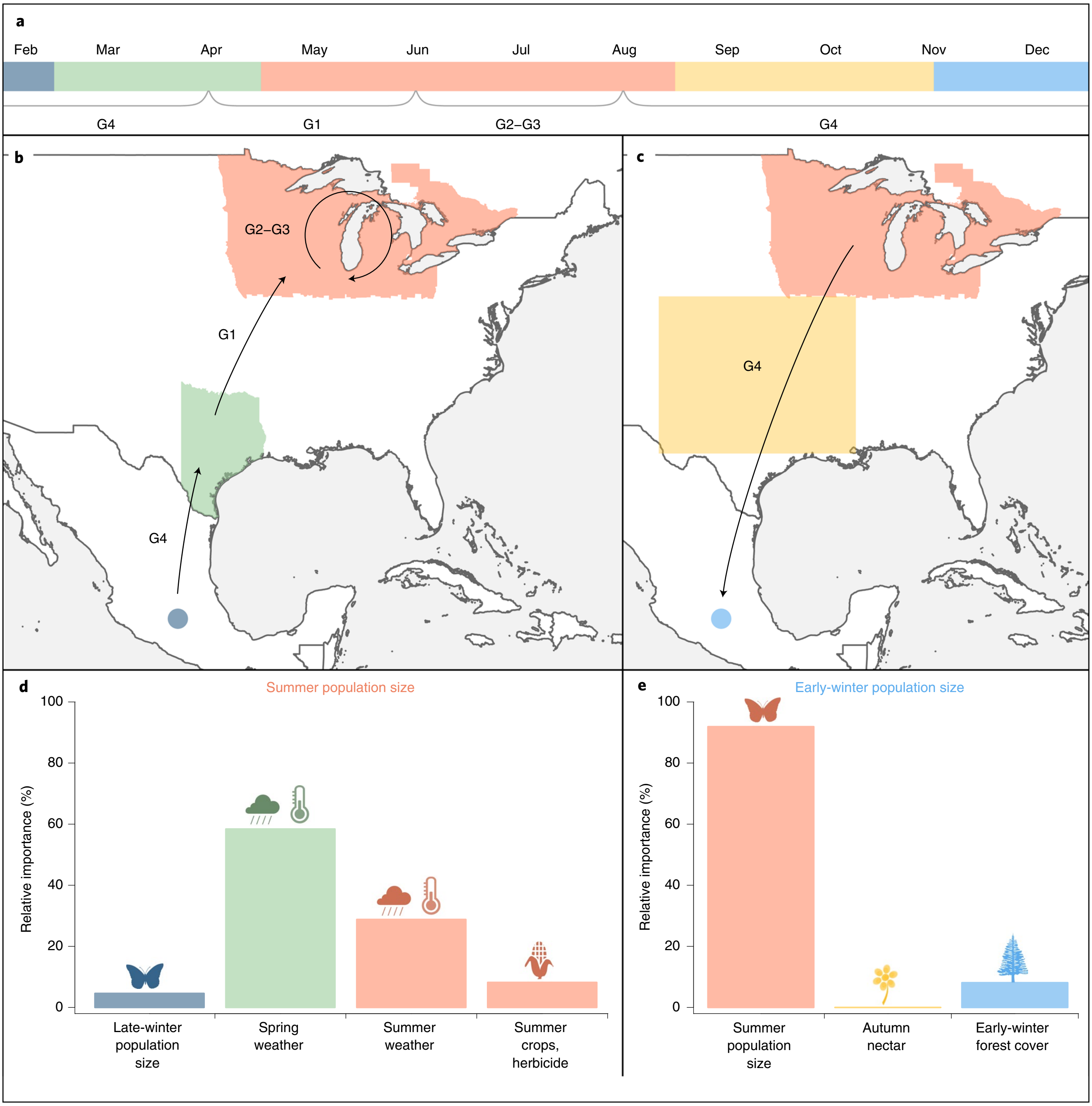

Fig. 2 | Relative importance of seasonal factors influencing the size of the eastern North American monarch population (2004–2018). a–c, Timing (**a**) and locations of the four monarch butterfly generations (G1–G4) as they migrate north and arrive on the spring and summer breeding grounds (**b**) and migrate south, returning to the overwintering grounds (**c**) (light and dark blue, overwintering grounds; green, spring breeding and migration corridor; orange, summer breeding grounds; yellow, autumn migration corridor). Coloured regions show the areas over which monarch and environmental data were summarized, not the complete geographic range of the population. **d**,**e**, Relative importance of factors affecting population sizes in summer (**d**) and early winter (**e**), 2004–2018.

Results

Monarch population between 2004 and 2018. We found strong support for the climate change hypothesis and comparatively little support for the other two hypotheses during the period from 2004 to 2018. Spring and summer weather conditions had the largest effects on summer population size, explaining 4.6 and 2.3 times more variation, respectively, than other factors combined (Fig. 2d). The relationships between spring weather variables and the subsequent summer monarch population size were nonlinear, with expected monarch counts lower when temperatures and precipitation deviated substantially from observed means (Fig. 3). Summer population size was positively associated with summer precipitation and summer temperatures (Fig. 4), except in the southern part of the breeding range, where high temperatures (annual GDD values

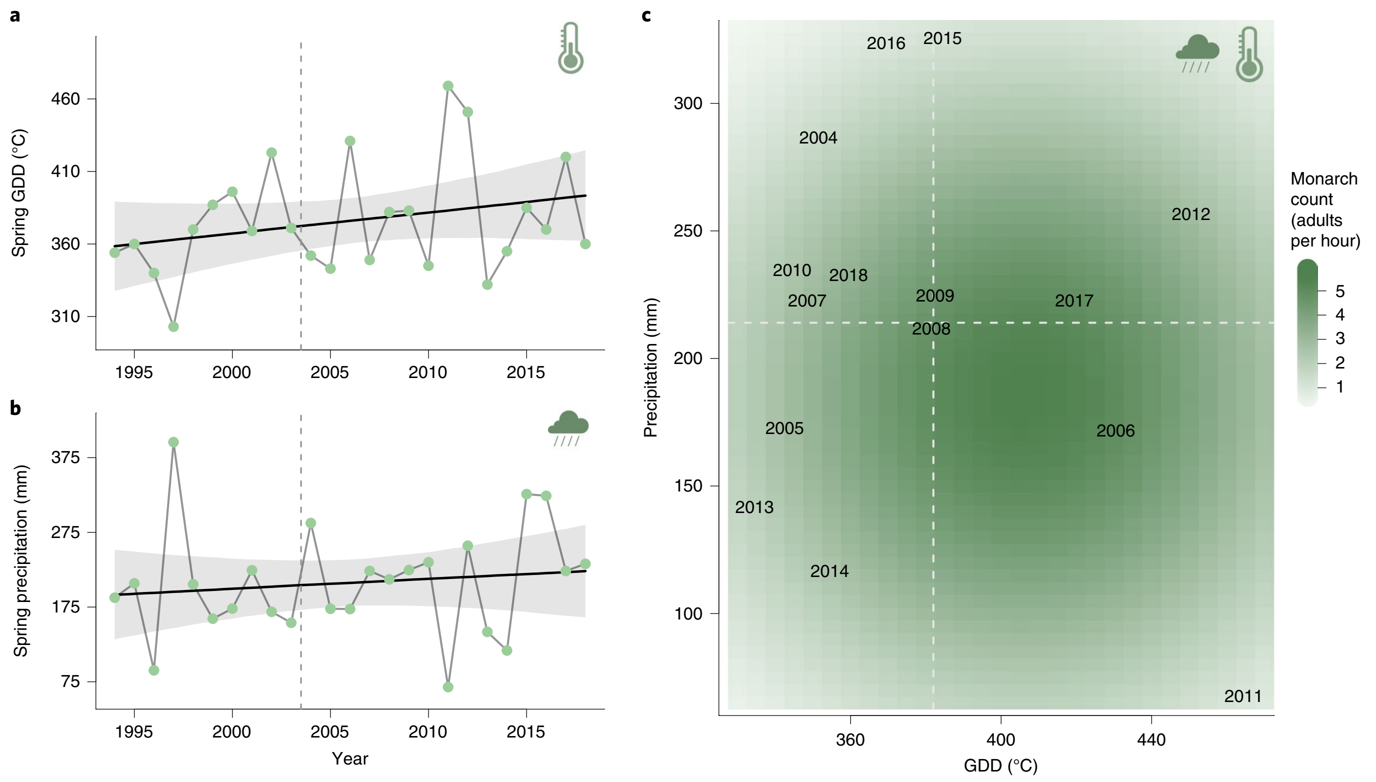

Fig. 3 | Spring weather (1994–2018) and estimated effects on summer monarch population size (2004–2018). **a**, Temperatures, measured as GDD (°C), accumulated 22 March to 2 May, in eastern Texas. **b**, Cumulative precipitation (mm) during February to April, in eastern Texas. Solid black lines and shaded areas show linear trends with 95% CI. Vertical dashed lines denote the break between our 1994–2003 and 2004–2018 analyses. **c**, Estimated marginal effects (posterior medians) of spring GDD and precipitation on expected monarch counts (adults per h) during peak summer (19 July–25 July), 2004–2018. Annual spring conditions indicated with their respective year labels; dashed white lines denote average values during 2004–2018.

well above normal) had a slight negative effect on monarch counts (dotted line in Fig. 4c). Summer monarch counts were also positively associated with agricultural areas and negatively associated with glyphosate use (Supplementary Table 3), consistent with the milkweed limitation hypothesis but these effects were small relative to the effects of breeding-season weather and contributed less to explained variation in summer population sizes (Fig. 2d). This was not unexpected, however, as glyphosate application rates had reached high levels by 2004 and were relatively stable over this 15-yr period (Fig. 1b)[21].

The size of the population in early winter was positively associated with peak-summer population size, with minimal effects of autumn nectar availability and forest cover at overwintering sites (Fig. 2e and Supplementary Table 4). In contrast to a previous analysis supporting the migration survival hypothesis[17], we found evidence of a decline in the summer breeding population via our model-derived estimates of peak-summer population size (Extended Data Fig. 2). Post-hoc linear regressions similarly revealed a strong association between the estimated index of peak-summer population size and the total area occupied across all colonies in early winter ($R^2 = 0.67$; Fig. 5a). This high correlation between peak-summer and subsequent early-winter population sizes, as well as the estimated decline in peak-summer population size, suggest that mortality incurred during autumn migration is not the principal driver of recent population changes. Taken together, these results underscore the value of integrating multiple sources of data to estimate summer population size rather than relying on raw counts from a single data source with limited spatial or temporal coverage[16–18]. We also found a moderately high correlation between the size of the monarch population at the beginning and end of the winter season ($R^2 = 0.43$; Fig. 5b), providing evidence that overwintering mortality, between late December and late February, is unlikely to have been one of the primary drivers of population change during this period. Indeed, the lowest correlation between seasonal population sizes occurred between late winter and peak summer ($R^2 = 0.31$; Fig. 5c), highlighting the importance of environmental conditions during the monarch's breeding seasons in determining annual population sizes.

Annual weather conditions on the spring and summer breeding grounds are shifting[30–32]. Between 1994 and 2018, there were modest increases in spring temperature and precipitation (Fig. 3a,b). Expected monarch counts on the summer breeding grounds were highest following mild springs (that is, slightly warmer and drier than average conditions in 2004–2018), while other combinations of temperature and precipitation resulted in lower expected counts (Fig. 3c and Supplementary Table 3). Across the summer breeding grounds, the direction and magnitude of weather changes varied geographically (Fig. 4a,b and Extended Data Fig. 3). In northern parts of the summer breeding range, where average temperatures are cooler and have changed little or even decreased since 1994, expected monarch counts were highest during the warmest and wettest summers (Fig. 4c,d). In the warmer southern portions of the summer breeding range, temperature increases were greater than those observed in other regions over both the short-term (2004–2018; Extended Data Fig. 3c) and long-term (1994–2018; Fig. 4a and Extended Data Fig. 3a). In contrast to northern parts of the summer breeding range, high summer temperatures in the south tended to have a slight negative effect on monarch counts (dotted line in Fig. 4c), indicating that these areas are becoming less hospitable for breeding monarchs[22].

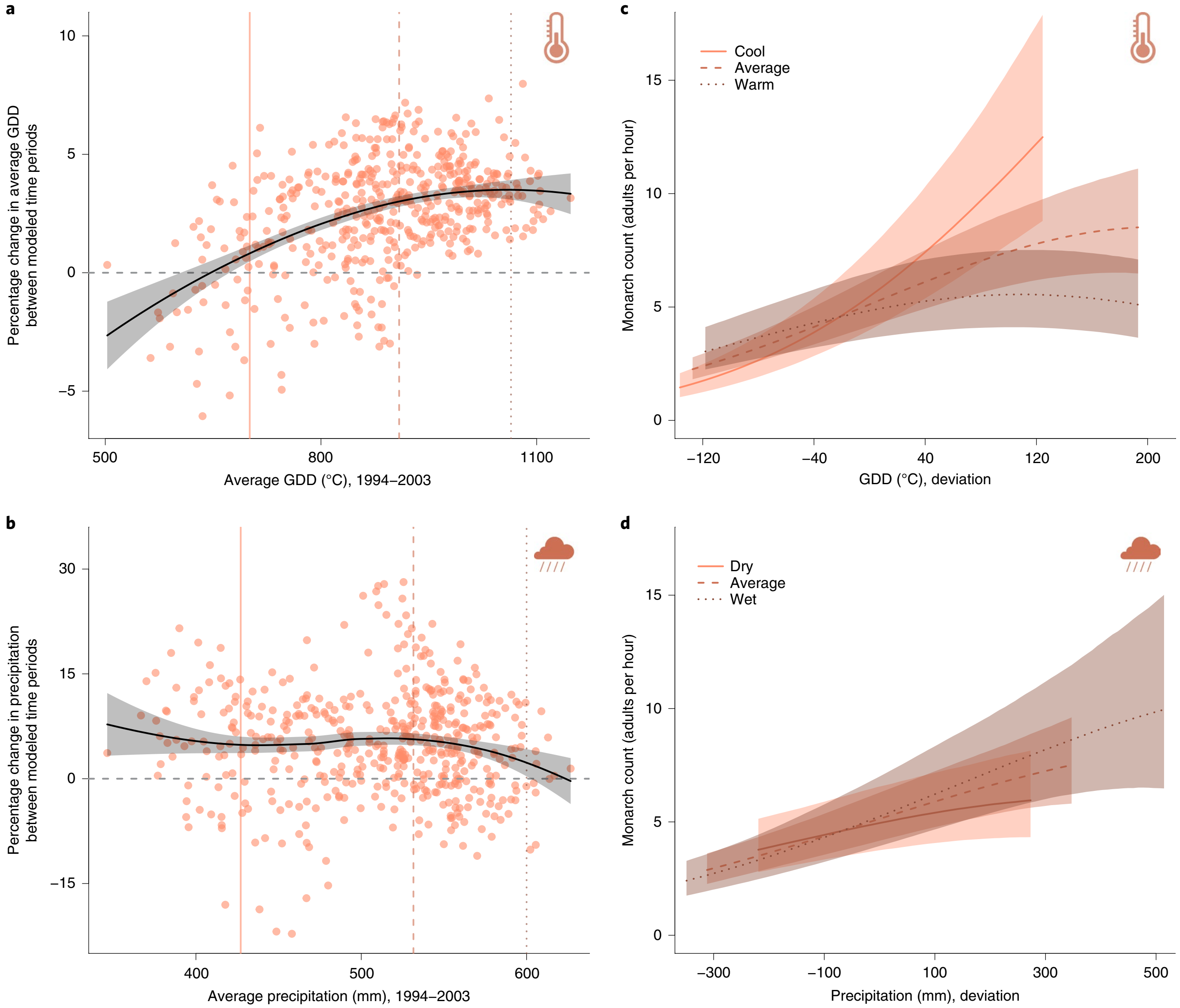

Fig. 4 | Summer weather (1994–2018) and estimated effects on summer monarch population size (2004–2018). a,**b**, Percentage change in average temperatures (GDD from 3 May to 15 August) (**a**) and precipitation (April–August) (**b**) for each US county in the summer breeding range between 1994–2003 and 2004–2018; positive values (above dashed horizontal lines) indicate an increase between time periods. Solid black lines and shaded areas show loess fits. **c**,**d**, Estimated marginal effects (median and 95% CI) of GDD (**c**) and precipitation (deviations from 15-year averages) (**d**) on expected monarch counts in peak summer (19 July–25 July), 2004–2018. Positive deviations indicate values that are warmer (**c**) and wetter (**d**) than 2004–2018 county averages, whereas negative deviations indicate values that are cooler (**c**) and drier (**d**). Vertical lines in **a** denote average GDD values associated with cool, average and warm counties depicted in **c**; similarly, the vertical lines in **b** denote average precipitation values associated with dry, average and wet counties depicted in **d**.

It is difficult to tease apart the extent to which weather and other environmental factors affect trends versus annual fluctuations in the eastern monarch population (Supplementary Information). While there is clear evidence that the overwintering population declined between 1994 and 2018 (−0.37 ha yr^{-1}, 95% credible interval (CI): −0.55, −0.19), the population declined only modestly over the more recent 15-yr period (−0.12 ha yr^{-1}, 95% CI: −0.36, 0.13), suggesting that factors in our 2004–2018 model may be explaining annual population fluctuations to a larger extent than systematic declines. That said, we found no evidence of a temporal trend in residuals from the winter component of the 2004–2018 model (−0.003, 95% CI: −0.014, 0.008; Extended Data Fig. 4), while a reduced model that excluded temporal covariates did have a slight negative trend (−0.013, 95% CI: −0.026, 0.000). Thus, our model largely explained the more recent, although modest, decline in the overwintering population between 2004 and 2018 while also producing unbiased estimates of yearly variations.

Monarch population between 1994 and 2003. We found large effects of breeding-season weather, particularly in the spring, on the size of the summer population during 1994–2003, providing evidence for the climate change hypothesis (Supplementary Table 4). Glyphosate use was negatively associated with summer population size in agricultural areas, although the magnitude of glyphosate-related effects was smaller than expected given the rapid increase in herbicide use and the concurrent decline in the

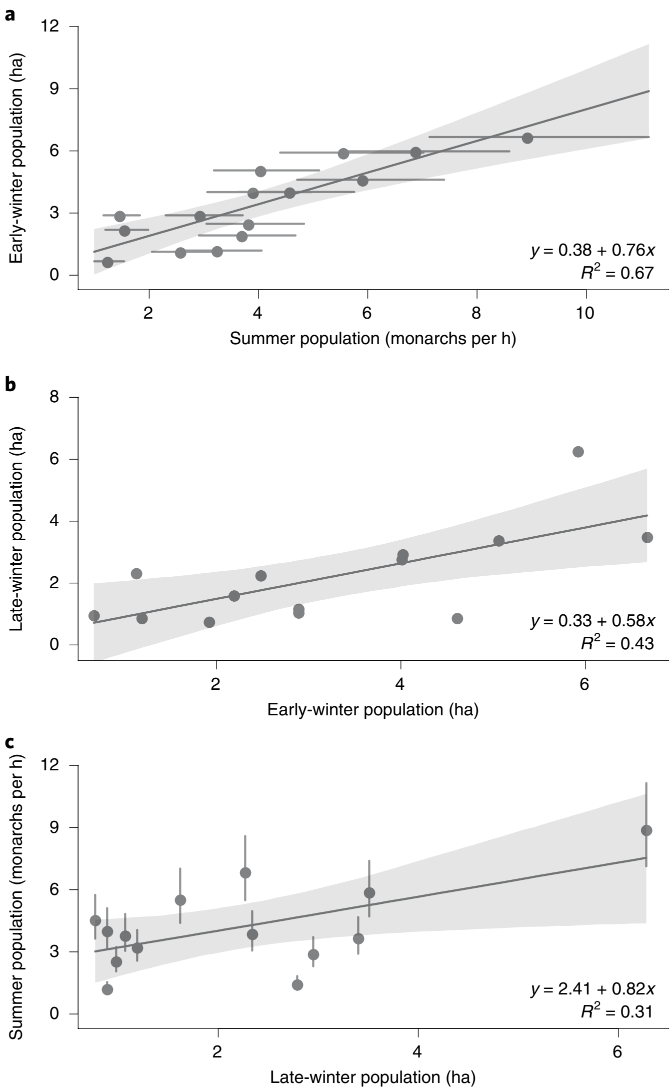

Fig. 5 | Relationships among monarch population sizes in summer, early winter and late winter between 2004–2018. a–c, Relationship between monarch population size during: peak summer (19 July–15 August) and the subsequent early winter (15–31 December) (**a**); early winter and late winter (15–29 February) (**b**); and late winter and the subsequent summer (**c**). Winter population indices represent the total area occupied across all monarch colonies in Mexico (data collected and reported with no associated measures of uncertainty). Estimates of summer population size are model-based predictions of the expected number of adult monarchs observed per hour on an average survey (posterior medians with 95% CI). Trends from post-hoc linear regression models with 95% CIs (shading) and associated R^2 values are also shown. **b** and **c** do not include 2004 because late-winter estimates were unavailable.

overwintering population (Supplementary Table 5 and Fig. 1). Unless additional and more representative data from this time period become available (for example, from sites within and adjacent to agricultural fields), definitively determining the primary driver(s) of the eastern monarch population decline before 2004 will not be possible. However, our results, which are based on the most comprehensive set of systematic survey data currently available, reveal a consistently strong effect of spring weather conditions on the summer monarch population over a 25-yr period and a growing importance of summer weather (Extended Data Fig. 5 and Fig. 4).

Discussion

Abundance in many insect populations varies greatly from one year to the next, depending in large part on weather conditions[33,34]. Monarchs are no exception, but the importance of cross-seasonal effects (for example, spring weather on summer breeding populations) adds a complex, temporal component to these relationships. Our understanding of the effects of weather on the eastern North American monarch population is further complicated by the immense geographic extent of their summer breeding range. Despite these challenges, our hierarchical, integrated modelling approach reveals that spring and summer weather conditions were more important than other factors in determining the size of the summer population during 2004–2018. In turn, summer population size was a strong predictor of the size of the overwintering population. These findings highlight the importance of a changing climate to recent, and probable future, monarch population dynamics.

Climate models predict that ambient temperatures will increase throughout much of the monarch's spring and summer breeding ranges[35] and we found evidence that these changes are already underway (Figs. 3a and 4a). The greatest increases in summer temperatures occurred at lower latitudes (40–44° N; Extended Data Fig. 3), consistent with global climate projections[36]. If future temperatures regularly exceed the optimal range for monarchs breeding at lower latitudes during the spring and summer, the size of the monarch breeding population will probably continue to decline. Predicted changes in precipitation on the spring and summer breeding grounds are more mixed[37,38]. Cumulative precipitation increased throughout much of the summer breeding range between 1994 and 2018 (Fig. 4b), which could benefit monarchs if continued increases lead to greater milkweed availability. However, it is difficult to predict how the population will respond if future precipitation or future temperatures deviate substantially from historic values.

The role of herbicides in the decline of monarchs has been a topic of debate in both scientific and public forums. While there is substantial correlative evidence linking glyphosate use to declines in milkweed and monarch populations before 2004 (Fig. 1)[15], we found little evidence that glyphosate use has been driving fluctuations and declines in the monarch population since that time. During 2004–2018, ~74% of variation in glyphosate use was attributable to differences among counties, with annual changes accounting for <26% of the total variation. We found no evidence that declines in monarch counts were more severe in counties with higher glyphosate use, which we would expect if glyphosate effects were cumulative or if recent use continued to degrade or eliminate remaining breeding habitat for monarchs (Supplementary Information). Rather, we suspect that milkweed abundance declined abruptly in the late 1990s and early 2000s in response to rapid adoption of glyphosate-resistant crops and glyphosate use since that time has largely prevented subsequent growth of milkweed (and possibly monarch) populations in agricultural areas.

Insect declines in temperate regions have often been attributed to habitat loss and agricultural intensification, whereas until recently, climate-related stressors had largely been viewed as secondary or exacerbating factors[39]. Yet, weather can play a pivotal role in driving not only insect population dynamics but also their declines[40,41]. Climate change thus poses a considerable threat to insects, especially because near-term weather conditions cannot be manipulated and climate change cannot be abated as readily as other stressors. Although the mechanisms and magnitude of climate-related effects on insects are likely to vary regionally (as we demonstrate here), changes in temperature and precipitation regimes are occurring worldwide, threatening not just monarchs but insect populations on a global scale. Understanding the extent and relative severity of these threats is paramount to mitigating current and future losses.

Methods

Data on the monarch summer breeding population. We integrated count data on adult monarch butterflies from multiple sources to characterize spatiotemporal variation in abundance on the summer breeding grounds. We defined the summer breeding grounds to include 545 counties in eight US states (Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Ohio and Wisconsin) and census districts (hereafter, counties) in Ontario, Canada above 40° N latitude (Extended Data Fig. 1). Our delineation of the summer breeding grounds was informed by recent isotopic evidence that suggests the majority of individuals arriving on the overwintering grounds originate from the Midwestern United States and southern Ontario, whereas a smaller proportion of individuals originate from the northeastern United States, the north-central United States and south-central Canada and the southeastern United States[42]. We excluded six counties in northern Ontario that extend north of 48° latitude, the approximate northern breeding limit of monarch butterflies, where no surveys were conducted[43].

We collated all available monarch count data between 1994 and 2018 from five monitoring programmes on the summer breeding grounds. First, we obtained count data from surveys conducted by the North American Butterfly Association (NABA). NABA surveys were located throughout the summer breeding range and were typically completed once per season (Extended Data Fig. 1 and Supplementary Table 2). During each NABA survey, one or more groups of volunteers searched within a circular area (25-km diameter) and recorded the total number of adult butterflies observed, by species[16,44]. We summed monarch counts from all groups to obtain a single count per survey location per sampling event. The remaining data sources were 'Pollard walk' surveys conducted by butterfly monitoring networks (BMNs) in four states on the summer breeding grounds: Illinois (surveys began in 1987), Ohio (1995), Iowa (2006) and Michigan (2011) (Extended Data Fig. 1). In the four BMNs, volunteers surveyed locations multiple times each summer (median = five surveys per summer), walking fixed transects and counting the number of adult butterflies observed within a predetermined distance of the observer (Supplementary Table 2)[16,44,45]. Although all BMNs used Pollard walk methods, slight variations in protocols (for example, maximum observation distances and transect lengths) probably resulted in systematic differences among counts, which we accounted for in our analyses. For each BMN survey, we used the total number of monarchs observed per survey location per sampling event.

To account for seasonal variation in monarch abundance on the summer breeding grounds, we sequentially numbered each week of the season, designating week 1 to begin on 1 March to correspond with the approximate time at which monarchs leave the overwintering grounds and begin their northward migration[20,21,46]. We included counts from summer surveys completed in weeks 16–24 (14 June–15 August) to capture the growth of the summer breeding population, but considered 'peak' summer abundance (our covariate in the winter submodel) to occur over a 4-week period, weeks 21–24 (19 July–15 August)[16–18]. Our 2004–2018 dataset included 1,393 NABA surveys at 145 locations in eight US states and Ontario, Canada, and 13,198 surveys conducted by four BMNs at 628 locations (Supplementary Table 2). Our 1994–2003 dataset included 577 NABA surveys at 108 locations in seven US states and 3,427 surveys conducted by Illinois and Ohio BMNs at 193 locations. We excluded Canadian surveys from the 1994–2003 analysis because corresponding covariate data were unavailable.

Data on the monarch overwintering population. We used data collected in Mexico in early winter (late December) as an index of monarch population size shortly after arrival on the overwintering grounds. By late December, butterflies form dense colonies in high-elevation forests in the central Mexican states of Michoacán and México[24]. Most colonies are located within the Monarch Butterfly Biosphere Reserve (MBBR), which was established in 2000 to protect forests inhabited by the overwintering population[47]. Monarch colonies are typically assigned names on the basis of the agrarian, state, federal or private property in which the colony is located (19 unique colony names between 1994 and 2018) (Supplementary Table 1). Only a subset of properties is occupied each year and the geographic location of a colony within a property, when present, varies over time.

Between 1994 and 2018, researchers surveyed each colony present in the region, both inside and outside of the MBBR. Although surveys were conducted intermittently at known overwintering locations before 1994, limited effort was spent locating new colonies and, as a result, these earlier estimates of population size were unlikely to represent the entire overwintering population[48]. Thus, we elected to analyse data from 1994 to 2018, during which time researchers delineated the perimeter of each colony and measured the total area occupied, in hectares, in the second half of December[48]. Because overwintering aggregations are dense and virtually impossible to census[24,25], we used measurements of the area occupied in late December as an index of population size, as previous studies have done. Between 1994 and 2003, observers from Comisión Nacional de Áreas Naturales Protegidas (CONANP) and the MBBR led data collection efforts, reporting annual estimates of the total area occupied across all colonies. The World Wildlife Fund–Mexico (WWF) in alliance with CONANP began leading data collection efforts starting in December 2004, reporting the area occupied in each colony instead of a single aggregate value[24]. For 2004–2018 analyses, we combined the late-December measures of area occupied among colonies in close proximity to one another and refer to these units as 'supercolonies' ($n = 13$) (Supplementary Table 1). We used expert opinion to delineate supercolonies rather than use estimates from the original 19 colonies, as has been done previously[18], because locations of several colonies were near one another, occasionally shifted within or among seasons and intersected property boundaries, suggesting that they were unlikely to function as independent units through time. Nevertheless, preliminary models fit to colony-level data produced inferences that were qualitatively similar to those from models fit to data that had been aggregated into supercolonies (results not shown). We thus chose the more parsimonious designation of supercolonies for the biological rationale stated above. There are technically only three supercolonies that represent the aggregation of multiple colonies (Supplementary Table 1); however, we collectively refer to the group of three supercolonies and ten colonies used in our model as supercolonies.

In addition to supercolony-specific estimates of area occupied in late December, WWF-CONANP also began reporting the total area occupied (summed across colonies) twice each month throughout the winter season beginning in the winter of 2004–2005[24]. We used measurements of the total area occupied in late February, before most monarchs leave the overwintering grounds to migrate north, as an index of monarch population size at the end of winter[21]. To include late-winter population values as a covariate in the 2004–2018 summer submodel, we imputed the predicted area for February 2004 on the basis of a linear regression relating estimates in February to the previous December, 2005–2018 (Bayesian $R^2 = 0.43$; Fig. 5b) and the reported area occupied in December 2003 (11.12 ha) (ref. [24]).

Overview of covariate data. We used the extensive literature on seasonal and annual factors influencing the eastern monarch population as a guide to determine which covariates to include in our models[11,15,17,18,20,21,26–28,46,49]. In the sections that follow, we detail each covariate included in analyses. Information about covariates we considered but ultimately excluded from analyses can be found in the Supplementary Information. Except where noted, covariates were calculated for the years 1994–2018 and were included in both the 2004–2018 full annual-cycle model and the reduced model for 1994–2003. We use the following notation to identify the spatial and temporal scale at which covariates were measured: i denotes survey locations ($i = 1, \ldots, m_c$) in county c ($c = 1, \ldots, n$) on the summer breeding grounds and k ($k = 1, \ldots, 9$) denotes weeks 16–24 in year t ($t = 1, \ldots, 15$ or $t = 1, \ldots, 10$ in 2004–2018 or 1994–2003 models, respectively). We use j ($j = 1, \ldots, 13$) to denote supercolonies on the overwintering grounds.

Spring covariates. In late February and March, monarchs leave the overwintering grounds, migrating north to the spring breeding grounds in eastern Texas and surrounding areas, where they lay eggs and subsequently die. Approximately 1 month later, adults that successfully develop from those eggs continue the northward migration towards the summer breeding grounds. We defined the spring breeding region as eastern Texas (94° W to 100° W, 26° N to 34° N) (Fig. 2b) because evidence suggests that most monarchs migrate through this region and comparatively few individuals migrate through the western part of the state, which is more arid[23,50]. We characterized temperatures and precipitation across the spring breeding region and used these weather-related covariates in the summer submodel to explain variation in counts of adults in subsequent generations on the summer breeding grounds.

Temperature. Like many Lepidoptera, the rate of monarch development from egg to adult life stages depends on ambient temperatures[19]. Temperatures may also affect monarchs indirectly by influencing availability and quality of their milkweed host plants. Similar to previous studies, we used GDD to characterize the thermal environment in the spring breeding region[51]. GDD measures the heat accumulated within a species-specific range of temperatures (11.5–33 °C for monarchs) that allows for development[19,51]. To calculate spring GDD, we obtained temperature data from Daymet[52], which provides daily climate data at a 1-km resolution across North America, from 1980 to the present. Specifically, we obtained daily minimum and maximum temperatures between 22 March and 2 May (weeks 4–9) for gridded points separated by 1° across eastern Texas. We computed GDD values for each location and year and then averaged values across locations to produce an annual GDD value for eastern Texas (spGDD_t)[20,21,46].

Precipitation. Cumulative precipitation in eastern Texas is likely to affect the quantity and quality of host plant resources available to breeding monarchs[23]. We obtained monthly precipitation totals (mm) from Daymet for the same gridded locations in eastern Texas in February, March and April because these months coincide with the growing seasons for native milkweed and monarchs[20,23]. We averaged values across locations in each month and summed the monthly values to produce an annual estimate of spring precipitation for eastern Texas (spPCP_t).

Summer covariates. Monarchs that originated in the Texas region begin arriving on the summer breeding grounds in May. On average, another three generations are produced on the summer breeding grounds between May and August before the last generation enters reproductive diapause and begins migrating south to the overwintering grounds[27]. We characterized weather, land cover and agricultural practices in the Midwestern United States and southern Ontario and used these covariates in the summer submodel to explain variation in counts of adult monarchs. With the exception of one summer covariate that was measured at each survey location and used to explain local-scale variation in counts (amount of unforested area; open$_i$), we calculated all covariates on the summer breeding grounds at the county level.

Temperature. Like spring temperatures, we expected that temperatures on the summer breeding grounds could affect larval monarchs directly and indirectly by influencing milkweed availability. We characterized spatiotemporal variation in temperatures on the summer breeding grounds in two ways. First, we used county-level measures of GDD accumulated throughout the entire summer breeding season, averaged across years, to characterize spatial variation in thermal conditions (avgGDD$_c$)[20,21,46]. Second, we used differences between weekly GDD values and long-term averages in each county to assess whether conditions were warmer or cooler than average in a given week and year (diffGDD$_{c,k,t}$). To calculate GDD values, we obtained daily minimum and maximum temperatures from Daymet for the centroid of each county between 3 May and 15 August (weeks 10–24). For each county and year, we calculated nine weekly GDD values, characterizing heat accumulated between week 10 and the end of each week in the summer breeding season (that is, weeks 16–24). We calculated diffGDD$_{c,k,t}$ as the difference between each weekly GDD value and the average for that period and county across all years included in the analysis (2004–2018 or 1994–2003). We calculated avgGDD$_c$ for each county by averaging GDD values associated with week 24 (that is, heat accumulated over the entire summer, between weeks 10 and 24) across years.

Precipitation. We used cumulative rainfall in April, May, June, July and August to explain variation in counts of adult monarchs because these months coincide with growth of native milkweed and monarchs on the summer breeding grounds[23]. We obtained monthly precipitation totals for the centroid of each county from Daymet. Similar to the approach we used to model variation in summer GDD, we characterized spatial variation in summer precipitation by averaging annual precipitation values in each county (avgPCP$_c$). We characterized temporal variation in precipitation (diffPCP$_{c,t}$) by calculating the difference between annual precipitation values and avgPCP$_c$.

Land cover. Milkweed, the primary host plant for larval monarchs, is associated with open and/or disturbed environments[15]. Through most of the twentieth century, milkweed was common in and adjacent to agricultural areas in the Midwestern United States and southern Canada[12,13,53,54]. We included county-level estimates of crop cover across the summer breeding grounds as a measure of potential habitat for monarchs. In addition to landscape-scale measures of crop cover, we assessed the relative amount of unforested area at each survey location. We included this local-scale measure because monarch abundance is likely to be positively associated with open areas and, importantly, observers may be more likely to detect monarchs when present in these environments.

We calculated percentage crop cover (crop$_c$) in each US and Canadian county on the basis of 30-m resolution data from the 2011 National Land Cover Database (NLCD) and 2010 North American Land Change Monitoring System database, respectively. We assumed values were constant over the study period because estimates of percentage crop cover in US counties on the basis of 2001 and 2006 NLCD databases were similar to those reported in 2011 (average difference from exploratory analysis <0.2). This finding corresponds with general patterns observed throughout the Midwest, where total crop cover has remained relatively constant over the last several decades despite changes in agricultural practices and crop composition[55,56]. To assess land cover at a local scale, we used the same data sources to calculate percentage area that was unforested within 12.5 km or 2.5 km of each NABA or BMN survey location, respectively (open$_i$). We classified deciduous forests, evergreen forests, mixed forests and woody wetlands as 'forested' and all other land cover categories as 'open'.

Herbicide use. Declines in milkweed on the summer breeding grounds have been linked to increases in the use of glyphosate on genetically modified crops, particularly corn and soybeans[15,57]. We used multiple data sources to estimate the proportion of corn and soybean crops in each county that were sprayed with glyphosate each year.

For each US county in our study region, we obtained the weight of glyphosate applied to all crops in each year and the proportion of glyphosate purchased in the associated state that was applied to corn and soybean crops from the US Geological Survey Pesticide National Synthesis Project[58]. We calculated the weight of glyphosate applied to corn and soybean crops in each county and year (weight$_{c,t}$) as the product of these two values. We then obtained annual estimates of corn and soybean acres planted in each county (acres$_{c,t}$) from farmer survey data provided by the US Department of Agriculture[59]. We used linear interpolation to impute missing values and assumed zero acres of corn and soybean were planted in counties where no values were reported between 1994 and 2018. We calculated the proportion of crops treated in each county and year (gly$_{c,t}$) as:

$$\text{gly}_{c,t} = \text{weight}_{c,t} \times \frac{1}{\text{app.rate}_t} \times \frac{1}{\text{acres}_{c,t}}, \tag{1}$$

where app.rate$_t$ represents glyphosate application rate, which we assumed was 0.75 lb acid equivalent (ae) per acre from 1994 to 2009 and 1.13 lb ae per acre from 2010 to 2018[21].

For each Canadian county in our study region, we acquired data to estimate glyphosate use from the Ontario Ministry of Agriculture, Food and Rural Affairs[60]. Because county-level estimates of corn and soy acres planted were unavailable before 2003, we did not include butterfly survey and covariate data from Canada in the 1994–2003 model. We used linear interpolation to generate estimates of the total amount of glyphosate applied to corn and soybean crops throughout Ontario between 2004 and 2018 on the basis of data that were available in 2003, 2008 and 2013; we assumed values in 2014–2018 were the same as those reported in 2013. We calculated county-level estimates of glyphosate use (weight$_{c,t}$) by multiplying provincial estimates of glyphosate use by the proportion of corn and soybean acres in Ontario that were planted in each county each year (assuming uniform application of glyphosate to all corn and soy crops). Finally, we assumed application rates were the same as those in the United States and calculated the proportion of crops treated in each county and year (gly$_{c,t}$) with the same approach used for US counties.

Autumn covariates. Unlike during spring migration, most monarchs do not breed during autumn migration. Most individuals that hatch from eggs laid in the Midwestern United States and Ontario in late summer enter reproductive diapause and migrate to overwintering sites in central Mexico, with surviving individuals arriving between late October and early December. A small but unknown proportion of migrating monarchs reproduce in the southern United States; they and their offspring may or may not reach the overwintering grounds in central Mexico[61]. We used autumn covariates in the winter submodel to explain variation in the area occupied by adults on the overwintering grounds in early winter, shortly after monarchs form well-defined colonies.

Normalized difference vegetation index. Flower nectar provides energy for monarchs to migrate from summer breeding grounds in the northern United States and Canada to the overwintering grounds in Mexico[62,63]. Previous work and preliminary analyses demonstrated that among potential drivers operating during autumn migration, variation in overwintering population size is better explained by vegetation conditions early in the migration as compared to later in the season[18]. We therefore used landscape greenness as a proxy for landscape-scale nectar availability in the first half of migration (between 15 September and 15 October), while monarchs are traversing the central United States migratory corridor (90° W to 105° W, 30° N to 40° N; Fig. 2c)[64]. Similar to previous studies, we used a remotely sensed measure of landscape greenness (normalized difference vegetation index; NDVI) at a region-wide scale[18,65]. We obtained NDVI values, at 250-m resolution, from Terra Moderate Resolution Imaging Spectroradiometer (MODIS v.006) Vegetation Indices (MOD13Q1)[66]. For each year, we extracted and averaged NDVI values within the corridor during the first half of migration, generating a single mean value for each year (nectar$_t$).

Early-winter covariates. Monarchs begin arriving on the overwintering grounds in late October and early November and form colonies starting in December[24]. We characterized the quality of habitat available to monarchs as they formed colonies and used these covariates in the winter submodel to explain variation in the area occupied in early winter.

Forest cover. Monarchs spend the winter in high-elevation forests, primarily aggregating in mature stands of oyamel fir (*Abies religiosa*), pine (*Pinus* spp.) and oak (*Quercus* spp.)[67]. These forests protect overwintering monarchs from extreme temperatures and precipitation, allowing them to survive and remain in reproductive diapause throughout the winter[68]. The primary threats to the high-elevation forests are illegal logging, fires and storm-induced damage[49,67,69–71]. Illegal logging has decreased since the late-2000s with the establishment of the MBBR and various conservation efforts[67,72], whereas fires and severe winter storms may become more frequent with climate change[73].

We estimated the availability of dense forest cover at each supercolony using maps developed to monitor long-term changes in land-use in the MBBR and surrounding areas[49,72,74,75]. We used grouped map categories to differentiate areas with dense forest cover (canopy cover >70%) from areas with open forest cover (canopy cover 40–70%), secondary shrubs and no forest cover. For each of the 19 colonies, we delineated a 100-ha 'critical area' that encompassed historical locations of the colony (elliptical-shaped and oriented downhill to account for microclimate and within-season movements of individuals) as well as a buffer that extended 500-m from the critical area boundary[18]. Before calculating covariate values for each supercolony (the spatial unit for which we had corresponding annual measures of the area occupied by overwintering monarchs), we created the union of overlapping critical areas and buffers for those supercolonies that represented the aggregate of multiple colonies ($n = 3$). For each year that maps were available (1993, 2000, 2003, 2006, 2009, 2012, 2015 and 2018), we then calculated the percentage of land area surrounding each supercolony (critical area plus buffer) that was comprised of dense forest cover. We used linear interpolation to estimate forest cover values for years when maps were unavailable (for example, 1994–1999, 2001–2002 and so on) to create an annual index of dense forest cover at each supercolony ($\text{forest}_{j,t}$). To include forest cover in the 1994–2003 model, when separate estimates of area occupied were not available for each supercolony, we averaged forest cover estimates among all supercolonies to produce an annual estimate of forest cover for the entire overwintering population (forest_t).

Supercolony location. The MBBR was created in 2000 to protect forests deemed essential for persistence of the monarch population and, as a result, most supercolonies (8 of 13) and those with the largest consistent aggregations are located inside the Reserve[24,47]. To account for this potential source of spatial variation, we included a binary variable in the 2004–2018 model that indicated whether the supercolony was located inside or outside of the MBBR ($\text{reserve}_j = 1$ or 0, respectively)[18].

Full annual-cycle model, 2004–2018. We modelled changes in the size of the eastern monarch population as a function of environmental covariates using a Bayesian, hierarchical framework. The full annual-cycle model is composed of two submodels. The summer submodel describes variation in counts of adult butterflies on the summer breeding grounds as a function of population size in late winter (delineated from surveys of the overwintering grounds in late February of the same year) and spring and summer covariates. The winter submodel describes variation in the area occupied by supercolonies in early winter (delineated from surveys of the overwintering grounds in December) as a function of population size in the last 4 weeks of the preceding summer (that is, estimated peak-summer population size) and autumn and early-winter covariates. The two submodels are linked through the estimate of peak-summer population size, which is a derived parameter in the summer submodel that is subsequently used as a covariate in the winter submodel. Thus, the two submodels are part of a single, unified analysis represented by different components within a joint likelihood. By estimating peak-summer population size as a derived parameter in a Bayesian framework instead of using an index based on raw counts, we account for uncertainty associated with estimates of peak-summer population size (by using the full posterior distribution of the derived parameter) and reduce potential biases resulting from uneven sampling effort.

Modelling variation in summer counts. We structured the summer submodel hierarchically, decomposing variation in monarch counts into that attributable to ecological factors operating at a landscape scale (variation among counties throughout the breeding range) and that attributable to survey- and detection-related factors operating at a local scale (variation within counties). We used this approach to reduce potential biases resulting from non-random survey locations (Extended Data Fig. 1). We modelled counts from surveys conducted between 14 June and 15 August (weeks 16–24). Similar to previous studies[21,46], we assumed a negative binomial distribution (specified as a Poisson-gamma mixture) for counts of adult monarchs, $y_{i(c),k,t}$, at each survey location i ($i = 1, \ldots, m_c$) in county c ($c = 1, \ldots, n$) during week k ($k = 1, \ldots, 9$) in year t ($t = 1, \ldots, 15$):

$$y_{i(c),k,t} \sim \text{Poisson}\left(\theta_{i(c),k,t}\right), \tag{2}$$

with mean $\theta_{i(c),k,t} = \lambda_{i(c),k,t} \times \rho_{i(c),k,t}$, where $\rho_{i(c),k,t}$ is a random variable drawn from a gamma distribution. We modelled $\lambda_{i(c),k,t}$, the expected count at location i in county c during week k in year t, as a function of the expected mean count on a NABA survey in county c ($\mu_{c,k,t}$), fixed effects allowing for differences in expected counts between BMN and NABA surveys (that is, $\text{IL}_{i(c)} = 1$ if survey $i(c)$ is part of the Illinois BMN and 0 otherwise; similar specification for Iowa (IA), Michigan (MI) and Ohio (OH) surveys) and the percentage of surrounding area that was unforested ($\text{open}_{i(c)}$). We used NABA as a reference level because NABA surveys were dispersed throughout the summer breeding range, whereas BMN survey locations were geographically restricted. We accounted for variation in survey effort by including the total number of search hours as an offset ($\text{eff}_{i(c),k,t}$):

$$\begin{aligned}\log\left(\lambda_{i(c),k,t}\right) = {} & \log\left(\mu_{c,k,t}\right) + \log\left(\text{eff}_{i(c),k,t}\right) + \beta_1 \times \text{IA}_{i(c)} + \beta_2 \times \text{IL}_{i(c)} \\ & + \beta_3 \times \text{MI}_{i(c)} + \beta_4 \times \text{OH}_{i(c)} + \beta_5 \times \text{open}_{i(c)} + \epsilon_{i(c)},\end{aligned} \tag{3}$$

where $\epsilon_{i(c)}$ is a random effect of survey location with mean 0 and variance σ^2_{survey}. We modelled the expected mean count in county c ($\mu_{c,k,t}$) as a function of week (week_k), overwintering population size in late winter (Feb_t), temperature and precipitation in eastern Texas in spring (spGDD_t and spPCP_t, respectively) and temperature (avgGDD_c and $\text{diffGDD}_{c,k,t}$), precipitation (avgPCP_c and $\text{diffPCP}_{c,t}$), percentage crop cover (crop_c) and glyphosate use ($\text{gly}_{c,t}$) in each county in summer:

$$\begin{aligned}\log\left(\mu_{c,k,t}\right) = {} & \alpha_0 + \alpha_{1,t} \times \text{week}_k + \alpha_{2,t} \times \text{week}_k^2 + \alpha_3 \times \text{Feb}_t + \alpha_4 \times \text{spGDD}_t \\ & + \alpha_5 \times \text{spGDD}_t^2 + \alpha_6 \times \text{spPCP}_t + \alpha_7 \times \text{spPCP}_t^2 + \alpha_8 \times \text{avgGDD}_c \\ & + \alpha_9 \times \text{diffGDD}_{c,k,t} + \alpha_{10} \times \text{diffGDD}^2_{c,k,t} + \alpha_{11} \times \text{avgGDD}_c \times \text{diffGDD}_{c,k,t} \\ & + \alpha_{12} \times \text{avgPCP}_c + \alpha_{13} \times \text{diffPCP}_{c,t} + \alpha_{14} \times \text{diffPCP}^2_{c,t} \\ & + \alpha_{15} \times \text{avgPCP}_c \times \text{diffPCP}_{c,t} + \alpha_{16} \times \text{crop}_c \\ & + \alpha_{17} \times \text{gly}_{c,t} + \alpha_{18} \times \text{crop}_c \times \text{gly}_{c,t} + \epsilon_c,\end{aligned} \tag{4}$$

where ϵ_c is a random county-level effect with mean 0 and variance σ^2_{county} and $\alpha_{1,t}$ and $\alpha_{2,t}$ are random coefficients with means α_{wk} and α_{wk2} and variances σ^2_{wk} and σ^2_{wk2}, respectively, that allow for annual variation in the time at which monarch counts reach a seasonal maximum. We explored whether the effects of weather in spring and summer were nonlinear by creating a model that included quadratic terms; we retained quadratic terms in the final model if 95% CIs for the coefficients excluded zero. We also included an interaction between summer temperature covariates (avgGDD_c and $\text{diffGDD}_{c,k,t}$) and summer precipitation covariates (avgPCP_c and $\text{diffPCP}_{c,t}$), which allowed the effects of GDD and precipitation to vary regionally. Finally, we included an interaction between crop cover and glyphosate use because evidence suggests that the influence of glyphosate on monarchs varies with amount of surrounding crop cover[21]. We standardized all covariates, in both the survey-level and county-level models (equations (3) and (4), respectively), by their respective means and standard deviations.

Modelling variation in size of supercolonies in early winter. Because every supercolony was not present every year, resulting in zero values for 28% of supercolony–year combinations, we used a hurdle model to estimate (1) the probability a supercolony was present and (2) the area occupied, conditional on presence[18,76]. Specifically, we used a Bernoulli distribution to model zero and non-zero values, where $\psi_{j,t}$ represents the probability of monarch presence in supercolony j ($j = 1, \ldots, 13$) in year t. We assumed a gamma distribution for the area occupied by supercolony j in year t ($A_{j,t}$), conditional on presence, resulting in the following probability function:

$$p\left(A_{j,t} \mid \psi_{j,t}, s, r_{j,t}\right) = \begin{cases} 1 - \psi_{j,t}, & \text{if } A_{j,t} = 0 \\ \psi_{j,t} \times \text{Gamma}\left(A_{j,t} \mid s, r_{j,t}\right), & \text{if } A_{j,t} > 0 \end{cases} \tag{5}$$

where s and $r_{j,t}$ represent shape and rate parameters, respectively. We assumed that probability of monarch presence varied randomly among the 13 supercolonies:

$$\text{logit}\left(\psi_{j,t}\right) = \psi_0 + \epsilon_{\psi,j}, \tag{6}$$

where $\epsilon_{\psi,j}$ is a random effect of supercolony with mean 0 and variance σ^2_{ψ}. We modelled mean area occupied, $\omega_{j,t} = s/r_{j,t}$, as a function of peak population size in the preceding summer (summer_t), nectar availability in autumn (nectar_t), as well as supercolony location (reserve_j) and extent of dense forest cover surrounding each supercolony ($\text{forest}_{j,t}$) in early winter:

$$\begin{aligned}\log\left(\omega_{j,t}\right) = {} & \gamma_0 + \gamma_1 \times \text{summer}_t + \gamma_2 \times \text{nectar}_t + \gamma_3 \times \text{reserve}_j \\ & + \gamma_4 \times \text{forest}_{j,t} + \epsilon_{\omega,j},\end{aligned} \tag{7}$$

where $\epsilon_{\omega,j}$ is a random effect of supercolony with mean 0 and variance σ^2_{ω}. We standardized nectar and forest cover values by their respective means and standard deviations. We used an estimate of peak-summer population size (summer_t), derived from the summer submodel, as a covariate in the winter submodel. Specifically, for each year and county in the summer breeding range (regardless of whether the county was surveyed or not), we generated expected monarch counts on NABA surveys in weeks 21–24 on the basis of the county-level model (equation (4)). We calculated a mean value across the 4 weeks in each county and year and then averaged values across counties, weighted by the amount of unforested land area in each county (a_c):

$$\text{summer}_t = \frac{\sum_{c=1}^{n}\left(a_c \times \frac{\sum_{k=6}^{9}\mu_{c,k,t}}{4}\right)}{\sum_{c=1}^{n} a_c}. \tag{8}$$

To improve convergence, we standardized the resulting annual values (summer_t) by a fixed mean (11.4) and standard deviation (6.0) that approximated expected values based on preliminary runs of the summer submodel[77].

Reduced annual-cycle model, 1994–2003. We used a 'reduced' version of the full annual-cycle model that accounted for data limitations to describe population dynamics between 1994 and 2003. Despite having comparatively less data, we sought inferences from this earlier period to assess the relative importance of environmental covariates on monarch population sizes during the period when the decline was most severe (Fig. 1a). We integrated count data from three monitoring programmes on the summer breeding grounds in the United States (Illinois and Ohio BMNs and NABA), the only systematically collected summer data available on adult monarchs during 1994–2003. We excluded data from Canada because county-level estimates of corn and soy acres planted were unavailable before 2003. We used the same hierarchical structure in the summer submodel as that used for 2004–2018 data (equations (2)–(4)) and included all the same covariates, with the exception of Feb_t because estimates of late-winter population size were unavailable before 2005. We simplified the structure of the winter submodel for 1994–2003 because we had only measures of the total area occupied in early winter rather than supercolony-level measures. Because zero values were no longer possible, there was no need for a hurdle model and, instead, we modelled annual estimates of the area occupied with a gamma distribution (that is, the same distribution used in the second part of the hurdle model for 2004–2018). We averaged values of dense forest cover across supercolonies to create an annual index of forest cover for the entire overwintering population (forest_t) and removed reserve_j from the model since it was no longer relevant. In addition, we excluded nectar_t from the model because NDVI values were unavailable before 2000. Finally, we confirmed that inferences about population size and covariate effects were robust to changes in model structure by verifying that estimates from the original 'full' model and a 'reduced' model were similar for data collected between 2004 and 2018 (Supplementary Tables 3 and 5).

Assessing relative importance of seasonal factors. We used hierarchical partitioning to assess the relative importance of seasonal factors in governing population dynamics of monarch butterflies[29,78]. Hierarchical partitioning uses differences between goodness-of-fit measures from nested models to assess the extent to which a covariate, or group of covariates, explains variation in a response variable independent of other factors under consideration[78,79]. Because assumed probability distributions and sample sizes differed for response variables in the summer and winter submodels (which would impact hierarchical partitioning results), we assessed the submodels separately. We used log-likelihood to assess model fit, calculating values for summer and winter submodels by summing log probability mass or density values across all surveys (equation (3)) and all estimates of area occupied (equation (5)), respectively. For each covariate group (see below), we began by averaging differences in log-likelihoods associated with each nested pair of models at each hierarchical level of model complexity (number of covariate groups in the model). We then averaged across hierarchical levels to generate the independent contribution of that covariate group to explained variation in the response variable.

To assess the relative importance of seasonal factors in the summer submodel for 2004–2018, we divided temporally varying covariates into four groups: late-winter population size (Feb_t), spring weather (spGDD_t, spGDD^2_t, spPCP_t, spPCP^2_t), summer weather ($\text{diffGDD}_{c,k,t}$, $\text{diffGDD}^2_{c,k,t}$, $\text{avgGDD}_c \times \text{diffGDD}_{c,k,t}$, $\text{diffPCP}_{c,t}$, $\text{diffPCP}^2_{c,t}$, $\text{avgPCP}_c \times \text{diffPCP}_{c,t}$) and summer land-use ($\text{gly}_{c,t}$, $\text{crop}_c \times \text{gly}_{c,t}$). If the independent contribution of spring and/or summer weather were large relative to the contributions of late-winter population size and summer land-use, that would provide evidence supporting the climate change hypothesis. If summer land-use was more important, that would provide evidence supporting the milkweed limitation hypothesis. We calculated log-likelihoods for 16 models that contained all possible combinations of the four covariate groups (thus, groups, not individual covariates, were included or excluded from each model). We included linear effects of time-invariant factors (avgGDD_c, avgPCP_c, crop_c) in all models because we were interested primarily in the capacity of factors to explain temporal variation in monarch counts. To ensure that random effects did not confound assessments of variable importance, we either removed random effects (ϵ_c, $\epsilon_{i(c)}$) or converted them to fixed effects ($\alpha_{1,t}$, $\alpha_{2,t}$). We used the same approach to assess the relative importance of seasonal factors in the summer submodel for 1994–2003, except we only assessed the relative importance of three covariate groups (spring weather, summer weather and summer land-use) given that estimates of late-winter population size were unavailable.

To assess the relative importance of seasonal factors in the winter submodel for 2004–2018, we calculated log-likelihoods for eight models that contained all possible combinations of three individual covariates: peak-summer population size (summer_t), autumn nectar availability (nectar_t) and forest cover at each supercolony location ($\text{forest}_{j,t}$). If the independent contributions of autumn nectar availability and/or forest cover were larger than the contribution of peak-summer population size, that would provide evidence supporting the migration survival hypothesis. Because summer_t is a derived parameter from the summer submodel, we ran the entire full annual-cycle model but only used log-likelihoods from the winter submodel to assess relative importance of the three covariates. We included all late-winter, spring and summer covariates in the summer submodel to generate summer_t, although including only a subset of covariates in the summer submodel did not qualitatively change hierarchical partitioning results for the winter submodel. As with the summer submodel assessment, we removed random effects (ϵ_c, $\epsilon_{i(c)}$) or converted them to fixed effects ($\epsilon_{\psi,j}$, $\epsilon_{\omega,j}$, $\alpha_{1,t}$, $\alpha_{2,t}$). We did not use hierarchical partitioning to assess the relative importance of factors in the winter submodel in 1994–2003 (summer population size and autumn nectar availability) because we had only a single, aggregate estimate of overwintering population size each year and thus data were quite limited.

Assessing trends in model residuals, 2004–2018. We evaluated the extent to which covariates in the 2004–2018 model explained the decline in the overwintering population by assessing evidence of temporal trends in the estimated residuals (posterior medians) from the winter submodel, excluding supercolony–year combinations when monarchs were not present. We presumed that covariates in our model sufficiently explained underlying population declines if there was no evidence of a decline in the residuals. We did not estimate trends in residuals from the 1994–2003 model because estimates of the area occupied in each supercolony were unavailable and, thus, there were only ten observations of the total area occupied (compared to 140 observations of supercolonies when monarchs were present during 2004–2018). See Supplementary Information for additional details on the difficulties of differentiating trends from annual fluctuations in short-lived, migratory populations, such as the monarch butterfly in eastern North America.

Evaluating relationships between population-level indices of seasonal abundance, 2004–2018. We calculated the extent to which population size in one season was associated with population size in the previous season with post-hoc linear regression analyses and Bayesian R^2 values[80]. We assessed the relationship between early-winter population size (total area occupied in late December; dependent variable) and population size at the peak of the previous summer (posterior medians of the estimated annual index values; independent variable), the relationship between late-winter population size (late area occupied in late February) and the preceding early-winter population size and the relationship between peak-summer population size and the preceding late-winter population size.

Model implementation and assessment. We used a Bayesian approach for analysis, fitting models in STAN executed from R using the package rstan[81–83]. We specified independent, diffuse prior distributions for model parameters. We ran three Markov chains initiated at random values for 3,000 iterations, discarded the first 500 iterations as burn-in and used the remaining 2,500 iterations (7,500 samples from the three chains) to summarize posterior distributions. We assessed model convergence by inspecting trace plots and checking that $\hat{R}$ statistics were <1.1 (ref. [84]). We assessed goodness-of-fit by verifying that posterior predictive P values for three summary discrepancy measures (mean and standard deviation of counts on the summer breeding grounds; mean of area occupied in early winter, conditional on presence) were ≥ 0.2 and ≤ 0.8 (ref. [85]).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Monarch data from the overwintering grounds and covariate data are available on Zenodo (https://doi.org/10.5281/zenodo.4085906). Monarch data from the summer breeding grounds are proprietary and were obtained from the North American Butterfly Association (https://www.naba.org/), the Iowa Butterfly Survey Network (https://www.reimangardens.com/collections/insects/iowa-butterfly-survey-network/), the Illinois Butterfly Monitoring Network (https://bfly.org/), the Michigan Butterfly Network (https://michiganbutterfly.org/) and the Ohio Lepidopterists (http://www.ohiolepidopterists.org/). These data may be available upon reasonable request to L.R. and with permission from the aforementioned programmes.

Code availability

Code needed to run analyses (R scripts and Stan model files) is available on Zenodo (https://doi.org/10.5281/zenodo.4085906) and Github (https://zipkinlab.github.io/#dataintegration2021Z).

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Author contributions

E.R.Z., L.R., K.S.O. and E.F.Z. conceived of the research. L.R., N.N., M.I.R., E.R.-S. and K.S.O. contributed data. E.R.Z, S.P.S., M.T.F. and E.F.Z. constructed the model. E.R.Z. ran analyses. E.R.Z. and E.F.Z. wrote the first drafts of the paper. All authors contributed to the interpretation of results and edits to the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to E.R.Z.

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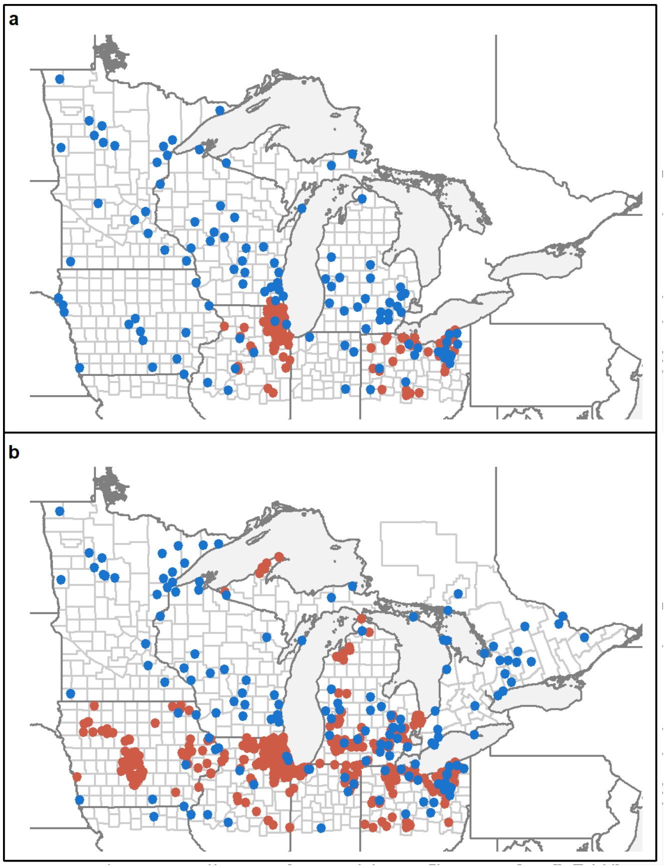
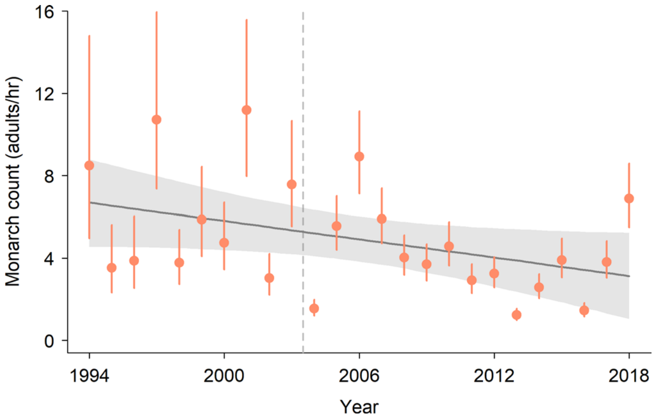
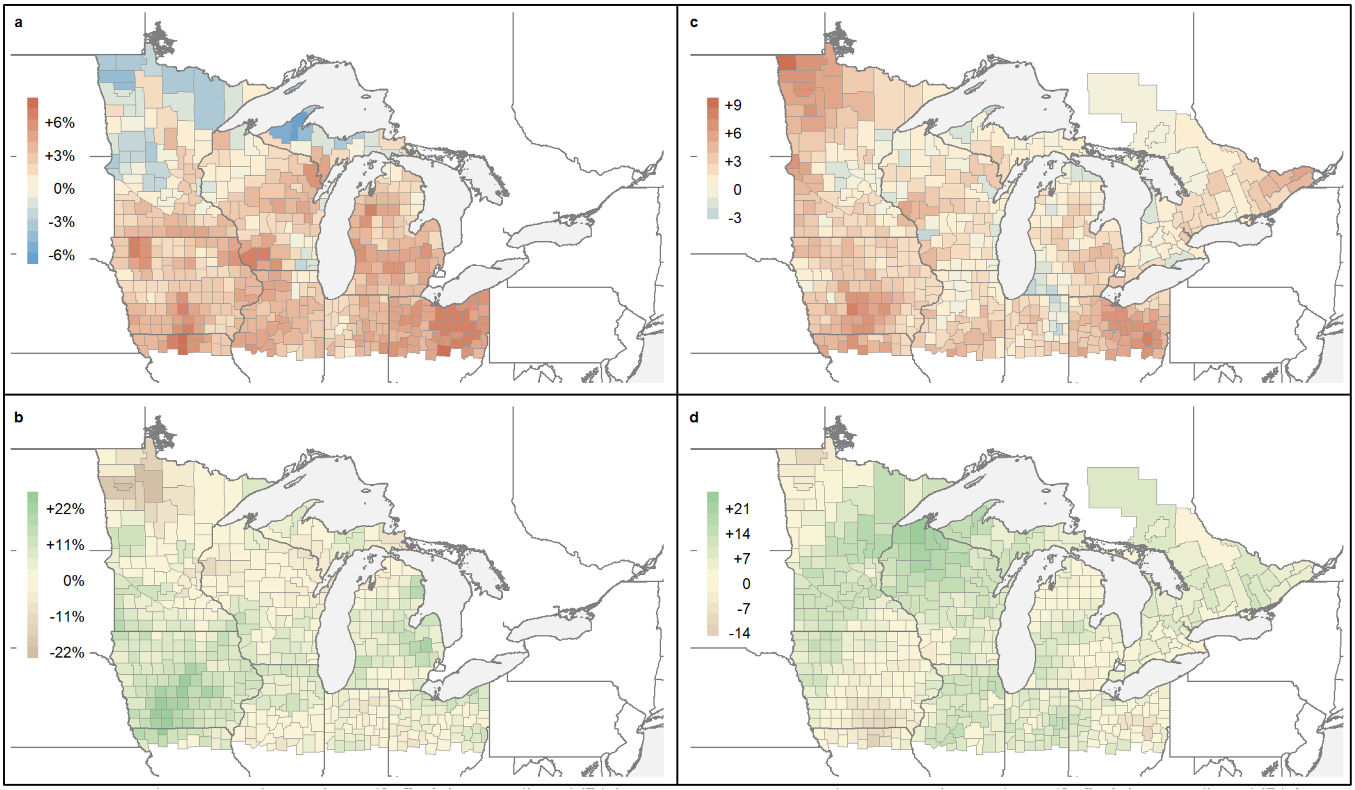


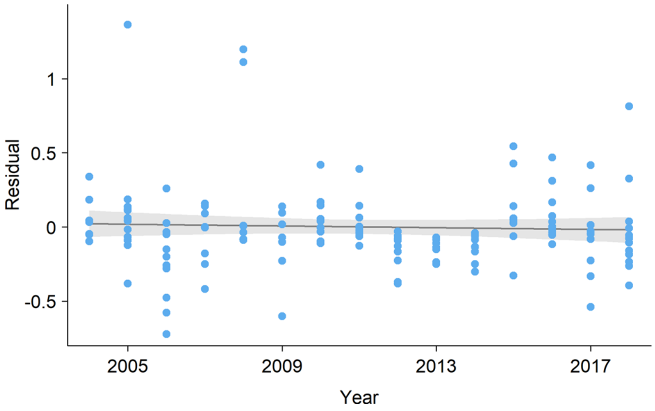
Extended Data Fig. 1 | Locations of monarch butterfly surveys on summer breeding grounds between 1994–2018. Locations of surveys conducted between 14 Jun–15 Aug by the North American Butterfly Association (NABA; blue) and state-specific butterfly monitoring networks (BMNs; red) in **a**, 1994–2003 and **b**, 2004–2018. Counties (U.S.) and census districts (Canada) that are included in our delineation of the summer breeding range for the 1994–2003 reduced annual-cycle model and the 2004–2018 full annual-cycle model are outlined in grey.



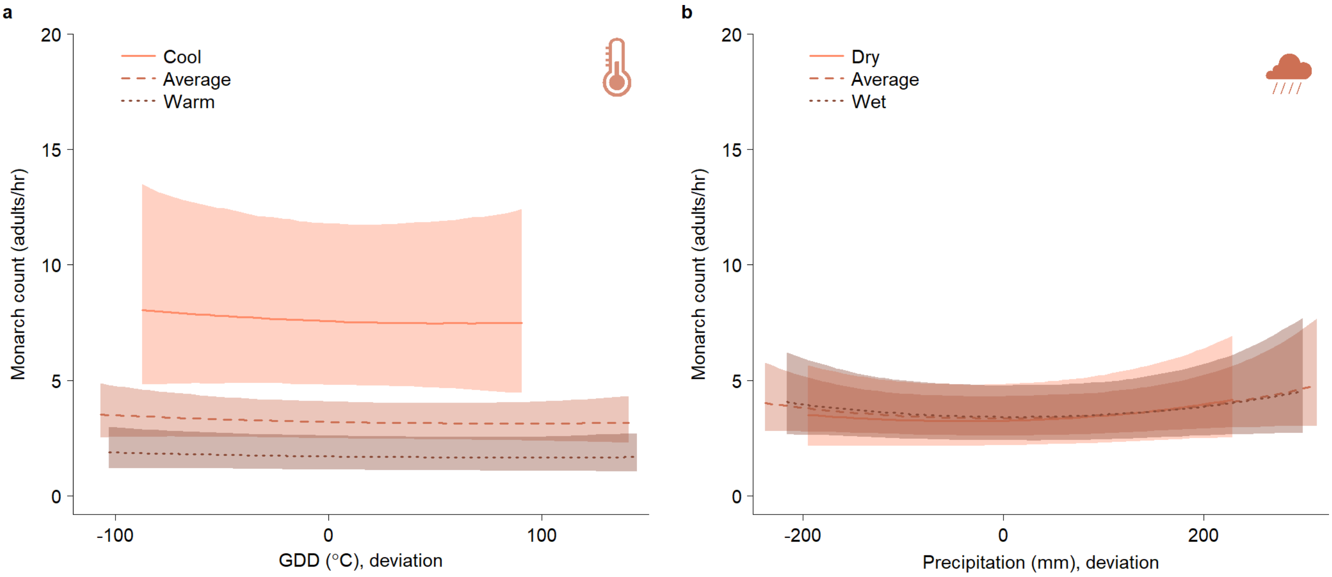
Extended Data Fig. 2 | Model-based index of monarch butterfly population size during peak summer, 1994–2018. Model-based predictions (posterior medians with 95% credible intervals [CI]) of the expected number of adult monarchs observed per hour on an average NABA survey conducted between 19 Jul–15 Aug, 1994–2018, with linear trend (grey line) and 95% CI (shaded area; slope = −0.15 adults/hr/yr, 95% CI: −0.30, 0.01). Vertical dashed line denotes the break between our 1994–2003 and 2004–2018 analyses.



Extended Data Fig. 3 | Changes in summer climate on monarch summer breeding grounds. Percent change between 1994–2003 and 2004–20018 in **a**, average temperatures (GDD from 3 May–15 Aug) and **b**, cumulative precipitation (mm, Apr–Aug) for each U.S. county included in our delineation of the monarch summer breeding range. Temporal trends over a recent 15-year period (2004-2018) in **c**, GDD (°C/yr), and **d**, cumulative precipitation (mm/yr). Positive values indicate increases or positive trends in weather variables; negative values indicate decreases or negative trends. Canadian counties were excluded from panels **a** and **b** because data limitations prevented us from including these regions in our 1994–2003 model of monarch population dynamics.



Extended Data Fig. 4 | Residuals from the winter submodel describing variation in the area occupied by monarch butterflies. Estimated residuals (posterior medians) from the winter submodel describing the area occupied by monarchs in each of the overwintering supercolonies, when monarchs were present in early winter, 2004–2018. Solid grey line and shaded area represent a linear trend with 95% credible interval (slope= −0.003, 95% CI = −0.014, 0.008).



Extended Data Fig. 5 | Effects of summer weather on monarch population size, 1994–2003. a, Estimated marginal effects (median and 95% credible intervals) of GDD (deviation from county 10-year average) on expected monarch counts during peak summer (expected mean count of adult monarchs per search hour, 19 Jul–25 Jul), for typical cool, average, and warm counties ($avgGDD_c$ = 711, 898, and 1033 °C, respectively) within the summer breeding range, 1994–2003. **b**, Estimated marginal effects of precipitation (deviation from county 10-year average) on expected monarch counts during peak summer, for typical dry, average, and wet counties ($avgPCP_c$ = 422, 525, and 578 mm, respectively), 1994–2003.