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Opposing global change drivers counterbalance trends in breeding North American monarch butterflies

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Abstract

Many insects are in clear decline, with monarch butterflies (*Danaus plexippus*) drawing particular attention as a flagship species. It is well documented that, among migratory populations, numbers of overwintering monarchs have been falling across several decades, but trends among breeding monarchs are less clear. Here, we compile > 135,000 monarch observations between 1993-2018 from the North American Butterfly Association's annual butterfly count to examine spatiotemporal patterns and potential drivers of adult monarch relative abundance trends across the entire breeding range in eastern and western North America. While the data revealed declines at some sites, particularly the US Northeast and parts of the Midwest, numbers in other areas, notably the US Southeast and Northwest, were unchanged or increasing, yielding a slightly positive overall trend across the species range. Negative impacts of agricultural glyphosate use appeared to be counterbalanced by positive effects of annual temperature, particularly in the US Midwest. Overall, our results suggest that population growth in summer is compensating for losses during the winter and that changing environmental variables have offsetting effects on mortality and/or reproduction. We suggest that density-dependent reproductive compensation when lower numbers arrive each spring is currently able to maintain relatively stable breeding monarch numbers. However, we caution against complacency since accelerating climate change may bring growing threats. Our data also suggest that increases of summer monarchs in some regions, especially in the west and far south, may reflect replacement of migratory with resident populations. Nonetheless, it is perhaps reassuring that ubiquitous downward trends in summer monarch abundance are not evident.

Keywords: monarch butterfly; population trends; decline; conservation efforts

Introduction

Despite considerable variability through time, between sites, and among taxa, it is increasingly clear that some of the world's insects are in steep decline. This is perhaps best documented among bees and other pollinators, whose loss would have devastating consequences for global ecosystems and the human food supply (Wagner, 2020). Beyond pollination, insects are key providers of a full suite of provisioning, regulating, cultural, and supporting ecosystem services. Human degradation of the environment, at a range of scales, is often implicated in falling insect numbers. A key local driver has been heavy herbicide and insecticide applications associated with agricultural intensification (Habel et al., 2019). Urbanization and associated automobile collisions (Baxter-Gilbert et al., 2015; Kantola et al., 2019) and light pollution bring additional challenges (Owens et al., 2020). At global scales, climate change can heighten physiological stress to insects while triggering spatiotemporal misalignment with, or reduced quality of, host plants or other resources (Bale et al., 2002; Jamieson et al., 2012), although even climate change can create variable regions of insect decreases and increases (Crossley et al., 2021; Koltz et al., 2018) such as when increased temperature enables faster population growth. Particularly damaging are cases where local and global drivers both are moving in harmful directions, for example when long-distance migrants must move through increasingly hot and dry regions that also are seeing more intense land use (Saunders et al., 2019).

Monarch butterflies (*Danaus plexippus*) in North America have become the public face of insect declines (Gustafsson et al., 2015), largely because of the well-publicized diminishing of winter colonies in Mexico and California (Boyle et al., 2019; Pelton et al., 2019). Monarchs are iconic insects due to their large size, attractive and distinctive coloration, wide range, host association with horticulturally popular milkweeds (*Asclepias* spp.), and fascinating long-distance seasonal migrations. This has led to the prominent use of monarchs as ambassadors to

engage the general public in insect conservation, for example, by facilitating the widespread planting of milkweed in home gardens (Thogmartin, López-hoffman, et al., 2017). However, some of these same traits that make monarchs so charismatic to humans also subject the butterflies to particular risk. Best documented is habitat loss and changing climate at concentrated overwintering sites, which has apparently led to an ongoing, multi-decadal decline of those colonies (Brower et al., 2012; Pelton et al., 2019; Thogmartin, Wiederholt, et al., 2017; Zylstra et al., 2021). A second widely-touted threat is removal of milkweed from agricultural fields within monarch's core breeding range in the American Midwest, following widespread adoption of glyphosate-tolerant corn and soybean (Stenoien et al., 2018). Thirdly, since migration in the human-dominated world is risky (Wilcove & Wikelski, 2008), their particularly long-distance movements could expose monarchs to multiple threats (e.g., deaths from traffic collisions, Kantola et al., 2019; McKenna et al., 2001). Additionally, agricultural and residential pesticides (Olaya-Arenas & Kaplan, 2019) and sensitivity to temperature and precipitation extremes as the climate changes (Lemoine, 2015; Saunders et al., 2018) may be adversely affecting monarchs at various stages of their life cycle.

Altogether, these perceived threats have led to the recent decision by USFWS that federal protection is warranted in the United States (USFWS, 2020). However, evidence is ambiguous whether monarchs continue to be in consistent, recent decline across the annual cycle (i.e., outside of the winter stage), with studies variously reporting steady or falling monarch numbers at different places and seasonal milestones (Brower et al., 2018; Davis & Dyer, 2015; Espeset et al., 2016; Ethier, 2020; Inamine et al., 2016; Ries et al., 2015). Uncertainty about whether breeding populations are continuing to steeply decline, or show some resiliency to overwintering

losses in at least some regions or at some stages, complicates efforts to target conservation

programs to points in the life-cycle where they will be most effective.

Here, we used the North American Butterfly Association's (NABA) summer citizen-

science counts to assess spatiotemporal patterns and drivers of relative abundance of breeding,

adult monarchs, and across most of their breeding range throughout the United States (east and

west) and southern Canada. Prior work with these or similar citizen-science datasets have

focused on specific regions of the country, such as the western U.S. (Forister et al., 2021), or the

Midwest (Zylstra et al., 2021). For a species like the monarch, which has a continental breeding

range, it is important to assess the population throughout this large area, so that local hotspots of

decline or increase do not bias the interpretation of the entire population's status. These NABA

data are broad in scope, collectively recording 135,705 monarchs at 403 sites across North

America, over time periods of 10-26 years from 1993-2018. We analyzed NABA data using

methods developed for a similar citizen-science program, the Audubon Christmas Bird Count

(Meehan et al., 2019), yielding monarch relative-abundance trends that accounted for spatial and

temporal variation in sampling effort as well as spatial and temporal autocorrelation among

neighboring counts. Our central goals were to (1) quantify trends in monarch relative abundance

among NABA sites throughout the USA and southern Canada, and (2) characterize relationships

between those trends and two dominant global change factors: agricultural intensification,

specifically glyphosate use, and climate change, specifically temperature and precipitation

change.

Methods

Butterfly data

We used direct counts of monarch adults from the North American Butterfly Association's summer citizen-science counts (https://www.naba.org/). Butterfly counts are made within a 15-mile (~24 km) diameter circle, typically in July, and are open to participation from the public. For each count event, the abundances of butterfly species are tallied and the sum of associated party hours (a measure of sampling effort that aggregates the number of hours spent by each observer) is recorded. To minimize bias due to differences among sites in the day of year when butterfly counts were conducted, we limited our analysis to butterfly counts that occurred between June 1-August 31. Prior to estimating trends in abundance, we removed sites that had < 5 years of monarch detections and that spanned < 10 years (Didham et al., 2020). Lastly, butterfly counts were assigned to 50 x 50 km (2,500-km2) cells on a uniform grid covering North America. The curated dataset recorded a total of 135,705 monarchs from 403 sites occupying 334 grid cells, over time periods of 10-26 years from 1993-2018.

Modeling relative abundance trends

We modeled monarch counts, $y_{i,k,t}$, in grid cell i encompassing count circle k during year t as a random variable from a negative binomial distribution. Expected values for counts per grid cell, $\mu_{i,t}$, were assumed to be a function of spatially structured grid-cell, count-effort, and year effects, plus unstructured variation among count circles. The linear predictor for $\mu_{i,t}$ took the form

$$\log\left(\mu_{i,t}\right) = \alpha_i + \epsilon_i\log\left(E_{i,k,t}\right) + \tau_i T_{i,k,t} + \gamma_{i,t} + \kappa_k$$

Parameters α_i were modeled as cell-specific random intercepts with an intrinsic conditional autoregressive (iCAR) structure. Parameters ϵ_i were modeled as spatially structured (iCAR), cell-specific, random slope coefficients for the local effects of effort $E_{i,k,t}$. Effort was represented

by $E_{i,k,t}$, the number of party hours expended during a count, where a party hour was the count

effort of one party of unspecified size for one hour. Pairing log-transformed expected counts

with log-transformed effort in the linear predictor yielded a power function for effort correction,

a flexible mathematical form that accommodated a decreasing, linear, or increasing impact of

effort on expected counts (Link & Sauer, 1999). Parameters τ_i were modeled as spatially

structured, cell-specific, random slope coefficients for a log-linear year effect. Year, represented

by T, was transformed before analysis such that $\max(T) = 0$, and each preceding year took an

increasingly negative integer value. Given the scaling of effort and year variables, $\exp(\alpha_i)$ could

be interpreted as a cell-specific expected count given one party hour of effort during the final

year in the time series. Parameters $\gamma_{i,t}$ were modeled as exchangeable random intercepts that

accounted for variation in relative abundance per grid cell and year that was not accounted for by

the log-linear year effect. The final term in the model, κ_k was an exchangeable random intercept

that accounted for variation in relative abundance among circles, possibly due to differences in

habitat conditions or observer experience.

This spatially-varying coefficient (SVC) model was analyzed within a Bayesian

framework using the R-INLA package in R (Rue et al., 2017; Lindgren, 2015; R Core Team,

2021). For parameters α_i, ϵ_i, and τ_i, with iCAR structure (Besag et al., 1991), precision matrices

were scaled such that the geometric mean of marginal variances was equal to one, and priors for

precision parameters were penalized complexity (PC) priors, with parameter values $U_{PC} = 1$ and

$a_{PC} = 0.01$ (Simpson et al., 2017). Precision for the zero-centered, exchangeable, random circle

effect, κ_k and grid cell by year effect, $\gamma_{i,t}$, were also assigned a PC prior with parameter values

$U_{PC} = 1$ and $a_{PC} = 0.01$ (Simpson et al., 2017). The overdispersion term for the negative

binomial count distribution, Φ, was assigned a PC prior with parameter value $l = 7$. (Rue et al., 2017)

Following trend model analysis, posterior medians and symmetric 95% credible intervals were computed per cell for α_i, ϵ_i, and τ_i and per cell and year for $\gamma_{i,t}$, by sampling the respective posterior distributions 5,000 times. Posterior summaries were then mapped to visualize spatial variation in abundance indices, effort effects, and relative abundance trends.

Explaining spatiotemporal variation in relative abundance

The North American monarch breeding range spans nearly the entire United States and southern Canada, which includes widely differing landscapes (see Fig. S1), including the heavily agricultural region in the Midwest. This region is where 38% of monarchs in Mexico come from (Flockhart et al., 2017), and this is where there has been significant losses of milkweeds due to application of glyphosate in crop fields (Brower et al., 2012). These losses have been proposed as one of the major reasons for the declines in winter colonies in Mexico, because of the temporal synchrony of glyphosate application and colony size decreases (Pleasants & Oberhauser, 2013). As such, determining the impact of glyphosate use on monarch abundance was a priority for us here. In addition, summer climate variables are also known to influence relative abundance of monarchs (Zylstra et al., 2021), and our analyses also incorporated such data.

We used posterior samples along with a subset of the linear predictor to calculate an annual relative abundance index, $\omega_{i,t}$, per year and grid cell, as $\omega_{i,t} = \exp\left(\alpha_i + \tau_i + \gamma_{i,t}\right)$. We then modeled relative abundance indices and their associated uncertainty for grid cell i during

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year t as a random variable from a gamma distribution. Expected values for annual abundance

indices per grid cell, $\Omega_{i,t}$, were assumed to be a function of spatially structured grid cell,

agricultural glyphosate use, average temperature, and cumulative precipitation effects (using data

summarized below). The linear predictor for $\Omega_{i,t}$ took the form

$$log(\Omega_{i,t}) = \beta_i + \rho_i P_{i,t} + \zeta_i Z_{i,t} + \nu_i N_{i,t}$$

Parameters β_i were modeled as cell-specific random intercepts with iCAR structure.

Parameters ρ_i were modeled as spatially structured (iCAR), cell-specific, random slope

coefficients for the local effects of glyphosate use, $P_{i,t}$. Agricultural glyphosate use was

calculated as the pounds of active ingredient applied in a county multiplied by the proportion of

the county planted in corn or soybean, to account for the expectation that the majority of

glyphosate use in a county that is negatively impacting monarch host plants is through

applications to corn and soybean acreage (Zylstra et al., 2021). Estimates of pounds glyphosate

applied were obtained from the United States Geological Survey – National Water-Quality

Assessment Project (USGS, 2022), and corn and soybean acreage were obtained from United

States Department of Agriculture National Agricultural Statistics Service (USDA-NASS, 2022)

using the 'rnassqs' R package (Potter, 2019). To obtain an estimate of agricultural glyphosate use

for each grid cell × year, values of glyphosate use offset by the proportion corn or soybean in

each county overlapping grid cell i in year t were multiplied by the proportion of overlap with

grid cell i. Spatial operations were done in R using functions available from the 'rgeos', 'raster',

and 'rgdal' R packages (Bivand et al., 2021; Bivand & Rundel, 2021; Hijmans, 2022). Maps of

glyphosate use (kg active ingredient per acre corn or soybean) in 1993 and 2017 are provided in

Fig. 1.

Parameters ζ_i were modeled as spatially structured (iCAR), cell-specific, random slope coefficients for the local effects of mean annual temperature, $Z_{i,t}$. Parameters ν_i were modeled as spatially structured, cell-specific, random slope coefficients for the local effects of cumulative precipitation, $N_{i,t}$. Mean temperature and precipitation data were obtained from CRU TS 4.03 (Harris et al., 2014), which provides monthly gridded estimates at 0.5° latitude/longitude resolution. Mean temperature for grid cell i in year t was calculated as the annual average of monthly mean temperature estimates in year t. Annual cumulative precipitation for grid cell i in year t was calculated as the sum of monthly precipitation estimates in year t. Maps of mean temperature and cumulative precipitation in 1993 and 2017 are provided in Fig. 1.

To propagate uncertainty in relative abundance indices, $\omega_{i,t}$, during covariate analyses, the analysis was repeated 5,000 times using randomly sampled values from the posteriors of α_i, τ_i, and $\gamma_{i,t}$. Estimates for ρ_i, ζ_i, and ν_i from each of the 5,000 replicates were then used to generate posterior medians and symmetric 95% credible intervals per cell for ρ_i, ζ_i, and ν_i. Posterior summaries were then mapped to visualize spatial variation in covariate effects.

Results

Considering all available NABA data for monarchs across the entire breeding range in eastern and western North America, the median of posterior distributions for relative abundance trends (τ_i) pooled across all grid cells suggested an overall annual increase in monarch relative abundance of 1.36% per year. However, there was an 84% chance of the global trend being > 0 and a 16% chance of the global trend < 0 (Fig. S2). Cell-specific relative abundance trends were generally the most negative in the US Northeast, parts of the Midwest, and in northwest California, and were generally the most positive in the US Southeast and Northwest (Fig. 2a).

Only 11 of the 334 grid cells exhibited relative abundance trends whose 95% credible intervals did not overlap zero, 10 of which were positive trends in Florida (Fig. 2a). Relative abundance in 2018 (α_i) was highest in the Midwest, and lowest in the Southeast (Fig. 2b), generally consistent with what is considered to be the main breeding range of monarch butterflies during the seasonal times of most NABA counts (Jepsen et al., 2015). The increase in expected monarch counts per hour of sampling effort (ϵ_i) was nearly linear ($\epsilon_i \sim 1$) throughout the Midwest and parts of the Northeast where monarchs are more abundant, while smaller values of ϵ_i in the West and much of the Southeast indicated near saturation of sampling space (Fig. 2c), as expected in areas where monarchs are not as abundant.

The effect of glyphosate use on monarch relative abundance was generally negative, especially in the Midwest, where the negative effects in 27 grid cells exhibited 95% credible intervals that did not overlap zero (Fig. 2d). Effects of cumulative precipitation varied spatially from positive to negative, but only one grid cell exhibited a significant local negative effect where the 95% credible interval did not overlap zero (Fig. 2e). Effects of mean temperature also varied spatially, with negative effects in warmer locations and positive effects in colder locations. Temperature effects were most pronounced in the Midwest, where positive effects in 43 grid cells exhibited 95% credible intervals that did not overlap zero (Fig. 2f).

Discussion

Our analysis of the North American Butterfly Association's citizen science data from summer monitoring at 403 sites distributed across the USA and southern Canada suggests that the *breeding* population of monarchs in North America are not showing strong evidence of widespread recent declines. Rather, decreases in adult monarchs were apparent in parts of the Southwest, Northeast, and Corn Belt regions of the USA (Illinois, Indiana, Ohio, southern

Wisconsin), while increases were evident throughout much of the US Northwest, Upper

Midwest, and Southeast. The lack of strong relative-abundance trends, particularly in the US

Midwest, could be partly attributed to opposing effects of increased agricultural glyphosate use

and increased ambient temperature due to climate change, where negative effects of glyphosate

appeared to be offset by positive effects of temperature.

The lack of strong trends in the species core breeding range is in contrast to studies that

focus on winter colony size as measures of population abundance, where there are clearly multi-

decadal declines that have not abated (Brower et al., 2012; Oberhauser et al., 2017; Semmens et

al., 2016; Thogmartin, Wiederholt, et al., 2017; Zylstra et al., 2021), but in general agreement

with various breeding season studies that have shown high variability in monarch abundance

trends (Table S1). For example, Zylstra et al. (2021) examined trends in breeding monarch

abundance using multiple citizen science datasets from the Midwest region. Their work showed

modest declines in that region, consistent with our findings. Meanwhile Ethier (2020) examined

temporal trends in migrating monarch abundance for the southern Ontario region, and concluded

there was no recent decline in the annual migratory cohort there, which is at the beginning of the

migratory journey. Similarly, Culbertson et al. (2021) found no evidence of declines over 30

years in the number of migrating monarchs in the Atlantic coast region. Our analysis considering

NABA counts from the entire breeding population suggests that monarchs may have some ability

to rebound from winter declines during the breeding season, perhaps providing some

counteracting upward movement of monarch numbers despite declines in the winter.

Our analysis indicated that glyphosate use, while an important contributor to local

monarch numbers, is significantly affecting only a portion of the summer breeding range

(portions of upper Midwest, Fig. 2d). The initial rapid increase in glyphosate use in midwestern

corn and soybean, which likely devastated weedy milkweeds in those fields, has now leveled

(Zylstra et al., 2021), such that harmful indirect effects of herbicides on monarchs may no longer

be increasing in magnitude. This suggests that the loss of agricultural milkweed in the U.S.

Midwest will not inevitably lead to ongoing drops in summertime abundances (Agrawal &

Inamine, 2018). A recent inventory of the western half of the USA revealed billions of

previously uncounted native milkweeds that are available for monarchs (Spaeth et al., 2022),

supporting the notion that there are sufficient hostplants to maintain a stable summer population

throughout much of the breeding range.

Recent analyses indicate that changing climate is driving increases and decreases in

overall butterfly numbers across North America (Crossley et al., 2021; Forister et al., 2021), and,

there is evidence that temperature and precipitation in North America is indirectly and positively

impacting abundances of overwintering monarchs (Zylstra et al., 2021). In line with this, we

found a pattern of increasing monarch relative abundance with increasing average temperature in

the northern USA, with the strongest effects evident in the midwestern USA (Fig. 2f), where

glyphosate use appeared to have the strongest negative effect (Fig. 2d). Positive and negative

effects of precipitation were also evident, but this signal was statistically less robust (Fig. 2e).

The eastern U.S. and Canada, the area corresponding to the major monarch summer breeding

ground for the Mexican long-distance migration subpopulation, has generally seen increases in

precipitation and only modest increases in summer temperature (IPCC, 2018), conditions that

have apparently been providing favorable conditions for many butterfly species (Crossley et al.,

2021). However, Texas and the northern portions of Mexico, a vital corridor region, have seen

recent pronounced increases in temperatures (Cuervo-Robayo et al., 2020) which could be

affecting survivorship during the arduous migration.

Overall, our findings suggest monarch populations may have some ability to recover, on average, from declines at overwintering colonies. Of course, the total loss of overwintering monarchs would make it impossible for any summer rebound to be ignited, and there almost certainly is some inflection point well before total winter extinction where spring migrants would be too few to reliably spark a summer resurgence. This would leave only the year-round resident monarch populations, with the loss of the epic migrations that inspire much human interest in monarchs as conservation icons. For those monarchs that do return northward in the spring, our results argue that following the winter period, monarchs experience high population growth, perhaps facilitated by reduced intraspecific competition among larvae. Indeed, monarch larvae are known to exhibit negative interactions with conspecifics, including egg cannibalization (Brower, 1961), aggression (Collie et al., 2020), and oviposition avoidance on optimal host plants (Jones & Agrawal, 2019), behaviors that are presumably reduced under the smaller population returning from recent years in winter migration. Considering the general lack of widespread breeding season declines found here, our evidence suggests, alongside the ongoing declines at winter colonies, that monarchs must be experiencing increasingly higher levels of mortality during their fall migration. Contrasting evidence of no change in the number of tagged monarchs returning to Mexico in the fall suggested otherwise (Taylor et al., 2020), but that finding remains contested due to difficulties in accounting for changing tagging effort through time (Fordyce et al., 2020). In support of our assessment, a recent study of the monarch parasite, *Ophryocystis elektroscirrha*, has shown that nation-wide prevalence has increased in the last 15 years, and that this increase is leading to migratory losses and corresponding reductions in winter colony sizes (Majewska et al., 2022). Therefore, conservation attention along the migration

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routes, and/or actions that reduce parasite transmission, may be more imperative for the

monarch's long-term survival compared to efforts directed at the breeding grounds.

Our data were collected by citizen scientists, a method that requires careful use (Burgess

et al., 2017). The number of party hours spent monitoring butterflies in the North American

Butterfly Association dataset increased on average by 1.2% (±0.3%) per year between 1993-

2017 (Fig. S3). However, our analyses accounted for annual variation in sampling effort while

allowing for a variety of relationships between increasing sampling effort and monarch counts,

following methods developed to analyze conceptually similar Audubon Christmas Bird Counts

(Meehan et al., 2019). Importantly, we did not find evidence of increasing or decreasing trends in

sampling effort around sites dominated by cropland or forest, suggesting that changes in

sampling effort have neither masked declines nor exaggerated abundance increases (Fig. S4).

Furthermore, we found that the local effects of sampling effort exhibited an increasing impact on

expected monarch counts in the Upper Midwest and Northeast (Fig. 2c), suggesting that NABA

counts are likely underestimating numbers of monarchs in the northern portion of their breeding

range. This contrasts with the notion that NABA counts are spatially tracking a dwindling

monarch population through the landscape, which would have yielded an asymptotic relationship

between sampling effort and numbers of expected monarchs, as observed in the western and

southern US.

Beyond monarchs, the conservation of insects has received far less attention than most

other taxa, despite the ubiquity of insects in terrestrial ecosystems. Undoubtedly, citizen-science

efforts targeting the charismatic monarch have exposed many non-scientists in North America to

the importance of insects and the value of their conservation. Given our results, we suggest that

there could be considerable ecological gain from broadening citizen scientists' attention to also

consider the many butterfly species who do appear to be experiencing major summer declines across North America. For example, the summer butterfly count data suggest that *Lycaeides melissa* is declining across much of its broad range (Fig. 3), and even the well-known west coast painted lady, *Vanessa annabella*, appears to be faring worse than the monarch (Fig. 3). In fact, of the 456 butterfly species tracked by NABA, there are 320 species with trends less positive than monarch butterflies (Crossley et al., 2021). More broadly, our results are consistent with other recent analyses of large-scale insect data, that have also revealed complex and heterogeneous spatiotemporal patterns of insect decline. For example, a warming climate in Europe is shifting some moth ranges northward, with species unable to do so declining, but leading to a net range increase overall (Fox et al., 2021). Similarly, recent drops in U.K. moths seem modest relative to increases seen over prior decades (Macgregor et al., 2019), leading to no net change over time. In North America, close examination of long-term insect counts revealed declines in some taxa, but increases in others (Crossley et al., 2020). The same is true with butterflies, where species declines in western North America may be at least partially offset by abundance increases elsewhere on the continent (Crossley et al., 2021), again, leading to no net change despite troubling declines in some locations and/or for some taxa. Our analyses show that for monarchs, for now, summer abundance increases appear sufficient to buffer winter declines. It will be increasingly important to understand complex interactions among species traits and mechanistic drivers, in order to understand and successfully predict how an ever-more-rapidly changing environment will impact the future persistence of monarchs and other insects.

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study monarch butterflies, and who we believe all have the same goal: to understand and identify

potential threats to the monarch population in North America.

Competing interests

The authors declare no competing interests.

Data availability statement

Data (relative abundances and environmental covariates) and R code supporting the findings of

this study are available on GitHub (https://github.com/mcrossley3/MonarchTrends). Raw data

are available from NABA.

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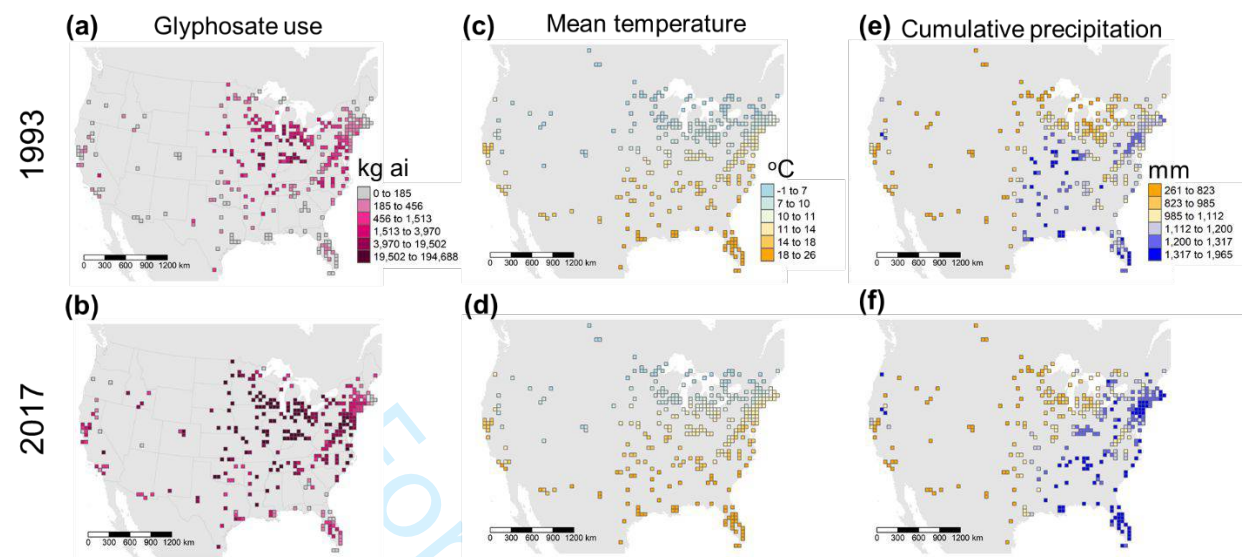
Figures

Figure 1. Maps of covariates considered in models of spatiotemporal patterns of monarch relative abundance in 1993 (earliest date when monarch data were available) and 2017 (latest year when glyphosate use data is available). **(a, b)** glyphosate use (kg active ingredient applied to corn and soybean). **(c, d)** Mean annual temperature. **(e, f)** Cumulative annual precipitation.
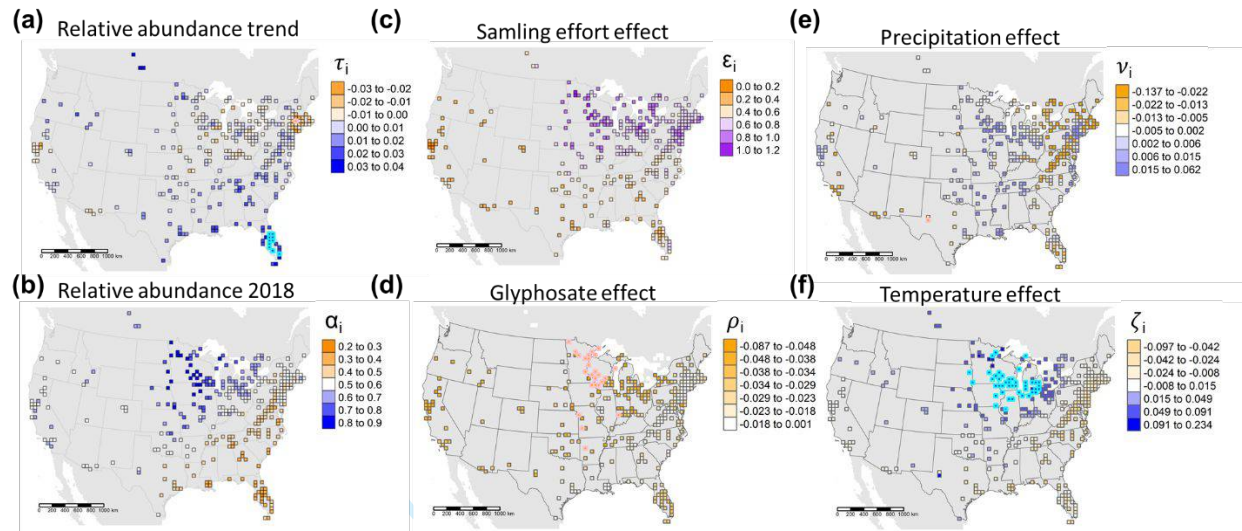
Figure 2. (a) Map of monarch relative abundance in 2018 (α_i). **(b)** Map of sampling effort effect (ε_i). Values of ε_i close to 1 indicate linear increase in butterfly counts per hour effort. Values of ε_i close to zero indicate an asymptotic relationship where number of butterflies counted levels off with increasing sampling effort. **(c)** Map of monarch relative abundance trends (τ_i) among grid cells. Cyan and pink highlighting denotes estimates whose 95% credible intervals were greater or less than zero, respectively. Maps of **(d)** glyphosate effect estimates (ρ_i), **(e)** cumulative precipitation effect estimates (ν_i), and **(f)** mean temperature effect estimates (ζ_i) among grid cells. For d-e, cyan and pink highlighting denotes estimates whose 95% credible intervals were greater or less than zero, respectively.
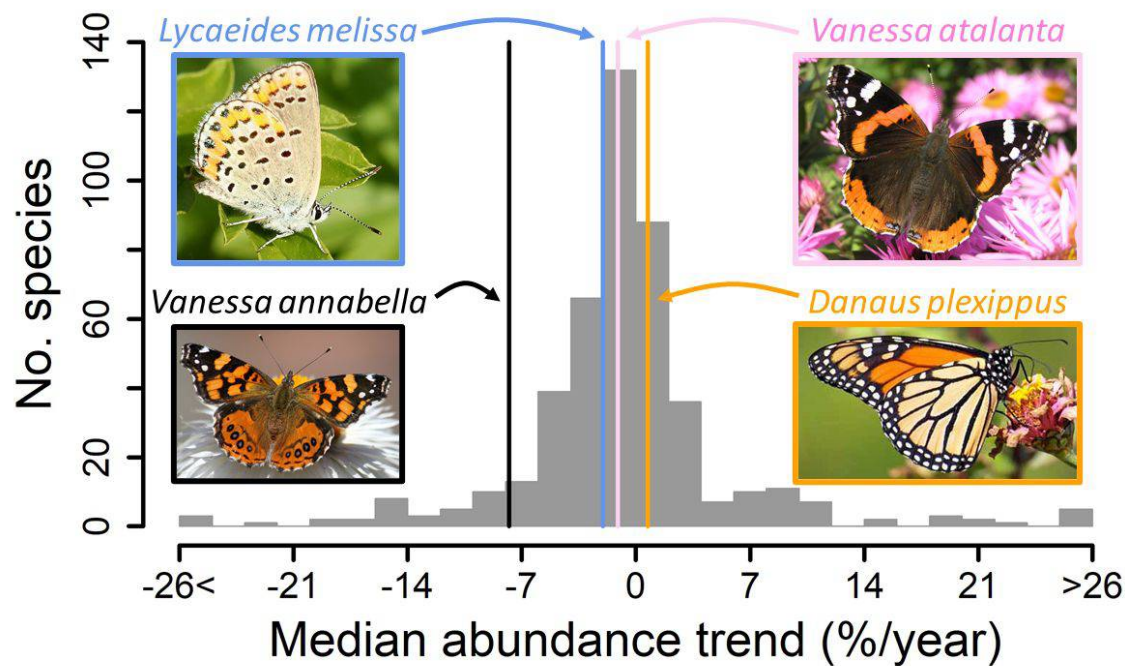
Figure 3. Monarch abundance trend compared to other common North American butterflies. Histogram depicts median abundance trends (%/year) of >450 species monitored by the North American Butterfly Association. Trend for *Danaus plexippus* (+0.7%/year) is highlighted and compared to three other well-known species, *Lycaeides melissa* (-2.0%/year), *Vanessa annabella* (-7.8%/year) and *Vanessa atalanta* (-1.1%/year). Trends based on sites where butterflies were recorded at least five times over a span of ten years. See Crossley et al. (2021) for details on trend estimation. All butterfly species trends are available in Supplemental Table 6.