Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

Population dynamics and drivers of the eastern monarch (*Danaus plexippus*) across its full annual cycle: a cross-scale synthesis of a model migratory species

Vaughn Shirey[1,2] and Leslie Ries[1]

The monarch butterfly is arguably the best-known butterfly species throughout its global range. Declines in the size of the overwintering colonies in Mexico have sparked controversy regarding the conservation of the species and this controversy has been heightened since the United States Fish and Wildlife Service and International Union for the Conservation of Nature concluded that the eastern monarch populations were threatened (or in the case of United States Fish and Wildlife Service, warranted listing). Drivers of decline vary through space and time. Here, we present a synthesis of longitudinal monarch abundance studies that aim to disentangle the putative drivers of decline from one another. We find remarkable consistency that suggests monarch populations are indeed declining and that potential drivers of such decline shift over time. We strongly encourage future work on the species paired with mechanistic, experimental designs to address some long-standing knowledge gaps.

Addresses
[1] Department of Biology, Georgetown University, 37th and O Streets NW, Washington, DC 20057, USA
[2] Marine and Environmental Biology Section – Department of Biological Sciences, University of Southern California, Allan Hancock Foundation Building, Los Angeles, CA 90089, USA

Corresponding author: Shirey, Vaughn (vmshirey@gmail.com)

Current Opinion in Insect Science 2023, **60**:101132

This review comes from a themed issue on **Special Section on Monarch butterflies**

Edited by **Christine Merlin** and **Karen Oberhauser**

For complete overview about the section, refer “Special Section on Monarch Butterflies (2023)”

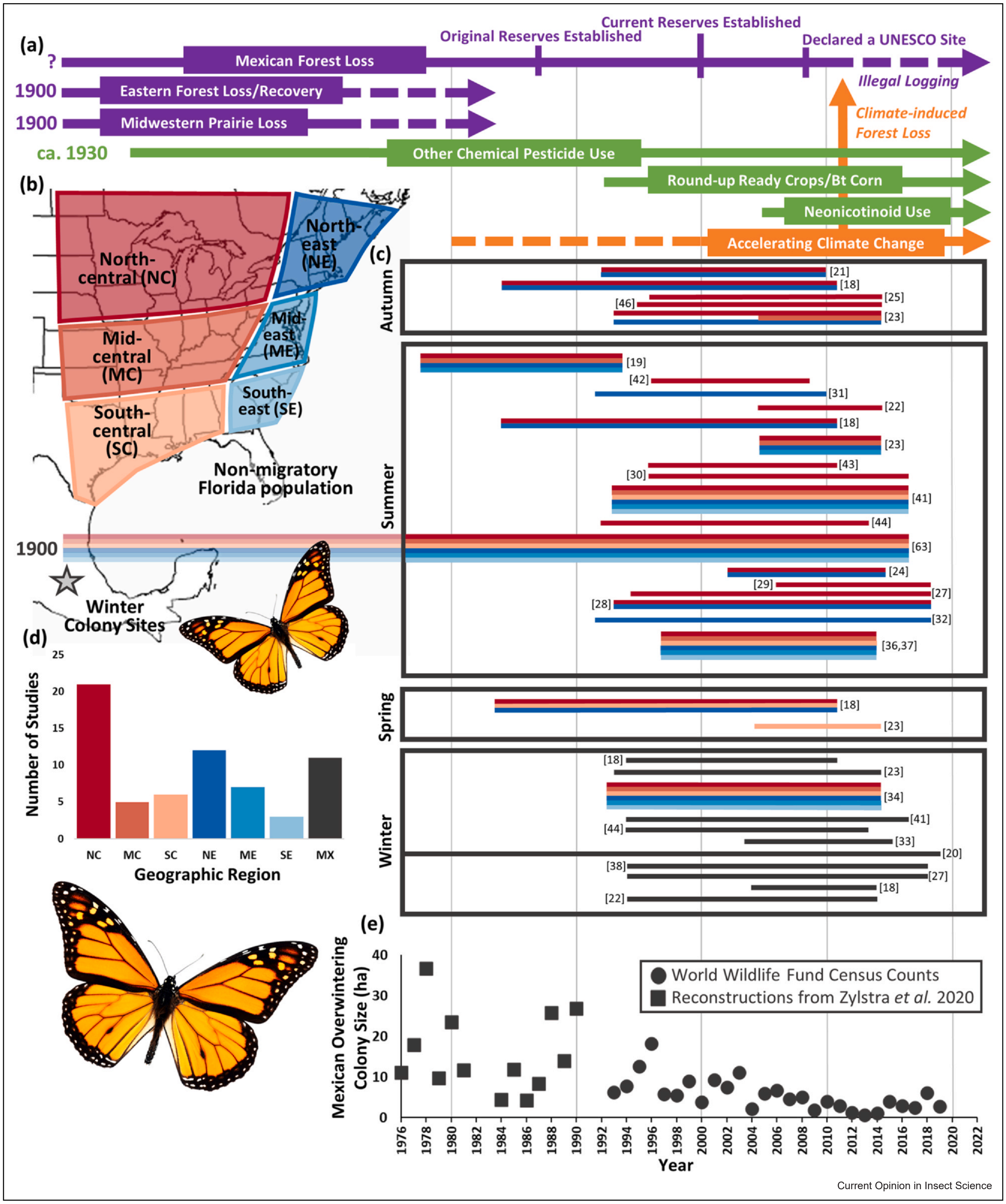
https://doi.org/10.1016/j.cois.2023.101132

Background

The monarch, *Danaus plexippus* (Lepidoptera: Nymphalidae), is arguably the best-known butterfly species throughout its global range [1]. A large part of its fame is due to the extraordinary life cycle of its two migratory North American populations, which are roughly divided by the Rocky Mountains. Both overwinter in dense colonies that occur in central Mexico for the eastern population and along the California coast in the West [2]. These populations are the only ones known to undertake multigenerational, round-trip migrations where they expand to the entire United States and southern Canada during their spring and summer breeding season, and then return to their respective overwintering locations in a single generation the following autumn [2]. Tracking changes in the abundance of monarch populations is of particular interest, not only to scientists, but also an intensely engaged public [1] that includes a large community of dedicated volunteers who monitor the monarch’s entire life cycle [3].

In the past 2–3 decades, the size of the overwintering monarch colonies has shown steep declines in both the western [4,5] and eastern populations (Figure 1e, see figure for reference numbers), and also among the non-migratory population in Florida [6]. Yet, characterizing changes in monarch abundance across studies has been challenging, especially determining which phase(s) of the migratory cycle is at the root of the decline and which stressor(s) are the most likely primary driver(s) [7,8]. The impact of these uncertainties has been heightened since the US Fish and Wildlife service concluded the eastern monarch population merited protected status under the ESA (but was ultimately designated as a candidate for listing with a final determination pending in 2024) [9] and the species as a whole was categorized as ‘endangered’ under the assessment criteria of the International Union for the Conservation of Nature [10]. Uncertainty in characterizing the drivers of the decline is due, in part, to the many studies that have been published over the past 20 years, which focus on different stages of the migratory cycle, occur over a range of temporal and spatial extents, use different data sources, and employ a variety of statistical methods. Synthesizing results across studies can be fraught with challenges; here, we compiled research focused on population trends and drivers for the eastern migratory population to evaluate the results across different spatial and temporal scopes and throughout their annual migratory cycle. We also provide key insights on gaps in analysis and highlight the importance of understanding multiple potential drivers and their shifting importance over time.

Figure 1



Current Opinion in Insect Science

A conceptual figure illustrating the most commonly cited putative drivers of eastern monarch declines along with an inventory of longitudinal monarch population studies at all stages of migration (*n* = *25* papers). Panel **(a)** indicates the drivers of decline and their putative dates of importance. Land cover-related drivers are shown in purple, agricultural drivers in green, and climate change in orange. We indicate the beginning of widespread aerial pesticide applications in the 1930s according to [17]. Panel **(b)** illustrates the migratory subregions that each study covered (the central flyway in warm tones, while the eastern flyway is in cool tones). Panel **(c)** shows the approximate temporal and spatial scope of select studies in our review where boxes indicate the migratory stage of the study, and the length of the bar indicates the temporal scope. Panel **(d)** counts these studies by subregion. Finally, panel **(e)** shows the size of the overwintering colonies in Mexico by year. Note that [63] reconstructed abundance trends back to 1900, whereas all other studies model monarch abundance post 1976.

Monarchs, such as any migratory species with continental-scale distributions, are inherently challenging to study because integrating dynamics across a species' entire migratory range is critical to understanding their population dynamics, but is also difficult [11]. Any point along its eastern North America range during its multigenerational cycle could represent a critical junction in the trajectory of one unified population, but the key stressors could also be a combination of multiple drivers, the so-called 'death by a thousand cuts' [12]. For monarchs, these key stressors have likely changed in importance through space and time (Figure 1a). Logging in the Mexico overwinter grounds was the primary activity first implicated as a threat to the eastern monarchs, but logging slowed after reserve establishment [13] (Figure 1a). Subsequent emerging threats, such as herbicide-tolerant crops, the increased use of insecticides, and climate change, present a shifting landscape of potential key factors and these likely differentially impact each life stage of the monarch (i.e., eggs, caterpillars, pupae, and adults).

Compounding these challenges is the reality that any comprehensive examination of range-wide monarch dynamics relies on volunteer-collected data, which originate from a variety of protocols that generally diverge from strict structured surveys and where uniform practices are challenging to enforce [3]. Further, as we strive to reconstruct trends and drivers across space and time, the changing stressors (Figure 1a) may be difficult to account for with linear statistical models or when key dynamics occur outside the temporal scope of a study [14]. Integrating data emerging from multiple programs is also particularly difficult and best practices for modeling are constantly evolving, complicating direct comparisons between results [15]. Despite these challenges, monarchs represent a unique opportunity to study the full annual cycle migratory dynamics because surveys on their winter grounds, conducted by the National Commission of Protected Natural Areas in Mexico (Comisión Nacional de Áreas Naturales Protegidas) since 1993 and with World Wildlife Fund-Mexico (WWF) since 2004 are better thought of as censuses rather than just a sample of a larger population [16]. This provides a metric that could be considered a 'gold-standard' reference point for tracking the historical dynamics of this population. Another benefit of working with the monarch is a rich history of research on factors such as host plant preferences, habitat use, movement ecology, thermal niche requirements, and disease ecology [1,3,7] and these mechanistic studies can be used to augment large-scale population studies that are necessarily observational in nature. To synthesize results across the history of studies on population trajectories and drivers of the eastern monarch population, we:

1. inventory population-scale studies on the eastern migratory monarch and summarize their main results and conclusions;
2. examine the congruence in results with a focus on cross-scale synthesis; and
3. contextualize these results within each component of the monarch's exceptional migratory cycle.

Methodology

We compiled a comprehensive library of studies on trends and/or drivers of the eastern migratory monarch population: these studies could be carried out at any spatial scale, but only those with at least 10 years of data were included. We started our search using literature from a prior comprehensive review of all monarch peer-reviewed publications beginning in 1945 [18], which has since been updated annually by the Monarch Joint Venture program (https://monarchjointventure.org/). Because statistical methodologies are constantly evolving and also can be a matter of dispute, we did not evaluate studies based on the analytical approach. We divided the migratory and breeding range into seven regions (Figure 1b) based on previously defined boundaries [18]: the overwinter colony sites (gray star), and the southern, middle, and northern zones of both the central (warm-colored) and eastern (cool-colored) flyways. We identified 23 papers that met our inclusion criteria (Table 1), with all published in the last 22 years, except one [19]. We scored each paper for the following information: 1) the migratory stage(s) modeled, 2) the study's spatial scope, 3) the years included, 4) the specific monarch datasets used in the analysis, 5) the main study results, and 6) the author's primary conclusions and details for each paper (Table 1).

Results and discussion

As expected, all studies that present results on the post-1993 trajectory of overwintering colony size showed a

Table 1

Summary of studies that assessed trends and drivers of eastern migratory monarch numbers.

Reference Spatial extent (data source) Year-span	Results summary (note that figure numbers showing results in the original article provided for reference)
Crossley et al. (2022) [28] America north of Mexico (NABA) 1993–2018	No region-specific analyses were done, but visual inspection of pixel-level trends is evident in NC and NE regions (Figure 2a), even though averaging pixel-based trends was not significant. Pixel-based inspection also showed glyphosate use had a negative impact in the NC region (Figure 2d). Warmer summer temperatures have a positive effect in cool regions and negative in warm ones (Figure 2f). The authors note that declines in the Midwest and Northeast may be offset by increases elsewhere.
Zylstra et al. (2021) [27] MEX, NC (NABA) 1994–2003 (reduced), 2004–2018 (full model)	For 2004–2018 model, spring and summer climate accounts for 58% and 29% of summer population size, respectively (Figure 2), but 92% and 6%, respectively, for 1994–2003 model (supplemental). Glyphosate use accounts for 8% in 2004–2018, but only 2% in reduced 1993–2004 model. Summer population size accounts for 92% of variability in overwinter size, and forest loss 8% (Figure 2). The authors conclude that climate is the most important factor driving declines and summer temperatures are becoming more important as they get hotter.
Michielini et al. (2021) [32] NE (MABC), 1992–2018	No decline observed (Figure 1f)
Thogmartin et al. (2020) [38]; MEX,1994–2018	Decline from 1994 to 2013, then increase from 2014 to 2018 (Figure 1). The authors conclude it is too early to determine if this is a true reversal of the decline.
Zylstra et al. (2020) [20] MEX,1976–2019	Based on an extrapolation of partial colony counts, based on 1994–2019 surveys, estimates were made based on colony surveys before WWF began regular monitoring. These extrapolations suggest a declining trend extended back to 1976.
Saunders et al. (2019) [33] MEX, NC (NABA) 2004–2015	The biggest contributor to winter population size is the size of the population at the end of the previous summer (Figure 3a), but autumn nectar (Figure 3c) and winter forest cover contribute as well (Figure 4b).
Wepprich et al. (2019) [30] NC (OH) 1996–2016	Summer monarch's population sizes are declining in Ohio (Table 2).
Crewe et al. (2019) [24] NC (ON Atlas) 2002–2014	Summer numbers are predicted by following (but not previous) winter and only for detrended values. This suggests a disconnect in summer and winter trends (Figure 2).
Kinkead et al. (2019) [29] NC (IA) 2006–2018	Summer monarch population sizes are declining in Iowa (Figure 5), but this was only using data from non-randomly placed surveys. Randomly placed surveys have slightly lower densities.
Boyle et al. (2018) [63] NC, NE, MC, ME, SC, SE (GBIF) 1900–2016	A decline in monarchs and milkweed is evident since the 1950s, whereas both were increasing as far back as 1900. The authors note that the timing of the decline means that the start of GMO crop use in the mid-1990s would not have initiated decline.
Saunders et al. (2018) [44] NC (IL) 1993–2013	Monarchs show a decline between two study periods (1993–2003, 2004–2013). In both periods, spring climate in TX is the strongest predictor of IL monarch size, but summer climate and land use were also factors. Glyphosate use was also associated with declines until application rates reached 75%, after which, they leveled off.
Thogmartin et al. (2017) [34] MEX 1993–2014	Glyphosate on the breeding ground was the main driver explaining overwinter colony size, but climate variables and neonics were also important.
Marini and Zalucki (2017) [41] NC, MC, SC, NE, ME (NABA, CM, PP, MLMP) 1994–2016	Populations throughout the eastern range were declining, but a substantial portion of variability could be explained by density dependence, a factor not accounted for in other studies.
Inamine et al. (2016) [23] NC, MC, SC, NE, ME (NABA, CM, PP, MLMP) 1993–2014	Declines were observed in Mexico and spring in the south, but not summer grounds (Figure 5). Summer levels were predicted by spring and spring by winter. But this was not the case for fall migration, where there was no connection between stages. This disconnect was seen as evidence for the migratory mortality hypothesis rather than milkweed limitation.
Saunders et al. (2016) [43] NC (IL, OH) 1993–2014	Spring climate is the most important factor overall, but there is a factor of summer climate, and moderate local temps are better.
Stenoien et al. (2015) [36] NC, MC, SC, NE, ME, SE (MLMP) 1997–2014	There are generally declining densities of eggs in the breeding season after 2006. Reduced area of overwintering colony size is negatively associated with the area of breeding ground covered in herbicide-tolerant crops.
Ries et al. (2015) [22] NC (IL, NABA) 1994–2014	Declines observed in winter only. But summer numbers showed a strong relationship for following winter colony size, but only a weak relationship with the previous one.
Ries et al. (2015) [18] NC, MC, SC (NABA, OH, IL, CM, PP, MLMP) 1984–2014	Spring recruitment (using early summer numbers as a proxy) predicts abundances the following summer, but that is not true between summer, fall, and the following winter.

Table 1 (*continued*)

Reference Spatial extent (data source) Year-span	Results summary (note that figure numbers showing results in the original article provided for reference)
Nail et al. (2015) [37] NC, MC, SC, NE, ME, SE (MLMP) 1997–2014	The authors find that survival rates appear to be declining between 1997 and 2014 and a density-dependent effect on the survival of immature stages.
Badget et al. (2015) [25] NC (PP) 1996–2014	Increase in fall counts suggests disconnect between stages.
Crewe et al. (2015) [46] NC (LP) 1994–2014	Increase, then decline with breakpoint at ~2004.
Breed et al. (2013) [31] NE (MA) 1992–2010	Summer monarch population sizes are declining in MA (Figure 1).
Davis (2012) [21] NC, NC (PP, CM) 1992–2010	Increase in fall counts suggests disconnect between stages.
Zipkin et al. (2012) [42] NC (OH) 1996–2008	Summer populations most strongly impacted by spring climate, but hotter summers at cooler sites or cooler summers at warmer sites increase populations.
Swengel (1995) [19] NC, MC, NE, ME, SE (NABA)	No obvious change in population size (no formal trend analysis).

Only studies with at least 10 years of data are included. For details on the spatial extent of each study, see Figure 1b and text.

decline since they were all based on the exact same WWF data (Figure 1e). Only one study [20] estimated colony size before standardized surveys began in 1992 and showed that winter population sizes may have been steadily declining since at least 1976 (square points in Figure 1b), but we note that these earlier surveys used inconsistent methodologies and only included a variable subset of the currently known colony locations [20].

Studies of population trajectories during other portions of the migratory cycle are considerably more difficult to carry out and thus to compare because they require spatiotemporally replicated surveys across the monarch's vast migratory and breeding ranges and so rely almost entirely on volunteer butterfly monitoring networks that vary in their protocols [3]. The primary volunteer-based programs used for these studies include the oldest and largest butterfly monitoring program in existence: the North American Butterfly Association's (NABA) count program, which was started in 1975 and establishes fixed-count circles (25-km diameter) where teams of volunteers record all butterflies seen during a single day [19]. More regional monitoring networks, where stricter surveys are performed along fixed transects multiple times within and across years, started in Illinois (IL) in 1987, then spread to Ohio (OH) (1996), Iowa (IA) (2007), and Michigan (MI) (2011) [3]. A continental-scale program surveying eggs and larvae, the Monarch Larva Monitoring Project (MLMP), was launched in 1998 and collects more fine-grained mechanistic data. Finally, during the 1990s, fall censuses were established on three peninsulas that funnel migrating monarchs on their journey south: Cape May in New Jersey, Peninsula Point in MI, and Long Point in Ontario [3].

The first study to examine long-term trends outside of the Mexico colonies was focused on the Cape May and Peninsula Point fall stopover sites and showed an upward population trajectory from 1992 to 2010 [21], highlighting the importance of comparative studies during different phases of migration. Three other studies [22–24] found no evidence of a directional trend in the summer breeding range from 1993 to 2015 and, together with the fall study [21], established a potential disconnect between trends seen in summer, fall, and winter stages of migration. Three hypotheses emerged to account for these disconnects: (1) observed winter declines are largely driven by mortality during fall migration [22,23,25]; (2) monarchs in the summer breeding grounds are actually in decline, but the effect was being masked by crowding into an increasingly small remaining habitat [26]; and/or 3) the statistical challenges of accounting for non-random placement of volunteer survey sites and variable protocols [22].

In an attempt to resolve the controversy, two recent studies using more advanced statistical approaches and including a longer time series (1994–2018) demonstrate regional declines in the northern, summer breeding portions of both the central [27,28] and eastern [28] flyways. These studies are consistent with smaller-scale regional studies showing monarch declines from 2006 to 2018 in Iowa [29], 1996–2016 in Ohio [30], and Massachusetts from 1992 to 2010 [31], but see [32]. Further, multiple studies have established strong links between the size of the population at the end of summer and the size of the colonies the following winter [22,27,33]. In contrast, studies specifically designed to examine loss during fall migration have found only minor impacts of drivers that could be linked to migratory loss, including disease [34], climate and/or nectar sources along the migratory flyways, and continued loss of forest habitat in Mexico [27,33]. Finally, studies of monarch tagging records show there is no trend in tag recovery rates of monarchs arriving in Mexico, which also suggests no downward trend in migratory success [35]. Based on these newer and more comprehensive studies, our opinion is that post 1993, declines in the size of the eastern migratory monarch population are driven primarily by lower recruitment rates during the spring and summer breeding season, rather than migratory loss. Indeed, evidence to support that egg density is declining has been reported over this timeframe [36] in addition to a reduction in survival rates from immature to adult butterflies [37]. Previous results showing a disconnect between summer and winter trajectories were likely due to the statistical challenges of analyzing data from volunteer surveys.

Pinpointing the specific causes of monarch declines during yearly recruitment is even more challenging than establishing patterns [38–41]. The first studies to specifically examine the underlying drivers of the substantial variability seen in year-to-year monarch population sizes showed that spring climate in the south central region was the primary factor explaining summer population growth in Ohio [42,43]. There was also a tendency toward higher local population sizes at cooler summer sites in warmer years and warmer summer sites in cooler years, suggesting an optimum summer temperature for growth [42]. Similar results were found for Illinois over a longer time period, 1994–2013 [44]. The most comprehensive study to date, incorporating conditions in winter, spring, summer, and fall along the central flyway, and integrating data from NABA, Ohio, Illinois, Michigan and Iowa surveys, showed climate as the primary driver of recent declines and supported the primacy of spring climate in the south. However, it also showed a growing role for hotter summer temperatures that appear to depress growth [27] and these results are supported by laboratory studies on thermal tolerances of developing monarch larvae [45]. Finally, forest loss in Mexico, while substantially slower, is associated with lower arrival rates in the winter colonies 2004 [20], but it is important to note that forest loss since 2007 is due largely to climate change rather than illegal logging [13] (Figure 1a). Notably, one study also found 2004 to be a breakpoint for declines at one local site in Ontario [46]. In aggregate, the evidence currently supports that climate, both directly and indirectly, is a primary, discernible driver of monarch declines post 2004 but potentially as far back as 1993.

Another putative driver of monarch declines is the deployment of herbicide-tolerant crops that allowed substantially increased applications of glyphosate starting in the mid-1990s [47]. Monarchs are expected to be especially vulnerable to increased glyphosate spraying because their favored host plant, *Asclepias syriaca* (common milkweed), grows primarily in a highly disturbed habitat, such as within row crops and along adjacent roadsides and fields. After the adoption of glyphosate-tolerant crops, it was estimated that 60–70% of these milkweed resources had been lost across the Midwest [48,49]. On the other hand, milkweed continues to be an extremely common plant on the landscape, causing some to doubt that it could be limiting as a food source [50]. Studies that link milkweed abundance to population declines are especially challenging because, unlike climate patterns, localized milkweed densities are unknown so they cannot be included as covariates in large-scale analyses. Further, data on chemical usage by the agricultural industry have been available, generally, since 1992 but not earlier [51,52]. Studies that combine these data with estimates of crop cover show mixed results for glyphosate usage. In more broad-scale studies, glyphosate (or the presence of herbicide-resistant crops) was a significant predictor in the decline of overwintering colony size [34,36] and on local monarch abundances in NABA counts in the Midwest [28]. The most detailed analysis of glyphosate use on local monarch abundances showed that glyphosate effects were significant predictors of decline up until glyphosate use leveled off in the mid-2000s [44], although a later analysis did not pick up the same signal throughout the Midwest [27]. However, based on (a) monarch's preferred use of common milkweed [53] and its dominance in a highly disturbed habitat, including adjacent to cropland and roadsides [48]; (b) better monarch survivorship in those locations [50]; and (c) the linkage between glyphosate use, crop cover, and localized monarch declines (especially during the period of the major adoption of herbicide-resistant crops [44]), our opinion is that milkweed loss was likely an important contributor to monarch declines between 1995 and 2005 and the current lower baseline size of their population.

Another major factor that could be impacting monarchs is pesticides. While these chemicals have been used for decades, the types of pesticides available and their modes of delivery are constantly evolving. This may mean that their impacts are shifting in ways that are difficult to predict [54,55]. Despite early concerns, corn genetically modified to express toxins from *Bacillus thuringiensis* (*Bt*) turned out not to be a threat to monarchs [56] and, indeed, the extremely targeted action means that this technology may be safer for insect communities. Lab-based toxicological comparisons between the current most frequently used insecticides suggest that pyrethroids are the most toxic at field-relevant levels to monarchs, while neonicotinoid exposure has the lowest toxicity. Use of neonicotinoid seed treatments was thus not expected to impact monarch populations due to larval [57,58] or adult [59] exposure because neonicotinoid concentrations in milkweed sampled immediate downslope of fields planted with treated seeds were 10–100 times lower than concentrations that cause no observable effects in toxicity studies. With regard to foliar and seed-treatment formulations, decreasing concentrations of neonicotinoids on milkweed would be expected with increasing distance downwind or downslope of the treated field, respectively. Despite this, an emerging literature on large-scale field correlations has indicated that use of neonicotinoid seed treatments has been implicated as a potential driver of butterfly declines [60,61], including monarchs [34]. A more recent examination of monarch population sizes throughout the Midwest indicates that neonicotinoids are the environmental factor most related to depression of local monarch abundance, while pyrethroids showed no relationship [55]. Further, on average, pyrethroid use has been relatively constant over 1998–2014 [62], which means they are unlikely to contribute to recent declines even if they do impact overall population sizes. Based on these studies, there appears to be a disconnect in risk estimates for neonicotinoid seed treatments, from laboratory toxicology studies compared with an emerging literature on field-based correlations between monarch population dynamics and county-level survey data of pesticide use. Resolving this disconnect should be a vital area of future research; however, our ability to examine this critical issue is at grave risk due to the cessation of reporting seed-applied neonicotinoid use in the USGS database after 2014 [62] as well as current proposals to scale back the USGS dataset further. This makes seed-treatment insecticide use difficult to include in any post-2014 long-term studies [20,27]; however, other datasets, such as those from the United States Department of Agriculture National Agriculture Statistics Service (https://www.ams.usda.gov/datasets/pdp), may be able to compensate for these data gaps.

Ultimately, our review of longitudinal monarch population trajectories revealed remarkable consistency across studies. Although the specific drivers of trends are still subject to debate, it is clear that the eastern population is experiencing a notable decline. Climate change is likely the primary driver of abundance trends beginning in the early 2000s, yet the role of recent insecticide and herbicide use in driving these trends is still controversial. Further, the studies that examined trends before 1993 provided evidence that monarch populations have been in decline before the most recent acceleration of climate change and the adoption of recent chemical pest control methods discussed above — a possible ‘death by a thousand cuts’ scenario [12]. This leaves forest loss in the Mexican overwintering grounds as the most likely driver of pre-1993 declines (and highlights the necessity of understanding how drivers may shift over space and time), yet we lack sufficient data about these populations to explicitly link these two factors due to the relatively recent collection of data from the overwintering grounds. Available data are notably sparse in the pre-1993 period and most studies examine monarch population trends in the critical transition phase between the mid-1990s and early 2000s, when a large majority of the decline has already been thought to have occurred (Figure 1c). Only three studies [19,20,63] sought to reconstruct trends in monarch populations before the 1990s (Figure 1b) and establishing pre-1990 baselines for monarch abundance is essential for understanding the true magnitude of declines compared with population estimates farther back in history. The farthest historical reconstructions [20,63] show declines occurring well before climate change and newer pesticide technologies, which is another indication that forest loss may be a major driver of more historical declines.

Examining year-to-year population trends for any wide-ranging migratory species is always a challenging endeavor, and this is partially due to notable gaps that occur differentially throughout the annual migratory cycle [11]. Based on our review of the literature, we have formed four core opinions regarding the nature of monarch decline:

(1) Pre 1990s, declines were likely driven by forest loss in the Mexican overwintering grounds, but formal hindcast analyses could disentangle these effects from other putative drivers.
(2) Declines from the mid-1990s to mid-2000s were likely driven, at least in part, by glyphosate use, but it is still difficult to demonstrate this definitively due to the localized scale of application and milkweed occurrence to tie to monarch survey data.
(3) Post 2005, the best evidence supports climate as the primary driver of monarch decline, but the full role of insecticide treatment is still unknown due to a lack of investigation and data limitations (primarily, county-level scale data).
(4) There is very little evidence supporting increased migratory mortality as a driver in monarch decline.

With respect to gaps in analysis, notably, only two studies in our review modeled spring abundance trends and this seasonal data gap in the migratory cycle is particularly problematic since the results show that spring climate is the largest driver of yearly recruitment. Filling these seasonal gaps will be an essential step forward for understanding the full migratory cycle and for potentially uncovering new drivers of abundance shifts previously masked by our overwhelming focus on summer and winter populations [11]. Altogether, we need to expand our scope of studies both forward and backward in time (forecasts and hindcasts), which will require us to leverage biased and sparse historical records from natural history collections with appropriate methodologies [64–66]. Additionally, other research approaches, such as studies involving the use of genomic data, may be a promising avenue for exploring trends in monarch abundance over thousands of years [67]. It is clear to us that future monarch research will benefit from the continued implementation of a range of techniques, including multiple and cross-scale modeling studies, reconstruction of historical trends, forecasting, and mechanistic experimentation, that directly investigate the role of climate and pesticides on monarch fitness and behavior. Synthesis of both large-scale models and mechanistic experimentation will undoubtably strengthen the causal linkages between potential drivers and monarch decline.

Funding

VS was supported by a United States National Science Foundation Graduate Research Fellowship (#1937959) and a David H. Smith Postdoctoral Conservation Research Fellowship while conducting this work. LR was supported by a National Science Foundation DEB #2017791 and the United States Geological Survey (#G21AC10369).

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

We the authors declare no conflict of interest in this work.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Gustafsson KM, Agrawal AA, Lewenstein BV, Wolf SA: **The monarch butterfly through time and space: the social construction of an icon**. *BioScience* 2015, **65**:612-622.
2. Brower LP, Fink LS, Van Zandt Brower A, Leong K, Oberhauser K, Altizer S, Taylor O, Vickerman D, Calvert WH, Van Hook T, *et al*.: **On the dangers of interpopulational transfers of monarch butterflies**. *BioScience* 1995, **45**:540-544.
3. Ries L, Oberhauser K: **A citizen army for science: quantifying the contributions of citizen scientists to our understanding of monarch butterfly biology**. *BioScience* 2015, **65**:419-430.
4. Espeset AE, Harrison JG, Shapiro AM, Nice CC, Thorne JH, Waetjen DP, Fordyce JA, Forister ML: **Understanding a migratory species in a changing world: climatic effects and demographic declines in the western monarch revealed by four decades of intensive monitoring**. *Oecologia* 2016, **181**:819-830.
5. Schultz CB, Brown LM, Pelton E, Crone EE: **Citizen science monitoring demonstrates dramatic declines of monarch butterflies in western North America**. *Biol Conserv* 2017, **214**:343-346.
6. Brower LP, Williams EH, Dunford KS, Dunford JC, Knight AL, Daniels J, Cohen JA, Van Hook T, Saarinen E, Standridge MJ, *et al*.: **A long-term survey of spring monarch butterflies in north-central Florida**. *J Nat Hist* 2018, **52**:2025-2046.
7. Agrawal AA, Inamine H: **Mechanisms behind the monarch's decline**. *Science* 2018, **360**:1294-1296.
8. Stenoien C, Nail KR, Zalucki JM, Parry H, Oberhauser KS, Zalucki MP: **Monarchs in decline: a collateral landscape-level effect of modern agriculture**. *Insect Sci* 2018, **25**:528-541.
9. United States Fish and Wildlife Service. Monarch (Danaus plexippus) Species Status Assessment Report. Version 2.1 96 + appendices, 2020.
10. Walker A, Oberhauser KS, Pelton EM, Pleasants JM, Thogmartin WE: **Danaus plexippus ssp. plexippus**. *The IUCN Red List of Threatened Species* 2022,.
11. Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM: **A call for full annual cycle research in animal ecology**. *Biol Lett* 2015, **11**:20150552.
12. Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D: **Insect decline in the Anthropocene: death by a thousand cuts**. *Proc Natl Acad Sci* 2021, **118**:e2023989118.
13. Vidal O, López-García J, Rendón-Salinas E: **Trends in deforestation and forest degradation after a decade of monitoring in the Monarch Butterfly Biosphere Reserve in Mexico**. *Conserv Biol* 2014, **28**:177-186.
14. Rollinson CR, Finley AO, Alexander MR, Banerjee S, Dixon Hamil K-A, Koenig LE, Locke DH, DeMarche ML, Tingley MW, Wheeler K, *et al*.: **Working across space and time: nonstationarity in ecological research and application**. *Front Ecol Environ* 2021, **19**:66-72.
15. Zipkin EF, Zylstra ER, Wright AD, Saunders SP, Finley AO, Dietze MC, Itter MS, Tingley MW: **Addressing data integration challenges to link ecological processes across scales**. *Front Ecol Environ* 2021, **19**:30-38.
16. Vidal O, Rendón-Salinas E: **Dynamics and trends of overwintering colonies of the monarch butterfly in Mexico**. *Biol Conserv* 2014, **180**:165-175.
17. Rattner BA: **History of wildlife toxicology**. *Ecotoxicology* 2009, **18**:773-783.
18. Ries L, Oberhauser K, Taron D, Battin J, Rendon-Salinas E, Altizer S, Nail K: **Connecting eastern monarch population dynamics across their migratory cycle**. Monarchs in a Changing World: Biology and Conservation of an Iconic Butterfly. Cornell University Press; 2015:268-281.
19. Swengel AB: **Population fluctuations of the monarch (Danaus plexippus) in the 4th of July Butterfly Count 1977-1994**. *Am Midl Nat* (2) 1995, **134**:205-214.
20. •• Zylstra ER, Thogmartin WE, Ramirez MI, Zipkin EF: **Summary of Available Data from the Monarch Overwintering Colonies in Central Mexico, 1976–1991**. US Geological Survey; 2021.

This report is a comprehensive compilation of all data that is available on the size of the overwintering colonies going all the way back to their discovery in 1976. This greatly expands the temporal scope of the pattern of decline in overwintering monarchs. The difficulty of these data is that they are fragmentary and use different methods than those initiated in 1993. The authors are all experts in the field of integrating difficult data sets across space and time and we believe that this report likely reflects the best estimation across the entire history of censuses in the Mexico overwinter grounds.

21. Davis AK: **Are migratory monarchs really declining in eastern North America? Examining evidence from two fall census programs**. *Insect Conserv Divers* 2012, **5**:101-105.
22. Ries L, Taron DJ, Rendón-Salinas E: **The disconnect between summer and winter monarch trends for the eastern migratory population: possible links to differing drivers**. *Ann Èntomol Soc Am* 2015, **108**:691-699.
23. Inamine H, Ellner SP, Springer JP, Agrawal AA: **Linking the continental migratory cycle of the monarch butterfly to understand its population decline**. *Oikos* 2016, **125**:1081-1091.
24. Crewe TL, Mitchell GW, Larrivée M: **Size of the Canadian breeding population of monarch butterflies is driven by factors acting during spring migration and recolonization**. *Front Ecol Evol* 2019, **7**:308.
25. Badgett G, Davis AK: **Population trends of monarchs at a northern monitoring site: analyses of 19 years of fall migration**

counts at Peninsula Point, MI. *Ann Èntomol Soc Am* 2015, **108**:700-706.

26. Pleasants JM, Williams EH, Brower LP, Oberhauser KS, Taylor OR: **Conclusion of no decline in summer monarch population not supported**. *Ann Èntomol Soc Am* 2016, **109**:169-171.

27. •• Zylstra ER, Ries L, Neupane N, Saunders SP, Ramírez MI, Rendón-Salinas E, Oberhauser KS, Farr MT, Zipkin EF: **Changes in climate drive recent monarch butterfly dynamics**. *Nat Ecol Evol* 2021, **5**:1441-1452.

This paper, which includes one of us (Ries) as a coauthor presents, in our view, the most comprehensive analysis of the population dynamics and their putative causes that exists for the monarch. This study uses an integrative approach that combines multiple sources of data, including more structured surveys that are not included in the Crossley paper.

28. •• Crossley MS, Meehan TD, Moran MD, Glassberg J, Snyder WE, Davis AK: **Opposing global change drivers counterbalance trends in breeding North American monarch butterflies**. *Glob Change Biol* 2022, **28**:4726-4735.

This is the most comprehensive study showing that across the entire North American range of the monarch, they do not appear to be declining. However, we note that if the spatial patterns of declines, increases, and areas with no apparent trends are examined in their results, there does appear to be a trend towards declines in the Midwest and Northeast, which encompass the main recruitment grounds of the overwinter population in Mexico. Thus, we feel that, despite the interpretation of the authors, our opinion is that this paper actually presents evidence that corroborates our conclusion of monarch declines, at least for the Eastern population.

29. • Kinkead KE, Harms TM, Dinsmore SJ, Frese PW, Murphy KT: **Design implications for surveys to monitor monarch butterfly population trends**. *Front Ecol Evol* 2019, **7**:195.

One of the main controversies surrounding the use of community science observations and surveys is that they are not randomly placed. Given that milkweed traditionally dominates in agricultural lands that are unlikely to be the focus of community science surveys, results from those surveys may underestimate any ongoing declines. This study suggests that randomly placed surveys are likely to find fewer monarchs, but that overall, there is little difference between survey methods.

30. Wepprich T, Adrion J, Ries L, Wiedmann J, Haddad N: **Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA**. *PLos One* 2019, **14**:e0216270.

31. Breed G, Stichter S, Crone E: **Climate-driven changes in northeastern US butterfly communities**. *Nat Clim Change* 2013, **3**:142-145.

32. Michielini JP, Dopman EB, Crone EE: **Changes in flight period predict trends in abundance of Massachusetts butterflies**. *Ecol Lett* 2021, **24**:249-257.

33. Saunders SP, Ries L, Neupane N, Ramírez MI, García-Serrano E, Rendón-Salinas E, Zipkin EF: **Multiscale seasonal factors drive the size of winter monarch colonies**. *Proc Natl Acad Sci* 2019, **116**:8609-8614.

34. Thogmartin WE, Wiederholt R, Oberhauser K, Drum RG, Diffendorfer JE, Altizer S, Taylor OR, Pleasants J, Semmens D, Semmens B, *et al*.: **Monarch butterfly population decline in North America: identifying the threatening processes**. *R Soc Open Sci* 2017, **4**:170760.

35. •• Taylor OR Jr., Pleasants JM, Grundel R, Pecoraro SD, Lovett JP, Ryan A: **Evaluating the migration mortality hypothesis using monarch tagging data**. *Front Ecol Evol* 2020, **8**:264.

This study provides mechanistic evidence, based on tagging, that the arrival rates on overwinter grounds have not declined over time, and so is an independent source of evidence that migratory loss is not likely a driver in the recently observed declines.

36. Stenoien C, Nail KR, Oberhauser KS: **Habitat productivity and temporal patterns of monarch butterfly egg densities in the eastern United States**. *Ann Èntomol Soc Am* 2015, **108**:670-679.

37. Nail KR, Stenoien C, Oberhauser KS: **Immature monarch survival: effects of site characteristics, density, and time**. *Ann Èntomol Soc Am* 2015, **108**:680-690.

38. •• Thogmartin WE, Szymanski JA, Weiser EL: **Evidence for a growing population of eastern migratory monarch butterflies is currently insufficient**. *Front Ecol Evol* 2020, **8**:43.

This study highlights the important point that understanding monarch population dynamics always requires a long view and that an apparent trend in any small subset of years may simply indicate the substantial variation in year-to-year abundances that are separate from any directional trends.

39. Belsky J, Joshi NK: **Assessing role of major drivers in recent decline of monarch butterfly population in North America**. *Front Environ Sci* 2018, **6**:86.

40. Agrawal AA: **Advances in understanding the long-term population decline of monarch butterflies**. *Proc Natl Acad Sci* 2019, **116**:8093-8095.

41. Marini L, Zalucki MP: **Density-dependence in the declining population of the monarch butterfly**. *Sci Rep* 2017, **7**:1-8.

42. Zipkin EF, Ries L, Reeves R, Regetz J, Oberhauser KS: **Tracking climate impacts on the migratory monarch butterfly**. *Glob Change Biol* 2012, **18**:3039-3049.

43. Saunders SP, Ries L, Oberhauser KS, Zipkin EF: **Evaluating confidence in climate-based predictions of population change in a migratory species**. *Glob Ecol Biogeogr* 2016, **25**:1000-1012.

44. Saunders SP, Ries L, Oberhauser KS, Thogmartin WE, Zipkin EF: **Local and cross-seasonal associations of climate and land use with abundance of monarch butterflies Danaus plexippus**. *Ecography* 2018, **41**:278-290.

45. Nail KR, Batalden RV, Oberhauser KS: **What's too hot and what's too cold**. Part III, 8 Cornell University Press; 2015:99-108.

46. Crewe T, McCracken J: **Long-term trends in the number of monarch butterflies (Lepidoptera: Nymphalidae) counted on fall migration at Long Point, Ontario, Canada (1995–2014)**. *Ann Èntomol Soc Am* 2015, **108**:707-717.

47. Swinton SM, Van Deynze B: **Hoes to herbicides: economics of evolving weed management in the United States**. *Eur J Dev Res* 2017, **29**:560-574.

48. Pleasants JM, Oberhauser KS: **Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population**. *Insect Conserv Divers* 2013, **6**:135-144.

49. Zaya DN, Pearse IS, Spyreas G: **Long-term trends in midwestern milkweed abundances and their relevance to monarch butterfly declines**. *BioScience* 2017, **67**:343-356.

50. Haan NL, Landis DA: **The importance of shifting disturbance regimes in monarch butterfly decline and recovery**. *Front Ecol Evol* 2019, **7**:191.

51. Baker NT, Stone WW: **Estimated Annual Agricultural Pesticide use for Counties of the Conterminous United States, 2008-12**. US Department of the Interior, US Geological Survey Washington, DC; 2015.

52. Stone WW: **Estimated Annual Agricultural Pesticide use for Counties of the Conterminous United States, 1992–2009**. US Geological Survey; 2013.

53. Pocius VM, Pleasants JM, Debinski DM, Bidne KG, Hellmich RL, Bradbury SP, Blodgett SL: **Monarch butterflies show differential utilization of nine Midwestern milkweed species**. *Front Ecol Evol* 2018, **6**:169.

54. Perry ED, Moschini G: **Neonicotinoids in US maize: insecticide substitution effects and environmental risk**. *J Environ Econ Manag* 2020, **102**:102320.

55. Van Deynze B., Swinton S.M., Hennessy D.A., Ries L.: **Adoption of modern pest control systems associated with declines in butterfly abundance across Midwestern monitoring network**, *bioRxiv*. 2022.

56. Sears MK, Hellmich RL, Stanley-Horn DE, Oberhauser KS, Pleasants JM, Mattila HR, Siegfried BD, Dively GP: **Impact of Bt corn pollen on monarch butterfly populations: a risk assessment**. *Proc Natl Acad Sci* 2001, **98**:11937-11942.

57. • Krishnan N, Zhang Y, Aust ME, Hellmich RL, Coats JR, Bradbury SP: **Monarch butterfly (Danaus plexippus) life-stage risks from foliar and seed-treatment insecticides**. *Environ Toxicol Chem* 2021, **40**:1761-1777.

This mechanistic study of toxicity effects of the current most commonly used pesticides in monarch larvae indicates that neonicotinoids show the lowest toxicity levels at field-relevant doses, whereas pyrethroids show the highest. These direct mechanistic studies contrast with emerging (but still preliminary) field studies showing that neonicotinoid field applications are associated with monarch declines, more so than pyrethroids. This mismatch between lab and field data demands that resolving the disconnect should be a primary focus of future research.

58. Krishnan N, Zhang Y, Bidne KG, Hellmich RL, Coats JR, Bradbury SP: **Assessing field-scale risks of foliar insecticide applications to monarch butterfly (Danaus plexippus) larvae**. *Environ Toxicol Chem* 2020, **39**:923-941.

59. Prouty C, Bartlett LJ, Krischik V, Altizer S: **Adult monarch butterflies show high tolerance to neonicotinoid insecticides**. *Ecol Entomol* 2023, **48**:531-543.

60. Gilburn AS, Bunnefeld N, Wilson JM, Botham MS, Brereton TM, Fox R, Goulson D: **Are neonicotinoid insecticides driving declines of widespread butterflies?** *PeerJ* 2015, **3**:e1402.

61. Forister ML, Cousens B, Harrison JG, Anderson K, Thorne JH, Waetjen D, Nice CC, De Parsia M, Hladik ML, Meese R, *et al.*: **Increasing neonicotinoid use and the declining butterfly fauna of lowland California**. *Biol Lett* 2016, **12**:20160475.

62. Douglas MR, Baisley P, Soba S, Kammerer M, Lonsdorf EV, Grozinger CM: **Putting pesticides on the map for pollinator research and conservation**. *Sci Data* 2022, **9**:571.

63. Boyle JH, Dalgleish HJ, Puzey JR: **Monarch butterfly and milkweed declines substantially predate the use of genetically modified crops**. *Proc Natl Acad Sci* 2019, **116**:3006-3011.

64. Ries L, Zipkin EF, Guralnick RP: **Tracking trends in monarch abundance over the 20th century is currently impossible using museum records**. *Proc Natl Acad Sci* 2019, **116**:13745-13748.

65. Shirey V, Khelifa R, M'Gonigle LK, Guzman LM: **Occupancy-detection models for natural history museum data: promise and pitfalls**. *Methods Ecol Evol* (2) 2022, **14**:402-414.

66. Larsen EA, Shirey V: **Method matters: pitfalls in analysing phenology from occurrence records**. *Ecol Lett* 2021, **24**:1287-1289.

67. • Boyle JH, Strickler S, Twyford A, Ricono A, Powell A, Zhang J, Xu H, Dalgleish HJ, Jander G, Agrawal AA, *et al.*: **Temporal matches and mismatches between monarch butterfly and milkweed population changes over the past 12,000 years**. *Curr Biol* 2023, **33**:3702-3710 e5.

This is an intriguing paper because it purports to examine population changes all the way back to our last glacial maximum, so would have the potential to capture any dynamics relative to the establishment and range dynamics of both monarchs and milkweeds. It is outside our expertise to know whether these types of inferences are reasonable, but the exploration of population dynamics reaching back this far is worthy of attention.