



Mapping monarch seasonal breeding patterns in Eastern North America to inform mowing strategies for roadsides and other rights-of-ways

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Abstract

Monarch populations have declined precipitously over the past decades, largely due to the loss of their breeding host plant, milkweed. One mitigation strategy is to plant milkweed along rights-of-ways. However, many rights-of-ways undergo routine mowing, which can result in egg, caterpillar, and chrysalis mortality. To minimize this risk, it is critical to time mowing activity to avoid the peak breeding activity of monarchs. In this study we used community science data to define breeding patterns and timing of monarch breeding throughout the United States and Canada. We identified four breeding patterns: (1) year-round, (2) spring-only, (3) summer, and (4) disjunct breeding. Year-round and disjunct breeding were concentrated around the Gulf of Mexico, including Florida, and the southern United States, respectively. As expected, we found that monarch breeding was later with increased latitude but with some longitudinal variation; for summer breeding regions, breeding occurred earlier in the western portion of the study area relative to the east, but the end of breeding was later in the east relative to the west, resulting in breeding seasons of similar duration. Additionally, in the east, breeding occurred later along the Appalachian Mountains. We suggest adapting our findings into mowing practices that benefit monarchs while considering the life histories of milkweed and the broader insect community.

Implications for insect conservation. Mowing and other maintenance activities in habitat where milkweed is present can be detrimental to monarch breeding. Our analysis provides guidance to minimize monarch mortality and loss of milkweed during peak breeding periods.

Keywords *Asclepias* spp. · Milkweed · *Danaus plexippus plexippus* · Monarch · Breeding date · Phenology · Rights-of-way vegetation management · Community science

Introduction

Eastern migratory monarch (*Danaus plexippus plexippus*) butterflies, which breed east of the Rocky Mountains and overwinter in central Mexico, have had a declining population since the early 1990's (Thogmartin et al. 2017). The risk of losing this monarch population and its migratory phenomenon has prompted the International Union for Conservation of Nature to list it as globally Vulnerable (IUCN 2023), Environment and Climate Change Canada to list monarchs as endangered in Canada under the federal Species At Risk Act (Canada Gazette 2023), and the U.S. Fish and Wildlife Service to propose listing monarchs as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 2024). The migratory phenomenon of monarchs includes a multi-generational springtime journey

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from the Oyamel fir forests of central Mexico to the breeding grounds in the Midwest and north-eastern United States and southern Canada, followed by fall migration to Mexico largely undertaken by a single generation (Oberhauser et al. 2017).

Loss of breeding habitat, primarily through declines in their host milkweed plants (*Asclepias* spp.) due to the use of herbicides in agro-ecosystems, insecticide use, loss of overwintering forest, and adverse weather events, are among the main threats to migratory monarchs (Hartzler 2010; Thogmartin et al. 2017; Wilcox et al. 2019). To reverse the monarch's decline, these threats must be addressed (Environment and Climate Change Canada 2016). While addressing the increased frequency of severe weather events requires a global effort to curb CO₂ emissions and sequester carbon, improving the quantity and quality of monarch habitat can be achieved by the actions of landowners and land stewards. Roadside verges, hydro-electric transmission corridors, and other lands that require regular mowing or brushing maintenance represent millions of hectares of potential habitat for monarchs and other insects (Baum and Mueller 2015; Kasten et al. 2016; Phillips et al. 2020). Eliminating mowing or brushing along roadsides is not feasible due to safety concerns, regulations, and invasive species and woody encroachment control, but reducing the frequency and timing the maintenance to avoid monarch breeding can reduce direct harm to monarchs and improve habitat quality (Baum and Mueller 2015; Knight et al. 2019). We recognize that, in many jurisdictions, vegetation in road sightlines must be maintained at a height that may not permit milkweed growth.

Knowing when to mow without harming monarchs is important knowledge that, if included in maintenance schedules, could improve many thousands of hectares of habitat and reduce mortality of likely large numbers of monarch eggs, larvae, and chrysalises. We used monarch breeding records collected by community scientists to map the spring and fall progressions of breeding across eastern North America to inform best practices regarding the timing of mowing for the maintenance of lands that have the potential to support monarch populations. Our work will complement the existing recommended management timing map for monarchs created by the Xerces Society and Monarch Joint Venture (Monarch Joint Venture 2019; Schultz et al. 2019). In addition to expanding the geographic scope northwards to include Canada, the use of differing methods and source data will help validate existing maps and provide insights into the breeding phenology of monarchs in eastern North America. Monarch breeding phenology also complements the suite of existing research and tools that provide guidance on mowing and roadside management for the benefit of monarchs (e.g., Hopwood 2013; Webb 2017; Cariveau et

al. 2019; Harris 2023; Meinzen 2023; Cariveau et al. 2024). Our approach to determining breeding phenology for the purpose of informing land management practices could also be applied to other insect species with a suitably large number of breeding evidence observations.

Methods

Data sources and study area

All spatial analyses were carried out in ArcGIS 10.8.2 (ESRI 2021) and statistical analyses were completed in Python. We collected monarch occurrence records with life stage information from iNaturalist (1978 to February 2024; iNaturalist community 2024a), Journey North (1997 to May 2024; Sheehan and Weber-Grullon 2021; Sheehan 2024), and Mission Monarch (2014 to February 2024; Mission Monarch 2024). We retained records of eggs, caterpillars, and chrysalises, but discarded observations of adult monarchs and those with coarse location accuracy (> 50 km), resulting in 126,513 records for North America east of the Rocky Mountains. We retained records from all years, however 327 records (0.3%) were from prior to the year 2000 and 14,103 records (11.1%) were from prior to the year 2010. Next, we used those records to refine the study area by performing a kernel density analysis to identify the core breeding range of the species in North America, defined by the 98% kernel density contour. The resulting range (Fig. 1) included 121,284 breeding records and covered an area from north-eastern Mexico in the southwest, north to Manitoba, and east to the Atlantic Ocean. Although the monarch breeding range expands beyond our identified core range, there were too few breeding records outside of the core range to complete the analysis in those areas. We then divided this range into 10,000 km² hexbins for the analysis ($n=519$; Fig. 1). We divided the monarch breeding range into hexbins because we needed dates of breeding to be associated with a single centre point in space (refer to estimation of kernel density rasters below) and hexagonal tessellations ensure the observations are as spatially close to the central point as possible when compared to square or triangular tessellations. The hexbin size was chosen by maximizing the number of hexbins while ensuring there were at least 20 observations per hexbin. Each retained record had an associated date and geographic coordinates, allowing us to map breeding phenology.

Breeding patterns

Prior to deriving the dates bounding the breeding period in each hexbin, we determined the seasonal breeding pattern

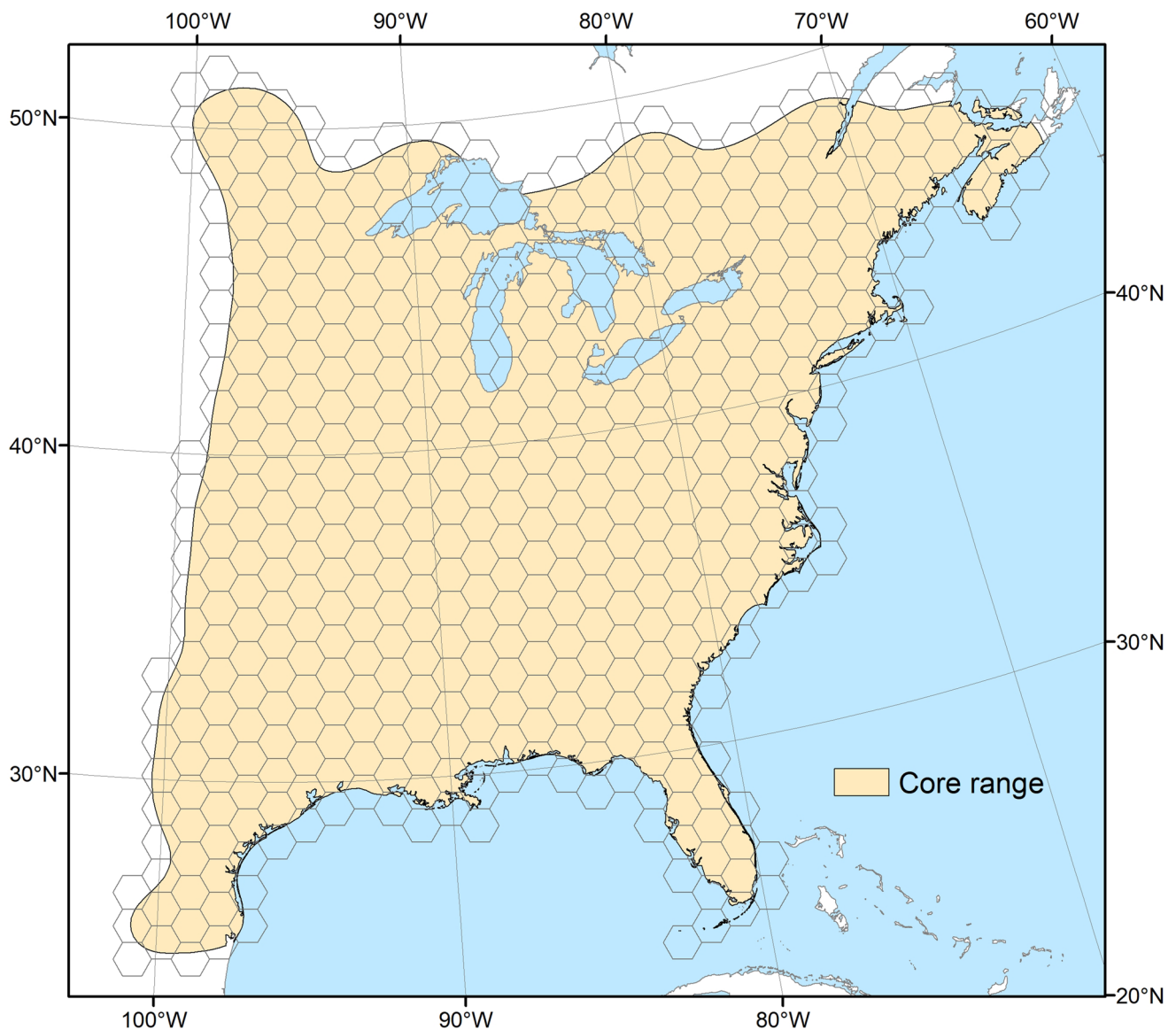


Fig. 1 The study area, which is the core range of the eastern migratory population of monarchs (*Danaus plexippus plexippus*), and associated hexbins. Range limits were defined by the 98% kernel density contour

for each hexbin across the study area. Monarchs in North America are known to have three main seasonal breeding patterns: (1) single season, which can further be divided into spring-only breeding and breeding from spring through the end of the summer (which from hereon will be referred to as spring-only and summer breeding, respectively), (2) disjunct, where the breeding season is interrupted by a non-breeding period, and (3) year-round, such as is found in southern Florida (Cockrell et al. 1993; Knight and Brower 2009; Oberhauser et al. 2017; Brym et al. 2018; Tracy et al. 2022). Assigning breeding patterns allowed us to identify and discard outliers, such as atypical early breeding records or fall and winter observations of old chrysalises, which are

included in community science projects such as iNaturalist that allow the collection of non-living occurrence evidence.

To assign a breeding pattern for each hexbin cell, we plotted cumulative breeding observation totals against observation ordinal dates for each hexbin with at least 20 observations ($n=394$). We chose a value of 20 observations because we found that hexbins with fewer than 20 observations made it challenging to define a breeding pattern and the plots were more susceptible to temporal sampling bias, a common issue with community science data (Courter et al. 2013). Plots of cumulative breeding observations by ordinal date for each hexbin were visually classified as spring-only, summer, disjunct, or year-round breeding (Fig. 2).

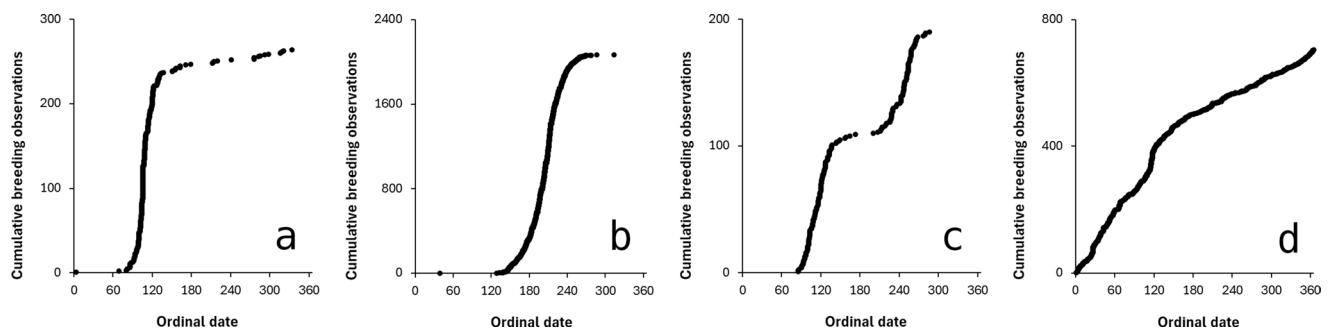


Fig. 2 Examples of the graphs produced for each hexbin that represent (a) spring-only breeding (b) summer breeding, (c) disjunct breeding, and (d) year-round breeding. Cumulative number of breeding event observations is on the y-axis and ordinal date is on the x-axis

Classification was done independently by two people and conflicting results were resolved by consensus.

Breeding dates

We calculated breeding dates for monarchs in all hexbins with spring-only, summer, or disjunct breeding. Hexbins with year-round breeding were not included because they lacked a defined breeding season. For spring-only and summer breeding we identified extreme breeding records by applying a linear regression of ordinal date of the breeding observation versus cumulative breeding observations and calculating residuals (Li et al. 2020). We defined extreme breeding records, i.e., very early or very late breeding records, as the highest 10% of residuals and removed the corresponding records from the data. In total, 10,606 records were identified as extreme breeding records. After extreme breeding records were removed, the lowest remaining ordinal date marked the beginning of the breeding season and the highest ordinal date the end of the breeding season. A similar method was used for disjunct breeding, but first the dates were split at ordinal 182 (July 1st), a day that fell within the break in the breeding season for almost all hexbins. The same outlier removal process was applied to each half of the data and the lowest ordinal date from the first half marked the beginning of the breeding season and the highest ordinal date from the second half marked the end of the breeding season.

Next, we interpolated breeding dates for hexbins that did not have data. For both the start and end dates of the breeding season we assigned the average date of the surrounding hexbins if this included at least three hexbins with data. The process was repeated and included the newly interpolated hexbins in subsequent interpolations until all hexbins had a value or until none of the remaining hexbins had three adjacent hexbins, in which case the interpolation was continued with two adjacent hexbins. A kernel density raster was calculated using a point from the centre of each hexbin with date as the population value, a cell size of 50 km,

and a search radius of 200 km. Breeding date contours were derived from the kernel density raster for the first and 15th day of each month, chosen because of the resulting spatial intervals and for ease of interpretation, and smoothed using the polynomial approximation with exponential kernel method and a 300 km tolerance, a method and tolerance that provided adequate smoothing without losing much detail. Anomalies smaller than the area of one hexbin (10,000 km²) were removed.

Results

Breeding patterns

In total, 394 hexbins were visually assessed. Twenty-two hexbins (6%) had conflicting results and conflicted hexbins were re-evaluated by the assessors and assigned a single category by mutual agreement. Conflicting results were predominantly from hexbins with a small number of breeding records or in the transition areas between breeding pattern types. In total, 237 (60%) of the hexbins were assigned as summer, 14 (4%) as spring-only, 113 (29%) as disjunct, and 30 (8%) as year-round breeding. The four seasonal breeding types followed distinct spatial patterns: summer breeding was found north of approximately 37° latitude, disjunct breeding was found between approximately 32° and 37° latitude, and year-round breeding was found in Florida and around the Gulf of Mexico coast (Fig. 3). Spring-only breeding was found in the south-western portion of the study area between approximately 30° and 34° latitude and west of approximately -92° longitude, however the boundary was less distinct. An additional area of disjunct breeding was found in far southern Texas and northern Mexico. Boundaries between breeding patterns were more distinct in the eastern half of the study area.

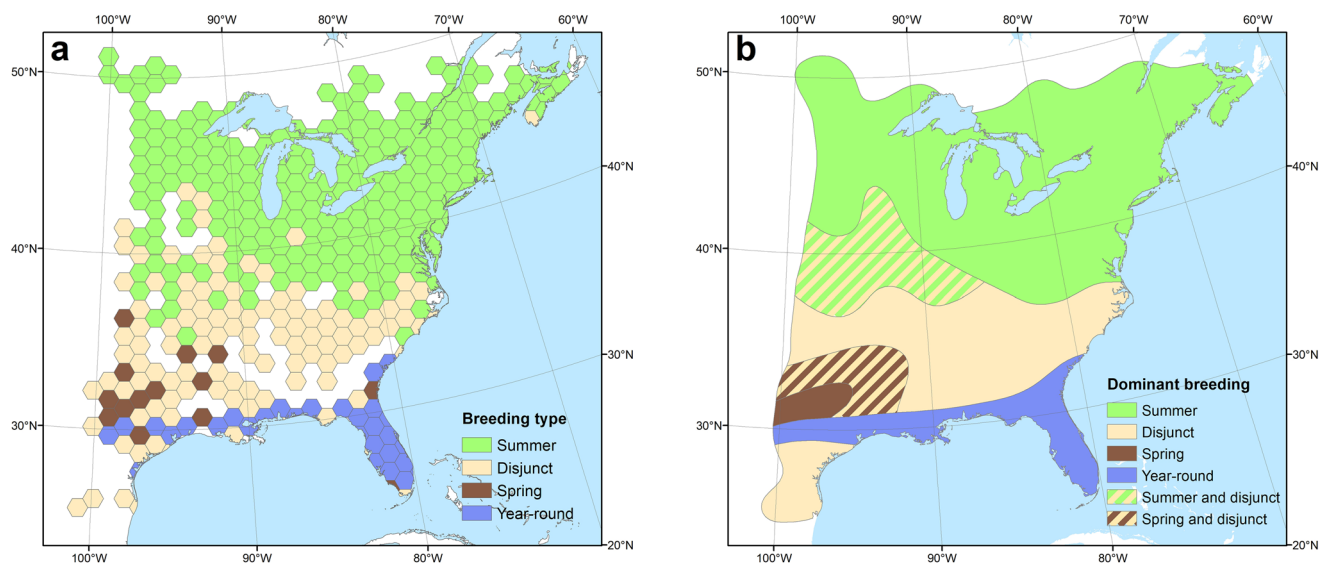


Fig. 3 Monarch (*Danaus plexippus plexippus*) breeding patterns by hexbin (a) and smoothed breeding pattern range (b). Green is summer breeding, light brown is disjunct breeding, dark brown is spring-only breeding, and blue is year-round breeding. The smoothed breed-

ing range was a visual approximation of the hexbin patterns and the hatched fill indicates locations where there is a mix of hexbins with different breeding patterns

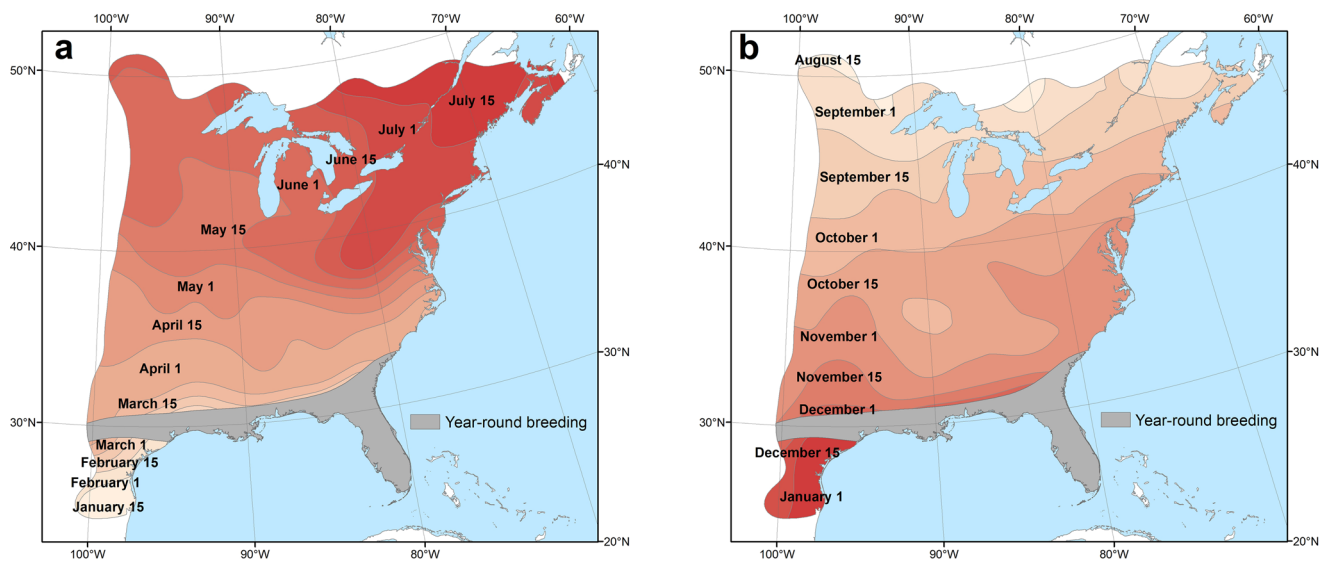


Fig. 4 Early spring breeding dates (a) and late fall breeding dates (b) for migratory monarchs (*Danaus plexippus plexippus*). Assigned dates refer to the northern extent of each band in the spring and the southern extent of each band in the fall

Breeding dates

The springtime progression of monarch breeding generally followed a strong latitudinal gradient with important longitudinal variation (Fig. 4, Supplementary Table 1). Breeding at more northerly latitudes began earlier (~one month) in the west than in the east, but breeding was later along the length of the Appalachian Mountains (~one month) relative to other observations at that approximate longitude. The end of breeding in the fall also followed a latitudinal gradient, however, breeding ended earlier in the western portion of

the study area (~one month). This resulted in approximately similar breeding season lengths in the east and the west of the northern portion of the breeding range.

Discussion

Breeding patterns

The summer breeding found in the north of the range coincided closely with the range of common milkweed

(*Asclepias syriaca*); common milkweed comprised 42% of all milkweed observations in the corresponding hexbins (calculated from GBIF.org 2024). Milkweed species such as green milkweed (*Asclepias viridis*; 22% of observations), butterfly milkweed (*Asclepias tuberosa*; 16% of observations), and antelope horns milkweed (*Asclepias asperula*; 12% of observations) are dominant in the disjunct breeding range (Tracy et al. 2022; percentages calculated from GBIF.org 2024). It is likely the phenology of the dominant milkweed species and high summer temperatures constrain reproduction and results in the disjunct breeding pattern we observed (refer to Cockrell et al. 1993; Goehring and Oberhauser 2002; Yang and Censer 2020; Tracy et al. 2022). Isotopic evidence suggests that monarchs breeding in the disjunct breeding areas could be migratory monarchs from further north (Flockhart et al. 2013), although this requires further investigation (refer to Tracy et al. 2022). Monarchs in Minnesota and Wisconsin were found to have all entered reproductive diapause by late August to early September (Goehring and Oberhauser 2002), so breeders in the disjunct portion of the range that originated from further north either never entered diapause, perhaps because they were early migrants, or came out of diapause. Evidence suggests they are early migrants, because the late summer/fall breeding period in the disjunct breeding range typically began between mid-August and early September, prior to the peak migration at latitudes further north. We could not find evidence as to why some locations within the south-western portion of the disjunct breeding range were limited to spring-only breeding, but explanations might include local climatic conditions or milkweed phenology/availability.

Breeding dates

Year-round breeding in Florida is hypothesized to be associated with the presence of tropical milkweed (*Asclepias curassavica*), a non-native species used commonly in horticulture, which is available year-round (Knight and Brower 2009; Majewska and Altizer 2019; Steele et al. 2023). Our results provide evidence that year-round breeding occurs along the Gulf of Mexico coast in Florida, Alabama, Mississippi, Louisiana, and Texas, which is also likely explained by the presence of non-native tropical milkweed in that area (Steele et al. 2023; Momeni-Dehaghi et al. 2024; iNaturalist community 2024c). An analysis of winter host plants based on community science photographs of monarch larva was attempted, but the difficulty of *Asclepias* spp. identification made for too much uncertainty. We acknowledge that egg observations from the Gulf of Mexico coast area are likely to be unreliable due to the presence of queen butterflies (*Danaus gilippus*) that have visually similar eggs (Scott and Kopachena 2024), however only 15% of the monarch

observations within the overlapping range (98% kernel density contour based on iNaturalist records; iNaturalist community 2024b) were of eggs.

There are three likely overlapping factors influencing the springtime and fall progression of monarchs outside the year-round breeding locations: (1) monarchs have thermal requirements for breeding (Malcolm et al. 1987; Cockrell et al. 1993) and thus cannot exceed the northward progression of appropriate climatic conditions but also may not be able to stay and continue to breed when temperatures drop at the end of summer and fall, (2) monarchs require milkweed for egg-laying and so cannot breed in advance of springtime milkweed emergence or after fall dieback (Cockrell et al. 1993; refer to Tracy et al. 2022), and (3) the time it takes to migrate from overwintering to breeding ranges may delay breeding at locations that are distant but otherwise have suitable breeding conditions. The first two factors are intrinsically linked and are the likely reasons for the delayed breeding along the Appalachian Mountains. The third factor may explain why breeding at the northern edge of the range occurs earlier in the spring in the west despite winter conditions lasting longer; the north-western edge is approximately 1000 km closer to the Mexican overwintering range than the north-eastern edge. The opposite is true for end of season breeding; breeding occurs later in the north-eastern part compared to the north-western part of the range, perhaps because of more moderate climatic conditions later into the fall in the northeast.

We did not assess yearly variation in breeding phenology nor the possibility that the phenology is shifting due to climate change. The yearly fluctuations in springtime and fall weather conditions means monarchs may begin breeding earlier or end breeding later at a given location over multiple years. Indeed, year showed a significant effect for first monarch sightings based on Journey North data (Howard and Davis 2015) indicating springtime migration is not consistent year over year. Yearly variability in peak fall migration has also been documented (Meitner et al. 2004), which suggests monarchs may leave the breeding grounds on different dates each year. Our method of identifying and excluding extreme breeding records controlled for early or late breeding in anomalous years. Long-term trends in monarch breeding timing may also be present. Howard and Davis (2015) noted that spring monarch sightings were getting later at a rate of 1 day per 4 years and hypothesized it may be a result of their declining population. Climate change may also play a role in influencing long-term trends in monarch breeding phenology. Our results are a snapshot based primarily on the last 14 years of breeding evidence (88.9% of records) and do not account for change over time.

For the United States portion of the study area, our results are comparable to the recommended management

timing map for monarchs published by the Xerces Society and Monarch Joint Venture (hereafter referred to as Xerces/MJV map; Monarch Joint Venture 2019; Schultz et al. 2019). During spring migration, the south edge of the management zones on the Xerces/MJV map coincides closely with the breeding dates we observed. However, north of approximately 40° latitude, the longitudinal variation we observed in springtime breeding is not reflected in the Xerces/MJV map. The 5° latitude bands used to separate regions on the Xerces/MJV map may have obscured some of the longitudinal variations in breeding that we observed. The fall results were more similar; our findings suggest that the end of fall breeding follows a latitudinal gradient more closely than spring breeding, which better matches the management regions used on the Xerces/MJV map.

Considerations for mowing

Although some breeding may occur at a given location outside the dates our analysis has identified, we recognize that much of the lands upon which monarchs breed are working landscapes that require vegetation management and the breeding dates provide a reasonable guideline for when to avoid activities that will directly harm monarchs. However, there are several considerations to adapt the breeding dates as mowing guidelines. Vegetation maintenance activities outside these dates may also harm adult monarchs pre- or post-breeding because of floral resource requirements for migration, for example, migrating monarchs in the fall are more likely to select roost locations with more abundant floral resources (Fyson et al. 2023). Additionally, milkweed may benefit from disturbance; optimally timed mowing can promote milkweed growth and produce higher quality plants for monarchs (Fischer et al. 2015; Knight et al. 2019). For example, in southern Ontario, monarch egg counts were highest 1 to 3 weeks after mowing common milkweed and maximized by mowing in mid-July prior to the peak breeding season (Knight et al. 2019), approximately four weeks after the beginning of the breeding season for that location. Mowing strategies to maximize egg counts may result in inadvertent mortality and should be weighed against management goals and species at risk regulations. Additionally, mowing too late in the season may result in the inability of common milkweed to set seed (Fischer et al. 2015) and some species of milkweed may be susceptible to mowing, for example Mead's milkweed (*Asclepias meadii*) declines in the Midwestern United States have been attributed to mowing (Betz 1989). Fischer et al. (2015) and the Monarch Joint Venture (Hopwood et al. 2022) advise that more research is needed regarding mowing timing, milkweed species, geographic location effects, and cost-benefit of mowing when it may directly harm monarchs. In southern

Great Plains, an area that experiences the disjunct breeding pattern, Dee and Baum (2019) suggest that mowing should be avoided during the spring flowering period of green milkweed (*Asclepias viridis*) but a mid-summer mow may benefit monarchs breeding in the late summer or early fall, however, additional research is necessary to determine the full impacts of mowing in the summer non-breeding period.

Mowing strategies should also consider the broader insect community. Mowing techniques, timing, and intensity have been shown to affect many insect taxa including Coleoptera, Hemiptera, Orthoptera, Heteroptera, Diptera, and Hymenoptera (Unterweger et al. 2018; Berger et al. 2024; Noordijk et al. 2009; van Klink et al. 2019). We have shown that, for monarchs, broad-scale analysis of large community science datasets comprised of local observations can provide information for management that local observations alone cannot. We believe our approach could be applied to other widespread insect species, or perhaps broader taxa, to provide valuable management information that can be applied locally for great conservation benefit.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-025-00676-6>.

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Data availability Data is provided within the manuscript and supplementary information files.

Declarations

Competing interests The authors declare no competing interests.

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