

TITLE: Continental breeding hotspots of migratory monarch butterflies revealed by coordinated community science partnership

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ABSTRACT:

The eastern migratory monarch butterfly (*Danaus plexippus plexippus*) has declined by more than 80% over the past two decades, highlighting the need for improved understanding of its breeding ecology. To address longstanding gaps in continental-scale data on monarch reproduction, the International Monarch Monitoring Blitz has mobilized community scientists across North America to monitor monarch reproduction. Using a hierarchical generalized linear model based on thousands of observations of larval density on milkweed across North America, we identified monarch butterfly mid-summer breeding hotspots. Our model suggests that such hotspots are broadly concentrated in the northeastern United States and southeastern Canada. Larval density was structured across multiple spatial scales, suggesting both local habitat conditions and broader regional factors contribute to variation. Our results demonstrate the power of coordinated community science to reveal large-scale ecological patterns and provide actionable information for monarch conservation across its breeding range.

MAIN TEXT:

Few insects have received as much scientific and public attention as the Eastern migratory monarch butterfly (*Danaus plexippus plexippus* L.). Celebrated for one of the most remarkable migrations in the animal kingdom, the eastern population cyclically departs from the oyamel fir forests of central Mexico each spring, recolonizes North America over the course of three to four generations, and then returns to the same forests in autumn to overwinter (1). These overwintering colonies have been monitored for decades and provide an unparalleled record of the eastern migratory monarch's population size (2,3).

Concerningly, data from the overwintering sites suggest that monarch populations have declined by more than 80% in the last two decades (2), increasingly putting the migratory phenotype at risk of extinction (4). In response, the monarch has been listed as Endangered in Canada (5), proposed as Threatened in the USA (6) and is recognized as a species at risk in Mexico (7).

Although essential for assessing population stability and extinction risk (Semmens et al. 2016), overwintering population size provides only an annual endpoint of the monarch's complex life cycle. In eastern North America, overwintering populations are largely driven by the preceding season's breeding population size (8). Thus, a robust and timely assessment of the eastern monarch's breeding population status could help predict the overwintering population size and clarify the indirect drivers of its change. Additionally, monarchs respond to environmental factors such as climate differently across life stages (9,10), emphasizing the importance of monitoring the full life cycle to best conserve this iconic species.

The protection and restoration of summer breeding habitats is considered a top priority to reverse monarch population declines (11). Yet, uncertainty surrounding the spatial distribution of summer monarch reproduction has made it difficult to identify which regions contribute most to annual recruitment, and thus where conservation actions are likely to have the greatest impact. Despite decades of research, continental-scale information on pre-imaginal stages (i.e., eggs, larvae, and pupae) of this population has remained remarkably sparse. This gap is perhaps unsurprising given the vast geographic extent over which reproduction occurs for this species. In contrast to the overwintering stage, where all suitable habitat occurs within 600 km² (12), summer breeding monarchs are distributed across millions of km². As a result, fundamental questions about the contribution of different regions and the environmental factors that drive variation in breeding success, remain difficult to address (13,14)

A unique continental community science partnership offers a solution to this challenge. The International Monarch Monitoring Blitz (hereafter, the "Blitz"; Fig. 1), initiated by the Montréal Insectarium in 2016, became a North American initiative with the support of the Commission for Environmental Cooperation (CEC) and national stakeholders. In collaboration with nine organizations (see Supplement), volunteers from across Canada, the USA and Mexico record monarch eggs, larvae, pupae, adults, and milkweeds (*Asclepias* spp.) during a period of 10 days from late July to early August. This period coincides with peak breeding season and the production of the generation that migrates south from the breeding grounds in the fall, overwinters in Mexico, and begins the northward migration the following spring. Strategic sampling in this narrow temporal window provides a standardized continental 'snapshot' of monarch reproduction at this time of year on its primary hostplant, milkweed.

Over the past decade, the Blitz has transformed local monarch monitoring into a coordinated continental network by harmonizing existing monitoring programs through a common survey window, standardized protocols, and data sharing. As participation has increased (Fig. 1B), so too has the geographic coverage of records of both the butterfly and its host plant, producing over 45,000 records (Fig. 1A,B) collected by over 20,000 participants across the continent, enabling the exploration of geographic patterns in monarch breeding that would have been otherwise beyond the reach of conventional research programs

To mark the 10th anniversary of this unique community science effort, we harnessed this remarkable dataset to ask a question that has been historically elusive: **where are monarch mid-summer breeding hotspots distributed across North America?**

Using the subset of standardized surveys that recorded both larval abundance and milkweed stems, we fit a hierarchical generalized linear model to partition variation in larval density (number of caterpillars per milkweed stem) across date, years, ecoregions, and five spatial scales (from ~25 km² to ~12,500 km²; Fig. 2). Unlike adult observations, which may reflect dispersing individuals, larval densities provide direct evidence of breeding activity. The nested spatial random effects account for the non-independence of nearby sites (see Supplemental Material), allowing us to distinguish broad-scale drivers of reproduction (e.g., climate) from finer-scale influences (e.g., land management), identify breeding hotspots, and quantify the spatial scales at which breeding varies most during the 10-day survey window. Finally, we examined whether interannual variation in breeding success was associated with climate by relating the year-specific random intercepts to that year's mean maximum temperature.

We found clear geographic signals of variation in reproductive activity across the monarch's range, with northeastern USA and southeastern Canada consistently emerging as regions with the highest larval densities across multiple spatial scales (Fig. 2A-E). Figure 2A highlights these continental-level hotspots of monarch mid-summer breeding success. The random intercepts shown in Fig. 2A-E predict, jointly with the other fixed and random effects, the total number of caterpillars at an individual site (Fig. 2G). The model explains approximately 60% of the variation in the data (Fig. 2F) and predicts an average of ~10.9 larvae for every 100 milkweed stems (Fig. 2G).

While fine-scale (~25 km²) differences accounted for the largest proportion of variance (~16%), these local effects primarily capture site-level heterogeneity, enabling more robust estimation of large-scale breeding success (which is also the scale with the lowest uncertainty, as each unit contains high sampling intensity; see Supplement). Importantly, substantial variation accounted for at broader spatial scales (e.g., ~10% between the ~12,500 km² and ~750 km² scales; Fig. 2F) indicates that regional drivers such as climate, land use, and other broad-scale environmental conditions strongly influence monarch breeding success. Consistent with this interpretation, warmer years were associated with greater larval abundance (Fig. 2F-H).

In all, these results support the notion that while local conservation can be meaningful, it is likely to be most effective when coupled with policies that address the broad-scale threats (15), such as habitat loss, pesticide exposure, and climate change. At the same time, the breeding hotspots identified here provide a framework for prioritizing habitat restoration and other local conservation actions across the breeding range. We note that this analysis required standardized estimates of larvae per stem, limiting it to sites within the mid-summer breeding range where this protocol has been implemented and leading to fewer grid cells considered in the analysis in the southern regions of the USA and in Mexico compared to the northeastern USA and Canada.

Looking forward, we suggest that our dataset has substantial potential for informing monarch conservation. Priority next steps include assessments of land use changes on larval density, or evaluations of spatial sampling biases to improve representativeness. We encourage researchers and conservation practitioners to continue drawing on these data to explore patterns in monarch reproduction.

More broadly, the Blitz illustrates the value of community science partnerships. Thousands of interested naturalists generate ecological data at a spatial extent (and for a difficult-to-study life stage) rarely achievable through traditional means. The Blitz demonstrates that community science is not only a tool for public engagement but an emerging framework for continental conservation evidence: one capable of generating ecological insights at scales necessary to address global biodiversity change into the future. We thank the volunteers and partner organizations whose contributions made this dataset possible, and we envision a future where strategic community science partnerships become integral components of conservation.

Acknowledgements:

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We also thank the organizations that have supported, coordinated, and promoted the Blitz across North America: the Commission for Environmental Cooperation (CEC), the Insectarium de Montréal |

Espace pour la vie, Environment and Climate Change Canada (ECCC), the Canadian Wildlife Federation (CWF), the Monarch Joint Venture, Journey North, the U.S. Fish and Wildlife Service (USFWS), the Xerces Society for Invertebrate Conservation, Profauna A.C., and Mexico's National Commission of Protected Natural Areas (CONANP). Their collaboration and long-term commitment have been instrumental in building and sustaining this trilateral community science initiative.

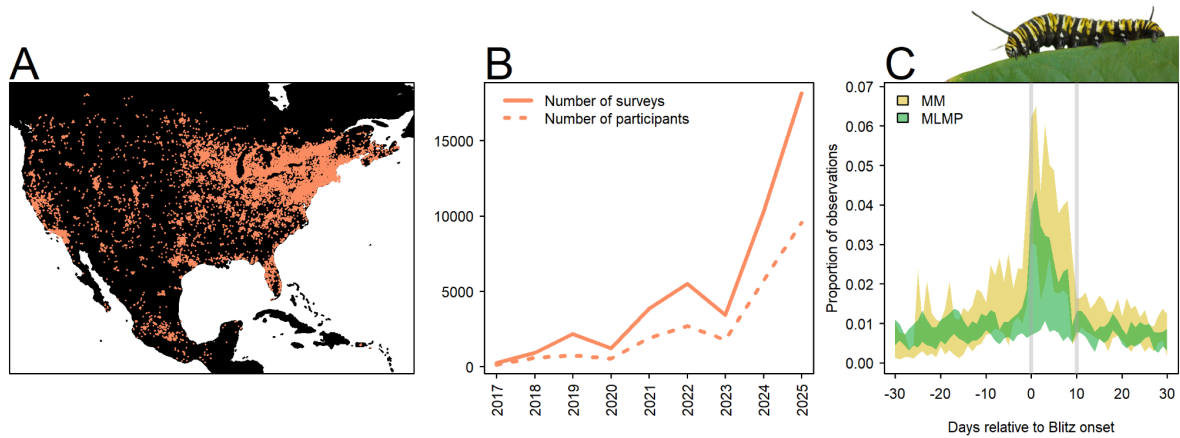


Figure 1. A) Map of the over 45,000 observations submitted during the International Monarch Monitoring Blitz from 2017-2025. B) Blitz participation throughout the monitoring initiative's history, showing trends in the number of participants (dotted line) and surveys (continuous line). C) The "Blitz Bump", illustrating the high volume of data gathered throughout the 10-day event (day 0 = start of the event; grey lines indicate event duration). Data from the Monarch Larva Monitoring Program (MLMP, in green) and Mission Monarch (MM, in yellow) are used as examples. Shaded areas represent temporal envelopes (min-max) across the years for both programs.

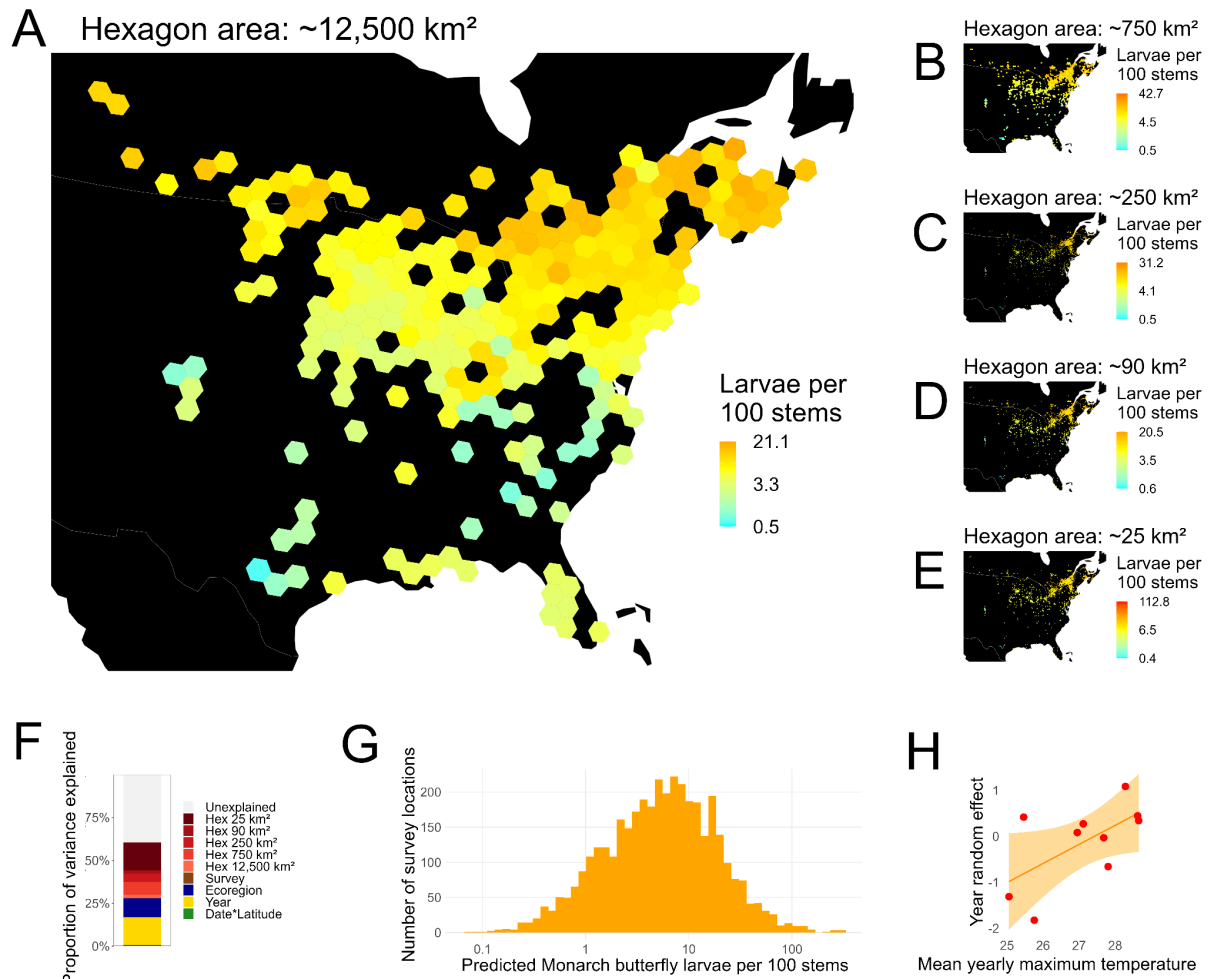


Fig. 2: A-E) The random intercepts estimated from the model for hexagonal grid units of ~12,500 km² (Panel A), ~750 km² (Panel B), ~250 km² (Panel C), ~90 km² (Panel D), and ~25 km² (Panel E) (n = 230 units, 540 units, 1050 units, 1652 units, and 2169 units, respectively). F) Proportion of variation explained by the different components of the model: Date*Latitude: 0.006; Year: 0.162; Ecoregion: 0.111; Survey < 0.001; 12,500 km² hex: 0.020; 750 km² hex: 0.075; 250 km² hex 0.047; 90 km² hex 0.112. G) Histogram of predicted Monarch butterfly larvae per 100 stems. H) Scatter plot of Year random effect vs Mean yearly maximum temperature.

0.020; 25 km² hex 0.162; Unexplained 0.397. G) Predicted monarch butterfly larvae across the 3824 samples modelled presented on a log-scale; H) The relationship between the random intercepts estimated for each year and that year's mean maximum temperature. Note that the colour scale for the maps in panels A-E are comparable, representing variation in the importance of the random intercept across spatial scales.

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Supplementary Material

Overview

The analysis was coded in software R version 4.5.1. The script is available at https://github.com/JaymeLewthwaite/Monarch_Breeding_Hotspot. We discuss below in detail (i) data preparation, (ii) the creation of nested, hexagonal spatial units underlying the model random effects, and (iii) the model assumption, formulation, and validation.

Data preparation

Our analysis is based on a subset of the International Monarch Monitoring Bioblitz data (Fig. 1). Specifically, we used only observations related to larval counts that reported an associated number of milkweeds sampled. 3 of the 9 total programs that contribute to the Blitz reported this information: Mission Monarch (Drapeau Picard et al. 2024), the Monarch Larvae Monitoring Program (Prysby and Oberhauser 1999), and the Integrated Monarch Monitoring Program (Cariveau et al. 2019). This allowed us to model larval density (# monarch larvae per milkweed stem, effectively accounting for sampling effort), the response variable in our model and our indicator of monarch breeding ground potential.

Initially, the data included 4724 observations. Because a subset of sites were visited multiple times in the same year during the 10 days window of the Blitz, but most sites only had one observation per year, we randomly selected one observation per year/site combination from the sites containing multiple visits in the same year. We decided to apply this filter because we knew that a small subset of community scientists tracked some larvae for part of the 10-day Blitz window, reporting daily observations of the same milkweed plant and associated monarch caterpillars. Such observations effectively duplicate the information contained in these samples, causing pseudoreplication.

Removing these pseudoreplicated observations resulted in a final dataset counting 3824 spatially-explicit observations, with one observation (density of monarch larvae per milkweed stem) per site per year, which constitute the base of our analysis. As a sensitivity analysis, instead of randomly selecting a sample from the sites with multiple sampling events in the same year as described above, we retained the observation with the highest number of caterpillars. Fitting the model presented in the manuscript with this slightly different dataset generates qualitatively identical results, with a high degree of correlation between random effect coefficients with the dataset where either a random sample or with the dataset where only the highest sample was retained. At the smallest grid size (25 km²), there was a correlation of 0.96 (and a total of 2169 levels for this variable); at 90 km², a correlation of 0.97 (1652 levels); at 250 km², a correlation of 0.97 (1050 levels); at 750 km², a correlation of 0.97 (540 levels); and at 12,500 km², a correlation of 0.97 (230 levels). For the effect of Survey ID, there were 3824 levels and correlation of 0.95. For ecoregion, there were 52 levels and a correlation of 0.98. For year of sampling, there were 10 levels and a correlation of 0.99. A previous model containing all data, including pseudo-replicated observations, also generated analogous results. Overall, we are confident that this step did not influence our conclusions.

In addition to counts of monarch larvae observed and number of milkweed stems sampled, each observation included the date of sampling. We extracted the Level III North American ecoregion for each site (Wiken et al. 2011); both variables were included as predictors in our model. Additionally, we extracted the corresponding nested hexagonal spatial units for each sampling location and used these to define nested spatial random effects.

Hexagonal spatial units

We created a set of five nested, hexagonal grids in R using the package h3jsr (O'Brien 2026). This corresponds to five levels of spatial overlap between hexagons of approximately 25, 90, 250, 750, and 12,500 km² areas. The hexagon shape was chosen because it is more efficient in representing

features of different spatial scales than squares or circles (i.e., it allows implementing a nested design, like squared pixels, while minimizing the distance between the center of a spatial unit and its sides, like circles; Birch et al 2007). Within a grid cell, pairwise average distance between surveys was 0.585 km, 1.740 km, 5.173 km, 13.056 km and 33.810 km for the 25, 90, 250, 750, and 12,500 km² grids, respectively. Because this is a pairwise metric, grids with only 1 survey were excluded from this calculation.

Every hexagon included in the model included at least one observation, and typically more. At the smallest grid size (25 km²), 29% of cells contained more than 1 observation; at 90 km², 37% of cells; at 250 km², 51% of cells; at 750 km², 64% of cells; and at 12,500 km², 74% of cells.

Modeling

We fit a generalized linear mixed effect model (GLMM) with a negative binomial distribution and log-link to predict the number of larvae observed in different samples, accounting for sampling efforts with an offset term based on the log-transformed number of milkweed stems assessed in that sampled. This effectively corresponds to modelling the density of monarch larvae per milkweed stem. The formula, in R, is specified as follows:

```
m_pheno_lat_max <- glmmTMB(
  LarvaeCount ~ 1 +
    poly(Day, 2) * scale(latitude) +
    (1 | SurveyID) +
    (1 | hex_12500km2/hex_750km2/hex_250km2/hex_90km2/hex_25km2) +
    (1 | Ecoregion) +
    (1 | YearCollected),
  family = nbinom2(),
  offset = log(StemCount),
  data = data_model_max)
```

We opted for a negative binomial distribution after testing four alternative model assumptions - negative binomial, Poisson, zero-inflated negative binomial, and zero-inflated Poisson. The model assuming a zero-inflated Poisson distribution failed to converge, whereas across the other three models, the negative binomial without zero-inflation performed best. The AIC score for the negative binomial model was 16920.5 (AICw = 0.73), whereas it increased to 16922.5 (AICw = 0.27) and 17024 (AICw < 0.01) for the negative binomial with zero inflation and the Poisson distributions, respectively.

The model includes two interacting fixed effects. First, it includes a quadratic term on date, to account for changes in the number of caterpillars during the time window through which the Blitz occurs. Second, this quadratic term interacts with latitude, recognizing that the timing of larval abundance varies across the study area depending on whether a sample occurred in different parts of North America. To further account for potential geographic variation in density of caterpillars, the model includes a random intercept on ecoregion, capturing spatial patterns in caterpillar abundance. The model also controls for variation in caterpillar abundance across years with a second, crossed random effect. The nested random effect with five hexagonal grid levels is designed to identify spatial hotspots and coldspots of monarch larval density after accounting for ecoregional and phenological (date) effects. In other words, such breeding hotspots are designed to estimate larval density after controlling for the spatial and temporal signature of monarch larval abundance. Finally, the survey ID random effect acts as an overdispersion correction to account for heterogeneity linked to, e.g., detectability, observer experience, or different microclimates.

Effectively, in addition to the interactive fixed effect terms, the model estimates a series of random intercepts that capture increases or decreases in the predicted larval abundance in space. This

means that the estimated hotspots and coldspots should be interpreted as additional sources of variation in local larval density after controlling for all the other sources of variation in the data. Therefore, the hexagonal spatial units are used to decompose variation in monarch larval density depending on the scale at which different spatial processes are hypothesized to influence local larval density (e.g., local landscape characteristics at finer grains, and macroclimate at the coarsest grains). Because many hexagonal grids contain only a few observations, as a sensitivity analysis, we plotted the relationship between the estimated random intercepts of the hexagonal grid units at the five different spatial scales, and the number of observations in those grids. The regression line was negative and suggests that grid cells with more observations were not more likely to be estimated as breeding hotspots. Instead, the fitted regression lines showed a weak tendency for more heavily sampled grid cells (which are often associated with high human population densities in community science datasets) to have lower random intercepts, suggesting they were, if anything, more likely to be estimated as breeding coldspots. This suggests that differences in sampling intensity alone are unlikely to explain the observed spatial pattern of breeding hotspots. This is the opposite pattern to what would be expected under a model that failed to distinguish sampling intensity and the underlying larval density that the model is designed to estimate, thus confirming that our inferences are not biased by different numbers of sampling sites in different hexagonal units.

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