



## Projected distribution shifts of resident monarch butterflies and consequences for migratory monarchs

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### ABSTRACT

The charismatic migratory populations of monarch butterflies have declined precipitously in North America. A contributing threat might be the expansion of winter breeding populations in the southern portions of their historical eastern and western summer breeding ranges. Recent research suggests individuals from winter breeding populations are prone to high parasite burdens, resulting in lower fitness compared to migratory counterparts. Temporal and spatial overlap between these individuals and migratory monarchs in both fall and spring mean that interbreeding and use of the same host plants could result in transfer of parasites, especially the debilitating neogregarine *Ophryocystis elektroscirrha*, increasing the parasite load in migrating populations. We aimed to predict how climate change could affect the distribution of winter breeding monarchs in North America. We used ecological niche modeling of monarch larval observations for winter and current climate data to predict the current and future distributions of winter breeding monarchs across North America. Our analyses predict up to a 38% and 160% increase and a 574 and 340 km northward shift in suitable area for winter breeding monarchs in response to climate change by 2100 for eastern and western migratory populations, respectively. Our results support concerns over potential risk of disease spread from resident monarchs to the migratory monarch populations. In both eastern and western migratory populations this is due to an increase in overlap between the resident population and the areas through which the migratory populations travel during fall and spring migrations. Our results support calls for controlling the spread of non-native tropical milkweed, as winter breeding monarchs depend on this plant for reproduction.

### 1. Introduction

The monarch butterfly (*Danaus plexippus plexippus*), Nymphalidae (Linnaeus, 1758), has a global distribution in 90 countries and islands across its native range in North, Central and South America, and its introduced range in Australia, Europe, northern Africa and southern Asia (GBIF-Secretariat, 2019; Nail et al., 2019). While not all populations are migratory, in North America monarchs are comprised mainly of two populations, western and eastern migratory monarchs, largely separated by the Rocky Mountains (although there is some natural interchange between these populations). In addition, there are at least two smaller, sedentary, winter breeding populations around the Gulf of Mexico and the West Coast of California, as well as in western

Mexico (Brower, 1995; Knight & Brower, 2009; Batalden & Oberhauser, 2015; Satterfield et al., 2016; James, 2018; Crone & Schultz, 2021; Steele et al., 2023).

Each year around mid-August, eastern migratory monarchs begin their fall migration from their breeding grounds in Canada and the US to their overwintering grounds in central Mexico – a migration that can be more than 4000 km long. Then, in early spring, the eastern monarchs move from Mexico into the southern US, where a new generation is produced. This generation spreads northward and repopulates the breeding range in the northeastern quarter of the US and in southern Canada. Two to three largely sedentary generations are then produced before a final, late summer generation migrates back to wintering sites in Mexico (Solensky, 2004). Western migratory monarchs overwinter in

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wooded groves along coastal California, USA, and breed as far north as southern British Columbia, Canada (Brower, 1995). The eastern and western populations are not genetically unique (Lyons et al., 2012; Talla et al., 2020), but their population sizes fluctuate independently (Espeset et al., 2016). Over the last several decades, both populations have undergone precipitous declines and the migratory phenomenon is at risk of disappearing (Brower et al., 2012; Vidal & Rendón-Salinas, 2014; Semmens et al., 2016; Schultz et al., 2017; Agrawal & Inamine, 2018; Crone et al., 2019).

Numerous factors are thought to contribute to the decline in migratory monarch butterflies in North America (Wilcox et al., 2019). These include habitat loss (Vidal & Rendón-Salinas, 2014; Crone et al., 2019), effects of pesticides on monarchs and their milkweed host plants (Pleasants & Oberhauser, 2013; Flockhart et al., 2015; Thogmartin et al., 2017; Solis-Sosa et al., 2021), vehicle collisions (Mckenna et al., 2001; Kantola et al., 2019; Mora Alvarez et al., 2019), disease (Satterfield et al., 2015, 2016), and climate extremes and climate change (Oberhauser & Peterson, 2003; Batalden et al., 2008; Agrawal & Inamine, 2018; Crewe et al., 2019; Saunders et al., 2019; Zylstra et al., 2021). With respect to climate, research suggests that warming temperatures are likely to result in (1) the loss and degradation of overwintering habitat in Mexico (Oberhauser & Peterson, 2003; Stevens & Frey, 2010; Barve et al., 2012; Sáenz-Romero et al., 2012; Ramírez et al., 2015; Fisher et al., 2018), (2) range shifts and degradation of breeding habitat in Canada and the US (Batalden et al., 2008; Lemoine, 2015; Faldyn et al., 2018; Saunders et al., 2019; Svancara et al., 2019; Zylstra et al., 2021), and (3) changes in the phenology of migration (Ethier & Mitchell, 2023).

Climate change may also indirectly affect North American migratory populations of monarchs by causing a range expansion of sedentary, winter breeding monarch populations (Zalucki & Rochester, 1999). In Florida and around the Gulf of Mexico, and on the West Coast of California, sedentary monarchs breed year-round, mostly on non-native tropical milkweed (*Asclepias curassavica*) (Malcolm et al., 1986; Brower, 1995; Farrey & Davis, 2004; Knight & Brower, 2009; Batalden & Oberhauser, 2015; Satterfield et al., 2016; James, 2018; Satterfield et al., 2018; Steele et al., 2023). Unlike their native milkweed host plant species, which senesce in fall (Batalden & Oberhauser, 2015), non-native tropical milkweed plants grow year-round in mild climates (Woodson, 1954; Batalden & Oberhauser, 2015), allowing year-round breeding (Satterfield et al., 2015).

Sedentary, year-round breeding monarchs in the US may represent a population sink for migratory monarchs due to their high infection with the parasite (McLaughlin & Myers, 1970) (OE), Apicomplexa. This parasite exists as inactive spores on the integument of adult butterflies, which can be shed into the environment, particularly onto milkweed leaves and egg chorions during oviposition. OE then reproduces within monarch larvae and pupae after being ingested by young larvae (Altizer & Oberhauser, 1999). Excluding winter breeding populations, on average, approximately 22 % of eastern monarchs and 51 % of western monarchs are either heavily infected with or contaminated by OE during different phases of their life cycle (Majewska et al., 2022). These rates fluctuate from year to year, but have been generally increasing over time (Majewska et al., 2022). The parasite infection rate is much higher in winter breeding monarchs, often at or approaching 100 %, than in migratory monarchs (Altizer et al., 2000; Satterfield et al., 2015, 2016, 2018; Kendzel et al., 2023). Monarchs infected with the parasite have reduced flight ability, fecundity, and survival (Altizer & Oberhauser, 1999; Altizer et al., 2000, 2015; Bradley & Altizer, 2005), making OE parasites a potential threat to monarch populations (Thogmartin et al., 2017). Infected monarchs easily spread spores to healthy monarchs during mating, and while transmission to the next generation is generally from parents to offspring, the offspring of healthy adults can consume spores transmitted by infected adults that have landed or oviposited on the host plants they are consuming (Satterfield et al., 2018). Thus, repeated use of the same host plants can lead to increased

levels of transmission to the offspring of healthy adults. Recent studies indicate that migratory monarchs experience a higher infection/contamination rate during the fall migration (September–November) compared to the breeding season (April–August; Bartel et al., 2011; Flockhart et al., 2018; Majewska et al., 2022) and this rate is typically higher at lower latitudes than at higher latitudes during both migration and breeding seasons (Flockhart et al., 2018; Satterfield et al., 2018) where the ranges of winter breeding monarchs and migratory monarchs overlap (Satterfield et al., 2018).

During fall migration, most monarchs are in reproductive diapause. However, non-native tropical milkweed at more southern latitudes, which typically does not senesce, can result in monarchs coming out of reproductive diapause to breed (Knight & Brower, 2009; Batalden & Oberhauser, 2015; Satterfield et al., 2018; Majewska & Altizer, 2019; Steele et al., 2023). These individuals can pick up OE spores by landing on milkweed plants recently visited by infected winter breeding monarchs or by mating with infected individuals. Although the offspring of winter breeding monarchs can be migratory (Freedman et al., 2018), similar to their parents they are more likely to be heavily infected with OE and thus less likely to complete the migration successfully. In addition, infected/contaminated individuals that do migrate to the overwintering habitats (Majewska et al., 2022) could transfer spores to healthy individuals in the high-density winter clusters, thus increasing the infection rate in the next generation.

During the multi-generational spring migration, the migratory population is most at risk of infection during its first generation in southern US, where overlap with the winter breeding population is highest. In contrast, by the time the population has reached the northern portions of its range the infection rate is lower because most of the heavily infected offspring of the first generation post-diapause are weeded out of the population, due to their low flight capacity and survival (Altizer & Oberhauser, 1999; Bradley & Altizer, 2005). Thus, northward range expansion of the winter breeding monarch populations in the future could increase the likelihood of exposing the more northerly second and third generations of the migratory populations to the OE parasite.

In this study, we use Ecological Niche Modelling (ENM) and participatory science data to understand how climate shapes the current distribution of winter breeding monarchs, separately for the eastern and western populations. We then use the resulting models to predict how these distributions will shift by 2040, 2060, 2080 and 2100, assuming low-, intermediate-, and high-emissions climate change scenarios. By understanding the potential range shift of winter breeding monarchs, we can better understand how the threat posed by these non-migratory populations to the migratory populations could change over time.

## 2. Methods

### 2.1. Study area

We defined the Rocky Mountains as a geographic barrier separating the eastern and western monarch populations. For the eastern population, the southern limit of their range was defined by their overwintering grounds in the Monarch Butterfly Biosphere Reserve, Mexico. Similarly, for the western population, the southern boundary was defined at the northernmost reaches of Baja California, Mexico, marking the limit of their overwintering area (<https://www.monarchjointventure.org>). To determine the northern limit for both populations, we used records of adult monarch sightings reported by participatory scientists through the Journey North platform (<https://www.journorth.org>) for all seasons between 1996 and 2020.

### 2.2. Occurrence data

Larval monarch occurrence data (1996 – 2020) were obtained from Journey North (<https://www.journorth.org>) and the Monarch Larva Monitoring Project (MLMP) (<https://www.monarchjointventure.org>).

[org/mlmp](https://mlmp.org/mlmp)), monarch participatory science programs that cover the North American range of monarchs. As our focus was on winter breeding monarchs, we limited occurrence data to larval observations recorded from November to January in North America, corresponding to the time during which migratory monarchs are not breeding. We did not include monarch egg records because the range of the Queen butterfly (*Danaus gilippus berenice*), Nymphalidae (Linnaeus, 1758), overlaps with monarchs in the southern US (Brower, 1961; Batalden & Oberhauser, 2015), and it is impossible to distinguish their eggs from each other (Batalden et al., 2008). After removing duplicates and five likely erroneous records that were in climatic zones where milkweed senesces in the fall (Lemoine, 2015), we retained 416 larval records for our analysis; 109 from the western population and 307 from the eastern population.

### 2.3. Sampling bias and background points

Participatory science data tend to be spatially biased towards regions with higher human populations. Failing to account for this sampling bias can result in highly biased predictions of occurrence (Pearce & Boyce, 2006; Phillips et al., 2009). To account for sampling bias, we selected background points (Phillips et al., 2009), with the same spatial sampling bias as the occurrence records (Phillips et al., 2009). We did this by laying a grid of cells over the region. We then randomly selected 10,000 background points, weighted relative to the density of occurrence data per cell rescaled between one and 10 so that a higher number of pixels used for background points were selected from areas where there were more occurrence data. Using this method, the output of our models is more likely to reflect the monarch's response to the available environment, rather than merely representing the sampling effort within the study area.

### 2.4. Current and future climatic variables

To populate our ENM, we used current and projected climatic data, including all 32 bioclimatic variables, which were down-scaled for North America to a 1-km resolution (Wang et al., 2016; AdaptWest-Project, 2022). The projections (2020–2040, 2040–2060, 2060–2080, and 2080–2100) were based on General Circulation Models (GCMs) of the Climate Model Intercomparison Project 6 (<https://pcmdi.llnl.gov/CMIP6/>). They include predictions for three different trajectories of greenhouse gas emissions (i.e. SSP2-4.5, SSP3-7.0, and SSP5-8.5, which we call “low”, “intermediate”, and “high” emissions). In the low scenario, CO<sub>2</sub> emissions are projected to stay close to current levels until 2050, after which they will start to decline, but will not reach net-zero by 2100; this scenario predicts a temperature rise of 2.7 °C by the end of the century. For the intermediate emissions scenario, CO<sub>2</sub> emissions are expected to double from current levels by 2100, leading to a 3.6 °C increase in temperature by the century's end. In the high scenario, CO<sub>2</sub> emissions will double by 2050, resulting in a 4.4 °C increase in temperature compared to current levels (Intergovernmental Panel on Climate Change, 2023).

It is generally better practice to fit ENMs based on a few biologically relevant predictors than on many predictors with unclear biological relevance (Santini et al., 2021). Moreover, many climatic variables are highly correlated to each other. Therefore, to reduce the number of variables in our ENMs, we calculated the pairwise Pearson correlation coefficients for all 32 climate variables and selected the following predictors, which are likely most biologically meaningful for the winter breeding monarchs and have low correlations to each other: winter mean temperature, precipitation as snow, winter precipitation, and relative humidity. We chose these variables because previous studies have shown that temperature, precipitation, and humidity are important factors affecting monarch distribution (Oberhauser & Peterson, 2003; Leong et al., 2004; Batalden et al., 2008). We limited the temperature and precipitation data to the winter season as our goal was to fit models predicting breeding monarch distributions in November through

January.

### 2.5. Current and future potential distributions

We fit our ENMs for eastern and western winter breeding monarchs using the maximum entropy method (Phillips et al., 2006; Phillips & Dudík, 2008) implemented in *dismo* V1.3–14 package (Hijmans et al., 2023) in R 4.3.2 (R Core Team, 2023). For tuning the MaxEnt parameters of our two models, we used the ENMeval V2.0.4 (Muscarella et al., 2014) package by testing 100 different combinations of Regularization Multipliers (20 different RM values from 0.5 to 10 in increments of 0.5) and Feature Classes (L, H, LQ, LQH, LQHP). We then evaluated the resulting models based on AICc. For the final MaxEnt run for each population, we selected the model with the lowest AICc. To assess model fit, we examined the differences between training and testing AUCs. Larger differences can be an indicator of model over-fitting (Muscarella et al., 2014). To predict the contemporary distribution of eastern and western winter breeding monarchs, we used a 10-fold cross-validation procedure using the 10,000 background points described above for eastern and western populations. We averaged the results across the 10 replications for each population. To predict the distribution of winter breeding monarchs in the future, we used our baseline ENMs and predicted occurrences based on predicted climatic conditions in 2040, 2060, 2080, and 2100 under the low, intermediate and high greenhouse gas emission scenarios. Finally, to convert the calculated continuous suitability layers into binary presence-absence layers, we derived a classification threshold by setting sensitivity and specificity equal for the model using the training data (Cantor et al., 1999; Liu et al., 2005).

## 3. Results

### 3.1. Model performance and climatic variable contributions

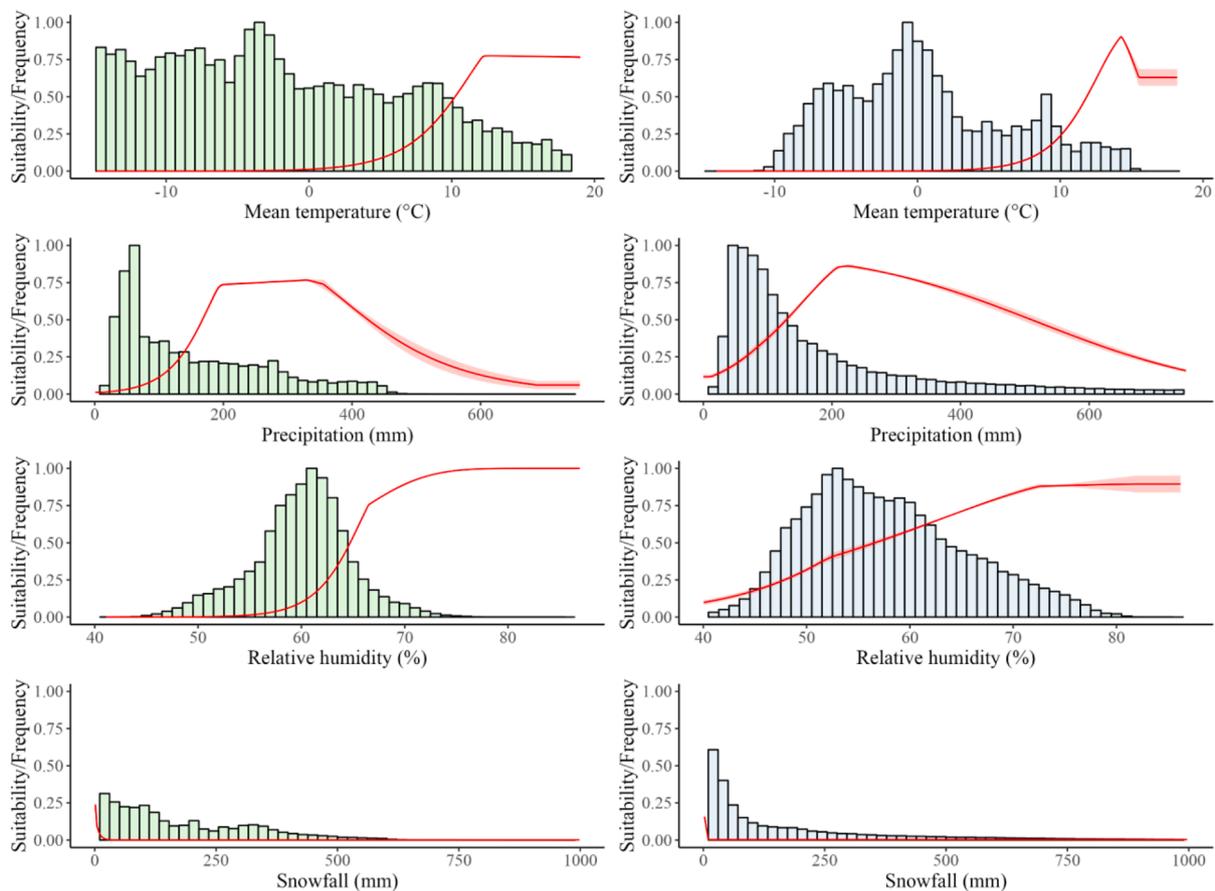
Contemporary winter breeding monarch distributions (November through January) were predicted with high accuracy ( $AUC \pm SD = 0.952 \pm 0.006$  SD for the eastern and  $0.961 \pm 0.011$  for the western population) based on the four climatic variables in each model. The successive permutation of variables and recalculation of AUC values indicated that for the eastern population, snowfall (74.0 %) and relative humidity (16.5 %) were the most important variables in the model. This permutation test for the western population indicated that mean temperature in winter (93.8 %) and rainfall in winter (5.0 %) had the highest contributions in the model. It is important to note that these percentages represent the relative contribution of each variable in the selected model and may vary between models. The response curves extracted from the two selected models are shown in Fig. 1.

### 3.2. Current distribution of winter breeding monarchs

Overall, 81 % (580,430 km<sup>2</sup>) of current predicted suitable areas in the study area for winter breeding monarchs were located east of the Rocky Mountains, and 19 % west of the Rockies (135,271 km<sup>2</sup>; Fig. 2). Suitable areas were mostly located in the southern portions of each region, mainly in Texas, Florida, and Louisiana for the eastern population and in California and Arizona for the western population (Supplementary Information, Fig S1 and S2).

### 3.3. Future distribution of winter breeding monarchs

For both eastern and western populations of winter breeding monarchs, our analyses predicted an increase in total suitable area by 2100 (Fig. 2). Thus, for both populations the areas of expansion will be larger than areas of contraction. These areas of expansion will be significantly farther north than the current distribution, e.g. expansion will occur in Arkansas, Missouri, Virginia, and Delaware for the eastern population and in Oregon and Washington for the western population (Fig. 2).



**Fig. 1.** Response curves (red lines) with standard deviation ranges (shaded areas) for the variables used in the ecological niche models of the winter breeding monarchs in eastern (left) and western (right) areas of North America from November through January. For visualization purposes, we plotted the same range of values for each variable for eastern and western populations. The background histograms show the distributions of the variables within spring and summer breeding ranges for eastern (green) and western (blue) populations.

Under the low emissions scenario, our models suggest a potential increase in the range of winter-breeding monarchs by 21.8 % in the east and 97.9 % in the west, with an average northward shift of 250.6 km in the east and 327.4 km in the west. Under the intermediate emissions scenario, the range of winter-breeding monarchs increased by 38.2 % in the east and 141.2 % in the west, with an average northward shift of 403 km and 302.8 km for the eastern and western populations, respectively. Under the high emissions scenario, the range expanded by 33.7 % in the east and 160 % in the west, with the eastern and western monarchs shifting northward by 573.6 km and 340.1 km, respectively.

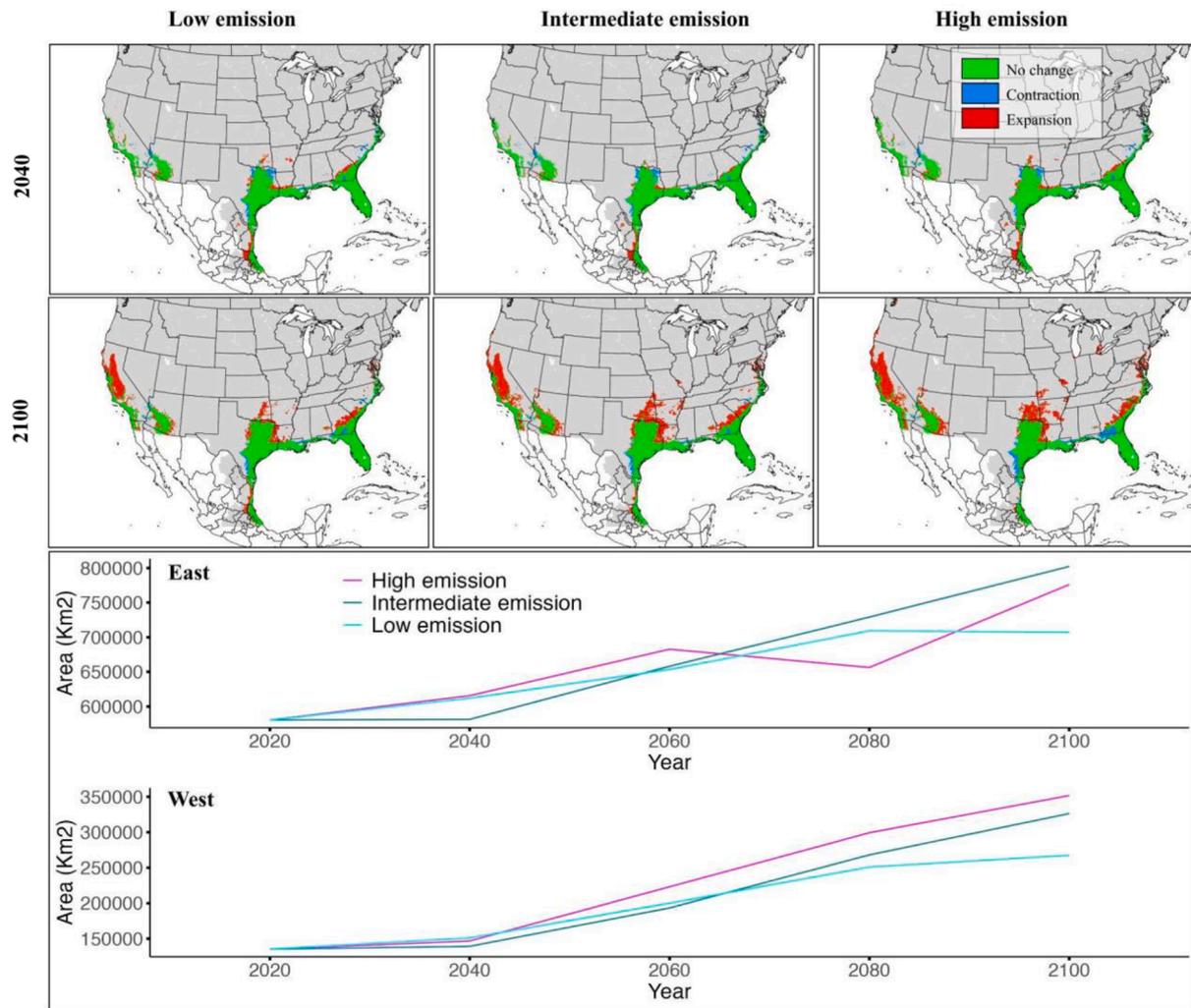
#### 4. Discussion

Our results suggest that climate change is likely to increase the exposure of migratory monarch populations to OE infection. For both the eastern and western North American populations this will happen during both the single-generation fall and the multi-generation spring migrations. This higher exposure is due to our predicted northward range expansion of both eastern and western winter breeding monarch populations. This means that, in addition to exposure during fall migration, during the spring multi-generation migration additional generations of migratory butterflies could be exposed to OE spores on milkweed that was used by winter-breeding monarchs as they move northward. This would result in larger infection rates overall than in the current situation where only the first generation post-diapause interacts with the winter breeding population.

Whether winter breeding monarch ranges actually shift as predicted will depend on the availability of milkweed in good condition within the

predicted range. As our projections are based on only climate variables, our conclusions depend on the assumption that tropical milkweed and winter breeding monarchs will respond in a similar way to shifting climate. This assumption is supported by [Lemoine \(2015\)](#), who predicts a northward expansion of tropical milkweed under various climate change scenarios. Management action to avoid the northward shift of the winter breeding monarchs should therefore include discouraging the sale and propagation of tropical milkweed in areas within the current and predicted range of winter breeding monarchs, thus reducing the potential exposure of migratory populations to the OE parasite. This management action is plausible because most tropical milkweed grows in human-tended gardens ([Steele et al., 2023](#)), and it rarely spreads by itself.

It is important to note that limiting the spread of tropical milkweed will not mitigate all impacts of climate change on migratory monarchs. Previous studies suggest that the increasing temperatures resulting from climate change may lead to a continuous decline in the population sizes of spring and summer breeding monarchs in North America ([Zylstra et al., 2021](#)). An additional significant impact of climate change on eastern migratory monarchs will be the loss of suitable overwintering habitat in central Mexico. Overwintering migratory monarchs require areas with reliably low temperatures that do not dip much below freezing ([Anderson & Brower, 1996](#); [Oberhauser & Peterson, 2003](#); [Williams & Brower, 2015](#)). The availability of these conditions is predicted to decrease with warming temperatures ([Oberhauser & Peterson, 2003](#); [Sánchez-Romero et al., 2012](#); [Zalucki et al., 2015](#)). This is largely due to unfavourable extreme climatic events associated with climate change, which are expected to increase on the wintering grounds,



**Fig. 2.** Predicted range expansion and contraction of eastern and western winter breeding monarchs under different climate change scenarios for 2040–2100. The predictions are based on different models for the two populations. The line charts show the area of suitable habitats for the 2020–2100 for eastern (top) and western (bottom) winter breeding monarchs in the study area (grey color in maps). We used equal sensitivity and specificity thresholds (0.25 and 0.20 for the eastern and western populations, respectively) to convert continuous suitability layers into binary representations.

resulting in large mass mortality events of monarchs (Oberhauser & Peterson, 2003; Barve et al., 2012) and loss of suitable habitat for the main trees species used by the monarchs for overwintering in the area (Sáenz-Romero et al., 2012; Cruzado-Vargas et al., 2021).

Comparisons between our analysis and previous distribution estimates of winter breeding monarchs suggest that climate change may have already caused increases in their range. Zalucki and Rochester (1999) used an ENM for monarchs in Australia to predict the distribution of monarchs in North America during the winter, spring, summer, and fall at that time (pre-1999) and into an unspecified future. Howard et al. (2010) also used participatory science observations to map the distribution of winter breeding and sedentary eastern monarchs in the US for the years 2002 to 2010. Compared to their predictions, our analysis estimates a larger contemporary (i.e. up to 2020) winter-breeding range as well as a larger predicted climate-induced range expansion. Zalucki and Rochester (1999) predicted that pre-1999 there was relatively little suitable habitat for winter-breeding monarchs in Texas. However, our analysis, along with existing occurrence data, suggests that Texas (including northeast Texas; see Supplementary Information, Fig. S1) and northeastern Mexico are now one of the most suitable areas for the winter-breeding monarchs. For western monarchs, the contrast between these two maps is even greater, as the Zalucki and Rochester (1999) pre-1999 distribution does not include monarchs in Arizona, while ours (up

to 2020) does. Finally, Zalucki and Rochester (1999) and Howard et al. (2010) suggested that the distribution of the eastern winter breeding population is restricted to the latitudes below 29°N and 31°N, respectively, while our results suggest that the potential current winter breeding range extends to 38°N for the eastern population and to 41°N for the western population. We suggest that the discrepancies between our current estimates and predictions from prior studies arise from a combination of factors, including increased prevalence of non-native milkweed in recent years (Majewska et al., 2022), a larger dataset of occurrence records reported by participatory scientists from diverse regions subsequent to the previous studies, and the influence of climate change.

The reason our models predict a decrease in suitability for areas with winter temperatures above 14 °C for western winter breeding monarchs (Fig. 1) is unclear. There is also considerable uncertainty regarding the behavior of winter breeding monarchs across different seasons. However, if we assume that these winter breeding monarchs are highly sedentary due to wing deformations caused by OE, we can infer that they need to withstand the summer temperatures in the same areas where they originated. Warmer winter areas likely have very high temperatures in the summer, making them unsuitable for the summer generations of sedentary monarchs.

Our ENMs suggest that winter-breeding monarchs are not found in

areas with high precipitation. Although the tolerance of winter-breeding monarchs to varying amounts of precipitation is not investigated yet, the negative impact of precipitation on the migratory populations of monarchs have been shown in previous studies on both their breeding grounds (Svancara et al., 2019) and wintering grounds (Anderson & Brower, 1996). Indeed, cool temperatures combined with precipitation have resulted in several mass mortality events on the wintering grounds in Mexico (Brower et al., 2004, 2017).

Discouraging the public from planting tropical milkweed in areas suitable for winter-breeding monarchs under current and future conditions (i.e. areas shown in Fig. 2 by red, green, and blue colours), will ultimately help reduce the range expansion of winter-breeding monarchs and mitigate their threats to migratory monarchs. In an effort to increase breeding habitat availability, in recent years the public has planted tropical milkweed, which is not indigenous to the U.S. (Luna & Dumroese, 2013). Planting tropical milkweed in the regions with a suitable climate for winter breeding monarchs will increase the contact zone between non-migratory and migratory populations, thereby raising the parasite load in the migratory population. Additionally, planting tropical milkweed may increase the risk of migratory monarchs becoming sedentary, possibly decreasing the size of the migratory monarch population.

It is important to note that, there is no evidence that non-native milkweed causes increased disease or changes in migratory behavior in more temperate areas where it dies back when native species senesce, e.g., in the northern portion of its summer breeding range. However, to avoid confusion among the public, we suggest the most straightforward management recommendation is to avoid planting non-native milkweed.

Multiple sources of uncertainty are present in the data and methods we used to predict winter breeding monarchs' current and potential distributions. Misidentification of species and sampling bias toward highly populated areas are some caveats tied to participatory science datasets. We minimized these problems, respectively, by using only larval records, which are typically reported by trained observers and are more distinctive than eggs, and by selecting background points with the same spatial bias as presence points. Another source of uncertainty is that the climatic data we used to predict future conditions are themselves predictions based on climate models. For this reason, we used data from three emission scenarios, all predicting relatively similar trends in the range shift of the winter breeding monarchs. Moreover, our predictions of range shifts did not account for future land use change or the current or future availability of suitable land covers that support milkweed and monarchs. Land use and land cover change will ultimately affect the amount of suitable milkweed habitat within the current and projected ranges and should be considered in future studies. Last, interpretation of binary maps should be made with caution. When converting a probability map of habitat suitability into a suitable/unsuitable map, the total area of suitable habitat highly depends on the selected threshold value. Selecting a very low threshold value will cause over-estimating the suitable habitat and a high false-positive error. In this study, we selected thresholds based on equal sensitivity and specificity. This approach is widely employed in ENM studies (Allouche et al., 2006; Riva et al., 2023). To investigate the impact of varying thresholds on our results, we reanalyzed our data applying stricter thresholds (Supplementary Information, Fig S3 and S4). Consistent with our findings, the binary layers generated using the stricter thresholds also showed that while the current range of winter breeding monarchs is significantly broader in the east compared to the west, there will be greater future range expansion in the western population than the eastern one.

In conclusion, our analyses predict that climate change is likely to result in an increase in suitable winter climate conditions for eastern and western winter-breeding monarch in North America. In addition, in both the eastern and western regions the model predicts northward shifts in suitable habitat. These shifts pose a threat to the migratory populations

due to increased disease exposure from the highly infected winter breeding populations. This increased infection is expected during both the fall migration and spring migration periods. Avoiding these impacts will require measures that discourage the public from planting the non-native milkweeds that support the winter breeding populations, especially in regions where there is or will be substantial overlap between migratory and winter breeding populations. We suggest establishing a bi-national program between the US and Mexico to enhance international collaboration for replacing non-native milkweed with native species. This would not only support the migratory population of monarchs but also aid in the recovery of declining populations of native milkweed species.

#### CRediT authorship contribution statement

**Iman Momeni-Dehaghi:** Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Lenore Fahrig:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Joseph R. Bennett:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Trina Rytwinski:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Karen S. Oberhauser:** Writing – review & editing, Methodology, Investigation, Data curation. **Nancy A. Sheehan:** Writing – review & editing, Data curation. **Greg W. Mitchell:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

All data used are freely available. Data on larval monarch occurrences are available from Journey North at [www.journeynorth.org](http://www.journeynorth.org) and the Monarch Larva Monitoring Project (MLMP) at [www.monarchjointventure.org/mlmp](http://www.monarchjointventure.org/mlmp). Current and future climate data can be accessed through the following link: <https://adaptwest.databasin.org/pages/adaptwest-climatena/>.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jnc.2024.126723>.

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