

Unravelling the annual cycle in a migratory animal: breeding-season habitat loss drives population declines of monarch butterflies

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Summary

1. Threats to migratory animals can occur at multiple periods of the annual cycle that are separated by thousands of kilometres and span international borders. Populations of the iconic monarch butterfly (*Danaus plexippus*) of eastern North America have declined over the last 21 years. Three hypotheses have been posed to explain the decline: habitat loss on the overwintering grounds in Mexico, habitat loss on the breeding grounds in the United States and Canada, and extreme weather events.

2. Our objectives were to assess population viability, determine which life stage, season and geographical region are contributing the most to population dynamics and test the three hypotheses that explain the observed population decline.

3. We developed a spatially structured, stochastic and density-dependent periodic projection matrix model that integrates patterns of migratory connectivity and demographic vital rates across the annual cycle. We used perturbation analysis to determine the sensitivity of population abundance to changes in vital rate among life stages, seasons and geographical regions. Next, we compared the singular effects of each threat to the full model where all factors operate concurrently. Finally, we generated predictions to assess the risk of host plant loss as a result of genetically modified crops on current and future monarch butterfly population size and extinction probability.

4. Our year-round population model predicted population declines of 14% and a quasi-extinction probability (< 1000 individuals) > 5% within a century. Monarch abundance was more than four times more sensitive to perturbations of vital rates on the breeding grounds than on the wintering grounds. Simulations that considered only forest loss or climate change in Mexico predicted higher population sizes compared to milkweed declines on the breeding grounds. Our model predictions also suggest that mitigating the negative effects of genetically modified crops results in higher population size and lower extinction risk.

5. Recent population declines stem from reduction in milkweed host plants in the United States that arise from increasing adoption of genetically modified crops and land-use change, not from climate change or degradation of forest habitats in Mexico. Therefore, reducing the negative effects of host plant loss on the breeding grounds is the top conservation priority to slow or halt future population declines of monarch butterflies in North America.

Key-words: agricultural intensification, annual cycle, conservation planning, genetically modified organisms, matrix modelling, migratory connectivity, transboundary conservation

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Introduction

Hemispheric migrations of wildlife involving billions of individuals each year are in widespread decline (Robbins *et al.* 1989; Bolger *et al.* 2008; Brower *et al.* 2012). Migratory animals face multiple threats at different portions of the annual cycle that are often separated by vast geographical distances (Webster *et al.* 2002), which pose enormous challenges for predicting population abundance and designing effective management plans (Martin *et al.* 2007; Norris & Marra 2007; Small-Lorenz *et al.* 2013). Underscoring good management is an understanding of how various environmental and anthropogenic threats interact to influence population dynamics, through their impact on vital rates, in the face of global change. Addressing threats to population viability of migratory animals therefore requires integrating detailed information of how individuals move, survive and reproduce throughout the annual cycle and respond to these threats (Webster *et al.* 2002; Norris & Marra 2007; Taylor & Norris 2010; Jenouvrier 2013).

Monarch butterflies (*Danaus plexippus*), which undergo a long-distance migration between breeding and non-breeding locations typical of vertebrates, have traditionally been considered most vulnerable to disturbance on the overwintering grounds. In Mexico, forest habitat loss (Brower *et al.* 2002) and severe weather patterns (Oberhauser & Peterson 2003; Brower *et al.* 2004) are known to affect local butterfly population abundance by increasing the probability of catastrophic mass mortality events (Anderson & Brower 1996; Brower *et al.* 2012). Alternatively, declines of monarch butterflies may also be attributed to habitat loss that could occur at multiple locations and time periods of the breeding cycle. Reduction in host plants (various milkweed species, *Asclepias*) due to land-use change (mostly urbanization) and agricultural practices, such as the adoption of genetically modified, herbicide-resistant corn and soybean crops, that lower density of host plants in agricultural fields on the breeding grounds (Oberhauser *et al.* 2001; Brower *et al.* 2012; Pleasants & Oberhauser 2013) is predicted to increase competition for food among larvae leading to decreases in immature survival (Flockhart, Martin & Norris 2012).

Given that the conservation of monarch butterflies, like many migratory species, is a responsibility shared by multiple countries (Commission for Environmental Cooperation 2008), a quantitative assessment of year-round population dynamics is critical for guiding effective trans-boundary conservation planning and assessing risk of extinction in the wild. Our objectives were to (i) assess the long-term viability trend and cumulative quasi-extinction probability (<1000 individuals) for monarch butterflies over the next 100 years given projected land-use changes that modify host plant abundance across the breeding grounds and concurrent future climate trends and deforestation rates that alter the frequency of winter mass

mortality events on the wintering grounds; (ii) use transient elasticity analysis (the relative sensitivity values which sum to 1) of the projected population to determine which life stage, season and geographical region across the annual cycle are contributing the most to explain population declines of migratory monarch butterflies; (iii) test the three hypotheses of population decline by comparing the singular effects of habitat loss on the breeding ground, habitat loss on the wintering grounds and climate change to a full model where all factors operate concurrently; and (iv) explore the effects of host plant loss on the breeding ground as a result of adoption of genetically modified crops on future monarch butterfly population size and the risk of extinction.

Materials and methods

Our population model required parameter estimates of survival, fecundity and migration throughout the annual cycle (Fig. 1). We considered one overwintering and three breeding regions (Fig. 2a) to parameterize a spatially structured, two-cohort, stochastic and density-dependent periodic projection matrix model (Hunter & Caswell 2005) for monarch butterflies. The model structure (Fig. 1) used a two-cohort approach to differentiate butterflies in diapause that migrate to Mexico from reproductively active butterflies because these cohorts have different physiological and demographic processes (Brower 1995). We therefore had five life stages: an immature stage that included all developmental transitions from egg to eclosion and then first- and second-month or greater (hereafter second month) vital rate estimates for each cohort of adults that captures differences in survival and reproduction (Fig. 1).

POPULATION MODEL

The model took the form $\vec{n}(t+1) = A\vec{n}(t)$ where the global transition matrix A at a given month t is used to project the population vector, that is, arranged as the spatial distribution of each

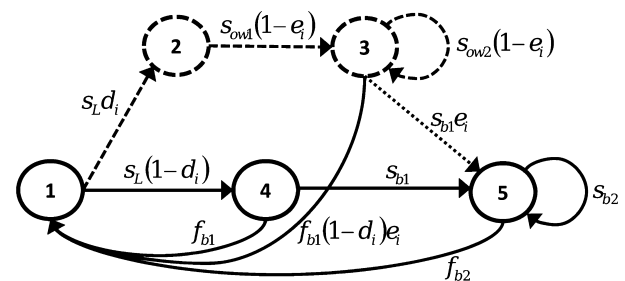


Fig. 1. The life cycle graph of monarch butterflies, characterized by five stages. The immature (1) stage includes egg, larval and pupal development until eclosion. Eclosed butterflies in their first (2) or second or more (3) month of life are in a reproductive diapause (dashed lines). Only eclosed butterflies in their first (4) or second or more (5) month of life in breeding condition (solid lines) produce offspring. The dotted line between (3) and (5) represents overwintered butterflies that emerge from diapause in April and become reproductively active in the South. Descriptions of the variables are provided in Table S1 (Supporting information).

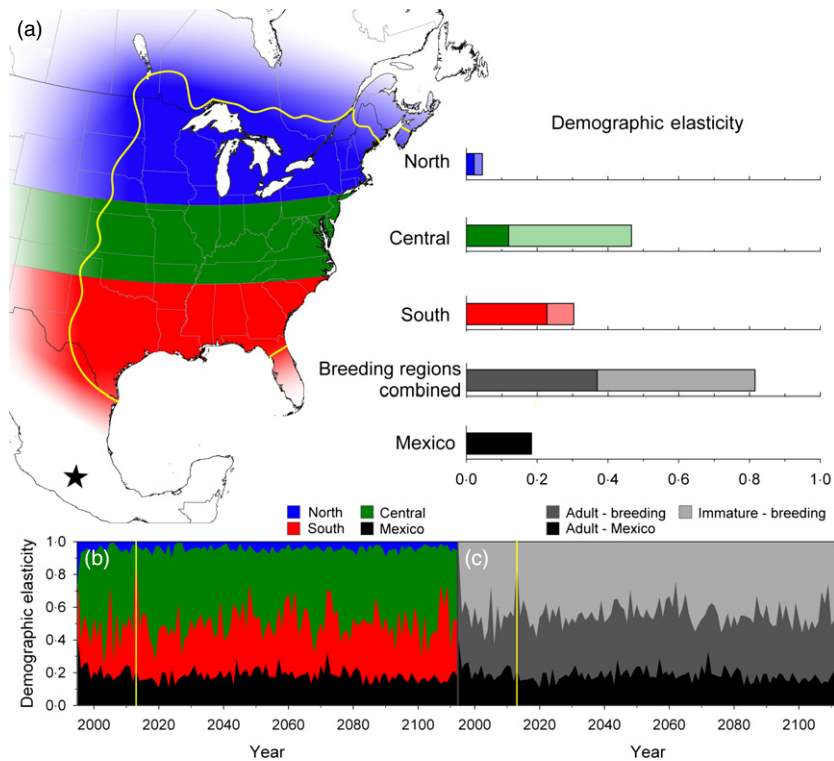


Fig. 2. The geographical regions occupied by monarch butterflies throughout the annual cycle in eastern North America and their associated long-term demographic elasticities between regions, seasons and life stages. (a) Butterflies overwinter in Mexico (black star) and breed in the South (red), Central (green) and North (blue) regions. The yellow outline indicates the monarch breeding habitat study area that was used to quantify milkweed abundance (See Supporting Information). Population abundance was most sensitive to vital rates in the North, followed by the South and Mexico, and least sensitive to vital rates in the Central region. The Central region was most sensitive to perturbation of immature vital rates (light green) compared to adults (dark green), whereas the opposite pattern was found in the South. Population abundance was more sensitive to vital rates on the breeding grounds (South, Central and North regions combined) than the non-breeding grounds (Mexico). On the breeding grounds, sensitivity was almost equal between adult (dark grey) and immature (light grey) life stages. (b) Annual trends of the demographic elasticity of monarch population abundance to perturbation of vital rates among regions and (c) between the breeding and non-breeding portions of the annual cycle. The annual demographic elasticity values vary annually owing to stochastic population processes; however, the sensitivity patterns to the left (historic) and right (future) of the vertical yellow line remain relatively consistent.

stage (Hunter & Caswell 2005), from $n(t)$ to $n(t + 1)$. Within each time step t of 1 month, A_t included both migration among and demography within the four geographical regions i of the five life stages using the block-diagonal formulation and vec-permutation approach (Hunter & Caswell 2005). In this arrangement, butterflies first move between regions before demographic events like reproduction occur, in order to reflect that females are reproductively active during the rapid re-colonization of eastern North America over successive generations (Malcolm, Cockrell & Brower 1993; Flockhart *et al.* 2013). The process is repeated for each of 12 months to project the population over an annual cycle.

The block-diagonal matrix organizes the demographic processes and transitions among life stages within regions (Hunter & Caswell 2005). The demographic vital rates represent survival of immature (s_L^i), overwinter survival for butterflies in their first and second month of diapause (s_{ow1}^i, s_{ow2}^i), survival of adults in their first and second month of breeding (s_{b1}^i, s_{b2}^i), and fecundity of breeding butterflies in their first (f_{b1}^i) and second (f_{b2}^i) months (Fig. 1). The terms d_i and e_i permit the transition of generations between reproductive to diapause life-history stages in autumn (which occurs during immature development; Goehring &

Oberhauser 2002) and the emergence from diapause to breeding condition at the end of the winter, respectively. The migration process was structured with the block-diagonal dispersal matrix that accounts for migration of adults between regions. For each adult cohort, migration included both the transition rate among regions (t_{ij}) and survival during migration between these same regions (s_{ij}). The Supporting Information provides details of the model structure.

VITAL RATE ESTIMATION

The population response to the effects of habitat loss and climate change, key environmental factors that are thought to strongly influence population size of monarch butterflies (Brower *et al.* 2012), occurs through changes to vital rates. We present the results of models to estimate milkweed abundance on the breeding grounds and weather-induced mass mortality events in Mexico that were incorporated into estimates of larval survival and adult winter survival probability, respectively. Detailed analysis of each vital rate estimate, as well as the milkweed abundance and weather-induced mass mortality models, is available in the Supporting Information.

Fecundity

We estimated fecundity of first-month and second-month adults (Table S1, Supporting information: f_{b1}^i, f_{b2}^i) using estimated lifetime egg output reported in Oberhauser (1997). We assumed that females laid 75% of their total eggs in the first month and 25% in the second month. Sex ratio of offspring was assumed to be 50:50.

Migration

Migration combines information on migratory connectivity (Webster *et al.* 2002; Norris & Marra 2007) and survival during migration (see below) to estimate the transition probability of adults flying between different regions at each time step. Following the two-cohort structure of the model, we differentiate rates between non-reproductive butterflies that are on fall migration to Mexico and reproductively active butterflies that can move between breeding regions.

The timing of migration of non-breeding butterflies to Mexico follows a relatively predictable pattern by latitude (Taylor 2013). We incorporated these temporal migration patterns in our model by assuming that butterflies depart to Mexico from the north during September, from the central during October and from the south during November. Collectively these butterflies arrived at the overwintering colonies in December where they remained until April when they became reproductively active (Brower 1995).

Reproductive monarch butterflies colonize the breeding grounds over successive generations (Malcolm, Cockrell & Brower 1993; Miller *et al.* 2011, Flockhart *et al.* 2013). We assumed the main cohort of butterflies colonized the south in April, the central in May and the north in June (Cockrell, Malcolm & Brower 1993) and the last breeding generation would occur in August in the north, September in the central and October in the south (Brower 1995; Calvert 1999; Baum & Sharber 2012; Flockhart *et al.* 2013).

We calculated migration rates (t_{ij}^r) of breeding butterflies based on published information in Flockhart *et al.* (2013) who used stable-hydrogen and stable-carbon isotopes to assign a geographical origin of captured butterflies. Using the assigned geographical region as the origin and the capture region as the destination, we cross-tabulated origin and destination regions to produce a contingency table of relative frequency by dividing the number assigned to each origin region by the marginal total of the destination regions. Using this approach, we calculated the migration between the four regions (origin included Mexico for butterflies that overwintered; see Supporting Information) for each month during the year.

Breeding-season survival

First- and second-month adult female survival (Table S1, Supporting information, Fig. 1: s_{b1}^i, s_{b2}^i) estimates came from longevity measures of captured wild female butterflies (Herman & Tatar 2001). Immature survival (s_L^i) was the cumulative survival from egg to eclosion as an adult butterfly and considered the product of a density-dependent survival relationship based on larval competition for milkweed host plants (Flockhart, Martin & Norris 2012), density-independent larval survival (Oberhauser *et al.* 2001) and pupal survival (Oberhauser 2012).

We applied the findings of Flockhart, Martin and Norris (2012) who showed larval survival probability declined as the average number of eggs per milkweed stem increased. Therefore, calculating the density-dependent response required an estimate of milkweed abundance in each region. To estimate the total number of milkweed stems, we multiplied the land area of different land-cover types (e.g. Taylor & Shields 2000) by the proportion of infested area for each land-cover type (e.g. Hartzler & Buhler 2000; Hartzler 2010; Pleasants & Oberhauser 2013) and the number of milkweed stems within infested areas (see Supporting Information). To understand milkweed abundance change over time, we estimated annual rates of land-cover conversion using data from 1982 to 2007 (U.S. Department of Agriculture 2009) and used nonlinear models to estimate the expected changes in adoption of genetically modified, herbicide-resistant corn and soybean crops (Hartzler 2010; Pleasants & Oberhauser 2013). Details of land-cover change and associated dynamic milkweed abundance are presented in the Supporting Information.

We calculated density-independent larval survival from egg to pupation using estimates from Oberhauser *et al.* (2001) who presented counts of 5th instar larvae relative to counts of eggs in non-agricultural areas, agricultural fields and field margins in four geographical regions that spanned the breeding range. Tachinid flies parasitize monarch larvae that results in mortality realized during the pupa stage, so pupal survival was assumed as one minus the marginal parasitism rate of fifth instars based on 11 years of data following Oberhauser (2012). Mortality during the pupal stage was therefore assumed to result solely from tachinid fly parasitism and provides a suitable way to incorporate this important source of immature mortality on monarch population dynamics (Oberhauser *et al.* 2007).

Migration survival

Evidence for Lepidoptera suggests mortality during migration to be low relative to the stationary portions of the annual cycle (Chapman *et al.* 2012; Stefanescu *et al.* 2013), whereas the opposite pattern has been found for vertebrates (Muir *et al.* 2001; Sillett & Holmes 2002). Few data exist to estimate these mortality rates directly and there is currently no published information for monarch butterflies. In the absence of empirical estimates, the opinions of experts can provide valuable information to understand population processes (Martin *et al.* 2012a).

We used an expert elicitation exercise to estimate the survival of monarch butterflies during both spring and fall migration (s_{ij}^f ; Table S1, Supporting information). The exercise consisted of independent elicitation of survival estimates, an anonymous review of the group results, and a second round of elicitations where experts were allowed to modify their original responses after having seen the group results (Martin *et al.* 2012a). Each expert provides a worst-case, average-case and best-case estimate of the probability of survival for (i) butterflies migrating to the overwintering colonies during autumn migration, (ii) overwintered adult monarch butterflies that migrate from Mexico to the south and (iii) first- or second-generation breeding butterflies born in the south that re-colonize the rest of the breeding distribution. We calculated the mean and standard deviation for the average-case values between each pairs of regions provided by experts and found that the variation of survival implemented into the matrix model contained both the mean worst-case and best-case estimates provided by experts, suggesting that the estimates

of survival during migration generated during simulations of the model captured a range of expected survival rates (see Supporting Information).

As survival during migration was the only vital rate used in the population model not based on empirical data, we present a sensitivity analysis in the Supporting Information of how well the worst-case, average-case and best-case survival estimates predicted the observed monarch butterfly population decline. The results suggest that both the average-case and best-case scenario estimates better reflect monarch butterfly population dynamics but that the predictions from models that incorporate the average-case scenario more closely reflect the observed population decline (see Supporting Information).

Overwintering survival

The probability of survival for overwintering adult butterflies (s_{ow1}^i, s_{ow2}^i) was a product of a baseline survival in the presence of predators (Brower & Calvert 1985; Glendinning, Alonso Mejia & Brower 1988) and catastrophic mortality events caused by extreme weather phenomena (Brower *et al.* 2004). Birds were estimated to kill about 9% of all butterflies in colonies (Brower & Calvert 1985), whereas mice are predicted to kill about 4% of the population (Glendinning, Alonso Mejia & Brower 1988). To estimate mortality, we divided the estimated number of depredated butterflies from Brower *et al.* (1985) and Glendinning, Alonso Mejia and Brower (1988) by butterfly densities (butterflies/ha) from the Jolly-Seber estimates in Calvert (2004) to correct for potentially biased estimates of population density in the wintering colonies. Assuming that predation by birds and mice is independent, multiplying the product of the two survival estimates yielded the baseline overwinter survival (see Supporting Information).

Stochastic mass mortality events in the overwintering colonies can kill significant numbers of the entire eastern population during a single storm (Brower *et al.* 2004). The magnitude of each mortality event is the interplay between ambient temperature, precipitation and exposure that determine body temperature, and hence freezing risk, of monarch butterflies (Anderson & Brower 1996). We used a logistic function to model the proportion of the total overwintering population that would die from extreme weather. The model included the effects of temperature, precipitation and changes in exposure (see Supporting Information). The addition of an exposure parameter incorporates the 'blanket effects' (Anderson & Brower 1996) offered by high-quality forest habitat that was assumed to be lost at 1.3% per year (Brower *et al.* 2002; Ramírez, Azcarate & Luna 2003; López-García & Alcántara-Ayala 2012; Vidal, López-García & Rendón-Salinas 2014).

Temperatures and rainfall patterns are predicted to change over the next 100 years in Mexico (Sáenz-Romero *et al.* 2010) and these changes are predicted to influence monarch mass mortality events (Oberhauser & Peterson 2003). Using the location and elevation of the monarch colonies (García-Serrano, Lobato Reyes & Mora Alvarez 2004), we extracted monthly (December to March) current and future temperature under the A2 scenario of the CGCM3 (T62 resolution) climate model that assumes high greenhouse gas emissions and a growing human population, presented in Sáenz-Romero *et al.* (2010). For each month, we fit a linear regression of predicted mean minimum temperature using data from the years 2000 (current), 2030, 2060 and 2090 as our predicted climate projection in the overwintering colonies. Variation in daily temperatures was assumed to remain consistent

over time and was estimated from daily minimum temperatures from five federal weather stations representative of the overwintering colonies (see Supporting Information). We assumed daily rain events >10 mm would result in butterflies being wetted and making them more vulnerable to freezing risk (Anderson & Brower 1996) and assumed that the probability of a rain event of >10 mm between December and March summarized from the weather station data would remain consistent. The matrix population model randomly selected a daily probability of a large rain event and a minimum temperature to calculate the daily survival between December 1 and March 30. The product of these daily mortality estimates represented the population-level stochastic mortality rate of each year of the model (see Supporting Information).

ANALYSIS

We initiated the population model using the population size observed in 1994 (Rendón-Salinas & Tavera-Alonso 2014) to assess the model fit from the first 19 years of the simulation (1995–2013) and then projected the population for 100 years and calculated the stochastic population growth rate ($\log \lambda_s$) and 95% confidence interval from 1000 simulations. Model fit was assessed by testing the standard deviates of the population growth rates from observed and projected population sizes (McCarthy *et al.* 2001). The cumulative probability of quasi-extinction was determined using a binomial model that regressed the counts of the number of simulations that had gone extinct by a given year. To test between the three hypotheses, we divided the mean population size from a simulation with each effect by the population size of the full model and used linear models to regress differences in population size against year. A slope different from zero indicates that threat alone would cause a larger (in the case of positive slope) future population than the full model that considers all threats simultaneously.

To understand the factors that limit population size of monarch butterflies, we estimated monthly transient elasticities (the relative sensitivity values which sum to 1) of the total species abundance to perturbation of the migration and demographic vital rates (Caswell 2007). To make general predictions of the sensitivity of population growth to changes in vital rates throughout the annual cycle, we summed the demographic transition elasticity values across life stages (immature, adult), life-history events (breeding, non-breeding) or regions (Mexico, South, Central, North). We ran all simulations using Matlab R2009.

Results

POPULATION TREND AND EXTINCTION PROBABILITY

Population size estimates from our model were not significantly different from the observed data ($t = -0.4889$, $P = 0.63$; Fig. 3a) and predict that, if land-use and climate change continue as expected, population size will decline by an additional 14% within the next 100 years (Fig. 3b). Furthermore, under these conditions, we predict that the cumulative probability of quasi-extinction of <1000 butterflies remaining in the population over 100 years is >5% (Fig. 3b). Overall, the stochastic population growth rate was predicted to be -0.0332 (95% CI: $[-0.4028, 0.3364]$)

(Fig. 3b) which is consistent with the population growth rate observed over the past two decades ($r = -0.048$, 95% CI: $[-0.186, 0.089]$; Brower *et al.* 2012; Rendón-Salinas & Tavera-Alonso 2014).

SENSITIVITY OF POPULATION ABUNDANCE

Population abundance was more sensitive to land-use and climate changes on the breeding grounds (mean 0.816 ± 0.004 SEM) than on the wintering grounds

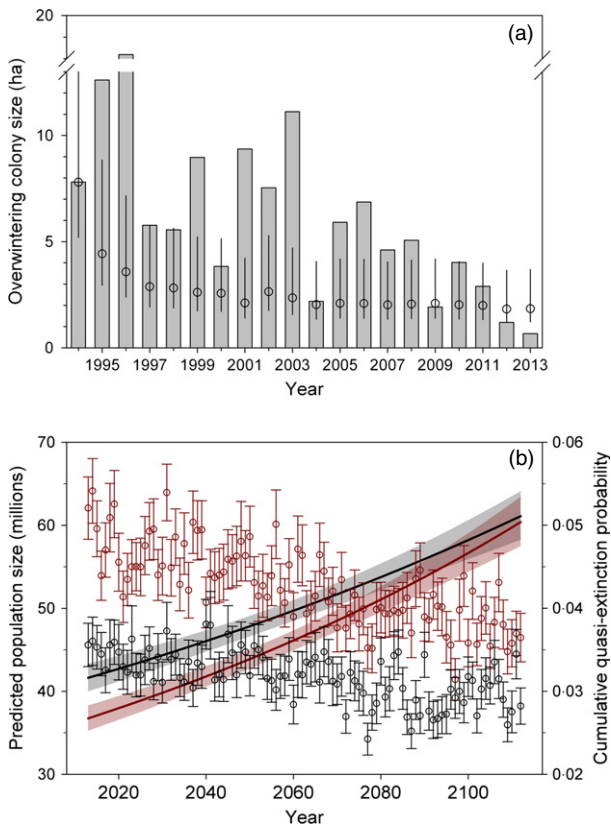


Fig. 3. Monarch butterfly population size is projected to decrease with a corresponding increase in quasi-extinction probability. (a) The model-derived mean predicted overwintering colony size (points) fit the observed monarch butterfly overwintering colony size (bars; Brower *et al.* 2012; Rendón-Salinas & Tavera-Alonso 2014). Overwintering population size is the area (in hectares) occupied by clustering monarch butterflies. For predicted colony size, the points represent the mean density ($50 \text{ million ha}^{-1}$), while the upper ($25 \text{ million ha}^{-1}$) and lower ($75 \text{ million ha}^{-1}$) error bars represent the observed lower and upper population density estimate (Brower *et al.* 2004) assuming a 1 : 1 sex ratio. (b) Projected mean population size (\pm SE, circles and error bars) and probability (\pm 95% CI, line and shading) of quasi-extinction (<1000 individuals) in eastern North America in December of each year from 2013 to 2112. The full model (black) which includes the effects of genetically modified crops is compared to a simulation with no genetically modified crops (red) and shows the presence of genetically modified crops predict monarch butterfly populations being lower with a higher probability of quasi-extinction over the next half-century. The population values represent the number of females since the model only considered female butterflies.

(0.184 ± 0.004 ; Fig. 2a). Decomposition of these sensitivities showed that larvae (0.446 ± 0.007) were more sensitive compared to adults (0.370 ± 0.007) on the breeding grounds (Fig. 2a). At a regional scale, the total butterfly abundance was more sensitive to land-use and climate change impacts on the vital rates within the Central breeding region (0.446 ± 0.010) than within the South breeding region (0.304 ± 0.010) or Mexico (0.184 ± 0.004), whereas butterfly abundance was least sensitive to impacts in the North breeding region (0.045 ± 0.002 ; Fig. 2a). Further decomposition between life stages and regions suggests that the patterns in the Central region resulted from sensitivity of perturbation of immature vital rates rather than adults (Fig. 2a). In contrast, in the South, butterfly abundance was more sensitive to disturbance of adult vital rates compared to vital rates of the immature stage (Fig. 2a).

Although annual elasticities varied between years, the historic and future sensitivity patterns were predicted to remain relatively consistent over time. For example, population abundance was about four times more sensitive to changes in vital rates on the breeding grounds than wintering grounds throughout the study (Fig. 2b) despite a reduced probability of mass mortality events in Mexico over time (Fig. S1, Supporting information). Furthermore, changes in butterfly abundance were about 1.3 times more sensitive to changes in vital rates of adults than those of larvae both at the start and end of the study (Fig. 2c) despite a reduction in milkweed abundance across the breeding distribution (Fig. 4).

THREATS TO POPULATION VIABILITY

Under current conditions, the annual probability of a mass mortality event on the wintering grounds was about

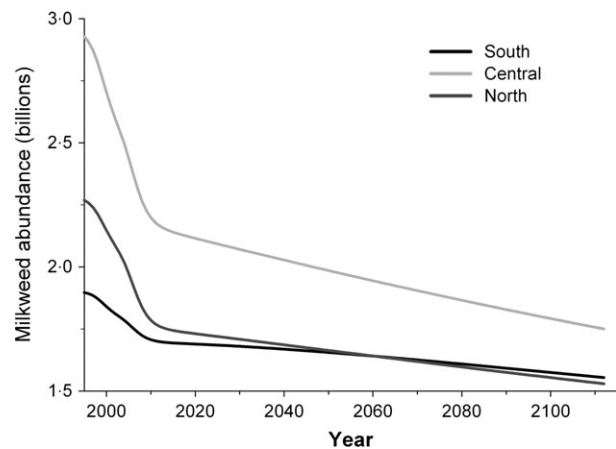


Fig. 4. Predicted changes of milkweed abundance in each breeding region between 1995 and 2112. In each region, milkweed was estimated by multiplying milkweed density by the area of different land-cover types infested with milkweed. Changes in milkweed abundance reflect predicted adoption rates of genetically modified, herbicide-tolerant corn and soybean crops and annual land-use changes.

11% and a reduction in forest cover increased the probability of these events (Fig. S1, Supporting information). Surprisingly, under projected climate change, the chance of butterflies being killed due to severe weather was predicted to decline. For example, winter mortality probabilities of adults under current conditions (11% per year) were eight times higher compared to 2030 (1%), 73 times higher compared to 2060 (<0.2%) and 665 times higher compared to 2090 (<0.02%; Fig. S1, Supporting information). However, over time, the decreasing probability of a mass mortality event caused by rising temperatures trumped any negative effects caused by reduction in forest cover (Fig. S1, Supporting information). Simulations of population dynamics that considered only the effects of forest loss or climate change in Mexico predicted higher population sizes compared to the full model that considered all effects simultaneously (Fig. 5).

Between 1995 and 2013, our model estimated that 1.49 billion individual milkweed stems were lost, representing a 21% decline in milkweed abundance (Fig. 4). Over the past two decades, the Central region, which was the most sensitive to perturbation of vital rates, had the most rapid loss of milkweed (Fig. 4) which resulted from recent widespread adoption of genetically modified, herbicide-resistant corn and soybean crops associated with industrial agriculture. Currently, we estimated there were more than 5.6 billion

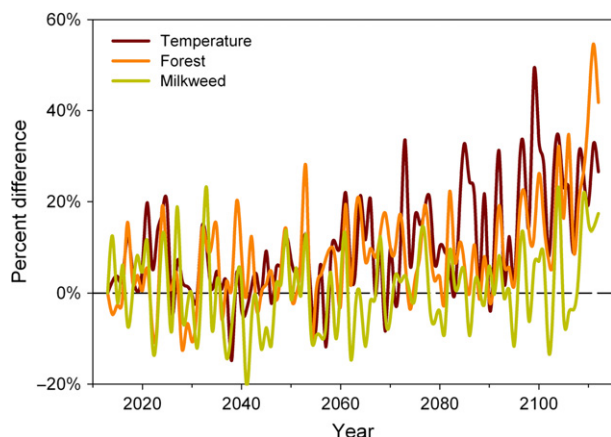


Fig. 5. Reductions in milkweed host plants drive monarch butterfly population decline. The proportional difference in projected mean population size of monarch butterflies over time under the effects of milkweed loss (yellow), forest loss (orange) or changes in temperature (red) relative to the full model that includes all three effects (dashed line). Linear models that regressed population size against year were significant for temperature ($\beta = 0.0023$, $P < 0.001$) and forest ($\beta = 0.0021$, $P < 0.001$) but not for milkweed ($\beta = 0.0005$, $P = 0.09$), indicating no difference in projected population sizes of the full model compared to one that only considered milkweed and hence milkweed is the driving factor of monarch population decline. The models for each effect controls for the others; for example, the milkweed model includes the effects of declines of milkweed host plant abundance on the breeding grounds while controlling for the effects of climate change (no change in temperatures over time) and deforestation (no deforestation over time) in Mexico.

milkweed stems in the study area with the majority (67%; 3.7 billion stems) occurring in agriculture-intensive landscapes (Table 1). Land held in the public trust for the maintenance of biodiversity (e.g. Conservation Reserve Program lands, road right-of-ways) contained 18% of all milkweed plants. Importantly, road right-of-ways accounted for almost 548 million plants (10% of all milkweeds; Table 1). Our model predicts the rate of milkweed decline to slow into the future with milkweed abundance being 14% lower than current conditions, although this still represents a loss of 770 million milkweed plants over the next 100 years (Fig. 4). Overall, genetically modified, herbicide-resistant crops have increased the current, and predicted future, extinction probability of monarch butterflies in eastern North America (Fig. 3b).

Discussion

Our results suggest both climate change and deforestation had less influence on projected population declines compared to the effects of milkweed declines on the breeding grounds. These results are contrary to the long-held belief that monarch butterflies were most vulnerable to disturbance on the wintering grounds since they congregate in a small area at high densities (Brower *et al.* 2002, 2004). Indeed, this was some of the motivation for multiple Mexican presidential decrees that protected butterfly overwintering habitats (Commission for Environmental Cooperation 2008) and recent successful efforts to curb illegal deforestation activities (Vidal, López-García & Rendón-Salinas 2014). Despite a reduced probability of catastrophic mortality events on the wintering grounds, sensitivity to this life-history stage compared to the breeding season remained relatively fixed because mortality is infrequent, stochastic and density-independent (Brower *et al.* 2004). In other words, even if monarchs adjust their behaviour to deal with changing habitat availability (Sáenz-Romero *et al.* 2012) or experience different future temperature and precipitation regimes (Oberhauser & Peterson 2003; Sáenz-Romero *et al.* 2010), population viability is expected to remain less sensitive to mortality on the wintering grounds than to changes in demographic rates on the breeding grounds.

Overall, observed monarch butterfly population decline and future increased extinction risk are largely driven by conditions on the breeding grounds, particularly in the Corn Belt region of the United States (Oberhauser *et al.* 2001; Brower *et al.* 2012; Pleasants & Oberhauser 2013). Given the demographic importance of the Central region and its direct link to overwintering population size in Mexico (Wassenaar & Hobson 1998; Flockhart *et al.* 2013), the rapid loss of milkweed projected for this region attributable to land-cover changes and shifts in agricultural practices is a large concern (Hartzler 2010; Brower *et al.* 2012; Pleasants & Oberhauser 2013). As monarchs are larval host plant specialists, changes in milkweed abundance directly influence vital rates, first through

Table 1. The proportion of milkweed stems in eastern North America in 2013. Estimates are among breeding regions, landscape protection classification and land-cover types. The total number of estimated milkweed plants was 5 604 106 046

	South		Central		North
Unprotected	0.84		0.84		0.76
Crop ^a		0.698		0.880	0.862
Pasture		0.117		0.083	0.108
Rangeland		0.046		0.016	0.024
Wetland		0.139		0.020	0.006
Protected	0.16		0.16		0.24
Crop ^b		0.177		0.282	0.544
Pasture		0.007		0.009	0.012
Rangeland		0.005		0.004	0.005
Wetland		0.224		0.108	0.006
Right-of-ways		0.587		0.597	0.433
Percentage of total	0.303		0.384		0.313
Total milkweed	1 696 459 725		2 154 696 122		1 752 950 199

^aIncludes the effects of genetically modified corn and soybean crops on milkweed abundance, see text for details.

^bCropland assumed to have milkweed density of Conservation Reserve Program lands.

intraspecific larval competition (Flockhart, Martin & Norris 2012) or alternatively, by preventing females from laying a full egg complement (Zalucki & Lammers 2010), although the latter has never been empirically demonstrated. Ultimately, understanding the mechanism by which milkweed reduction limits population abundance will have important implications towards conservation planning.

Our results imply that conserving monarch butterflies by addressing the negative impacts of changing land-use and the adoption of genetically modified, herbicide-resistant crops on host plant abundance is the highest conservation priority. These conclusions should not be misconstrued as implying that efforts towards improving the social, economic and environmental conditions on the wintering grounds are not important, but rather, that inaction in one location during a portion of the annual cycle can undermine conservation efforts in other portions of the annual cycle (Myers *et al.* 1987; Martin *et al.* 2007; Sheehy *et al.* 2010; Vidal, López-García & Rendón-Salinas 2014). Specifically, increasing host plant abundance in the South and Central regions of the United States is expected to translate into the largest benefit to species viability. While planting milkweeds in gardens of private citizens and publicly held lands such as road right-of-ways may be the easiest locations to focus immediate conservation efforts given the limited supply of milkweed seeds, overall, these efforts may be insufficient to negate the ongoing annual loss of milkweed plants let alone address the massive habitat losses observed over the last two decades due to industrial agricultural practices (Hartzler 2010; Pleasants & Oberhauser 2013). Furthermore, the spatial arrangement of milkweed may influence population response (e.g. Zalucki & Lammers 2010) highlighting that both recovery efforts and threats are dynamic and spatially explicit (Brower *et al.* 2002, 2012; Commission for Environmental Cooperation 2008); thus, stochastic population dynamics should be incorporated into cost-effective conservation planning options

(Baxter *et al.* 2006; Martin *et al.* 2007; Pichancourt *et al.* 2012) to aid monarch butterfly population recovery.

Limited data will affect what we can infer about how ecological relationships interact to influence population dynamics across space and time. In extreme cases, no data exist to estimate vital rates. For example, there are virtually no empirical estimates of survival during migration for any terrestrial migratory animal (for rare exceptions see: Ward *et al.* 1997; Sillett & Holmes 2002; Chapman *et al.* 2012). In such cases, we may be limited to using educated guesses or surveys of experts as to the likely range of empirical values (Martin *et al.* 2012a). Drawing inference from model results based on sparse data must therefore be done cautiously, particularly when the sensitivity of data-limited vital rates is high, but is often necessary when investigating steep population declines of threatened species and where conservation success depends on timely decision-making (Martin *et al.* 2012b). For monarch butterflies, subsequent sensitivity analysis suggests that the values elicited from butterfly experts were robust to observed population dynamics and that true survival during migration is expected to be equal or slightly higher than what was provided by experts.

Population declines among migratory species have generated hypotheses that populations are limited by conditions on the breeding grounds (Robinson *et al.* 1995), the non-breeding grounds (Robbins *et al.* 1989; Sherry & Holmes 1996), during migration (Bolger *et al.* 2008) or a combination of these factors (Kareiva, Marvier & McClure 2000; Brower *et al.* 2012). However, quantifying which environmental and anthropogenic factors drive population dynamics at global extents is a complex issue because it depends on how we integrate migratory connectivity and population processes across the annual cycle (Sherry & Holmes 1996; Kareiva, Marvier & McClure 2000; Faaborg *et al.* 2010) and the quality of the data available.

Overall, the general modelling approach we promote could be applied to any migratory species because it

incorporates recent methods to delineate migratory connectivity (Webster *et al.* 2002), how seasonal interactions influence vital rates via density dependence (Norris & Marra 2007), and established approaches of evaluating spatial population dynamics across the annual cycle (Hunter & Caswell 2005; Caswell 2007). Ultimately, the ability to quantify contributions to population growth rate across the annual cycle provides a tractable way to measure the robustness of international conservation programmes (Bull *et al.* 2013) and has important legal implications for conserving threatened wildlife that migrate between countries that classify and protect species-at-risk differently (Fischman & Hyman 2010).

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Author contributions

D.T.T.F., D.R.N. and T.G.M. designed the research. D.T.T.F. analysed the data. J.-B.P. wrote the code of model. All authors wrote the paper. [Correction added on 28 July 2014, after first online publication: final sentence changed to 'All authors wrote the paper.']

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed description of methodology.

Fig. S1. The annual probability of a mass mortality event (>1% mortality of total population) under different proportions of habitat forest cover on the wintering grounds over time.

Fig. S2. Daily minimum temperature used to describe temperature patterns at the overwintering colonies in Mexico between December and March.

Table S1. Key to notation used in the spatial periodic matrix model for migratory monarch butterflies (*Danaus plexippus*) in eastern North America.

Table S2. Sample sizes of monarch butterflies captured in each region for assigning migratory connectivity (Flockhart *et al.* 2013).

Table S3. Monthly transition of monarch butterflies between destination region where they were captured and their region of origin based on stable isotopes.

Table S4. Survival of monarch butterflies during migration.

Table S5. Data used in the Geographic Information System used to calculate milkweed abundance in eastern North America.

Table S6. Land-cover classification.

Table S7. Milkweed density ($\text{m}^2 \text{ha}^{-1}$) for different land-cover types in eastern North America.

Table S8. Results of models used to explain road and right-of-way widths in eastern North America.

Table S9. The width of roads in eastern North America.

Table S10. The width of road right-of-ways in eastern North America.

Table S11. Transition matrix of annual land-cover change based on data between 1982 and 2007.

Table S12. The proportion of total row crops grown as corn and soybean among the three breeding regions in eastern North America.

Table S13. Parameter estimates used in a logistic regression to predict changes in the adoption rates of genetically modified corn and soybean crops over time.

Table S14. Monthly weather in monarch butterfly overwintering colonies in Mexico.

Table S15. Future monthly mean minimum temperatures in monarch butterfly overwintering colonies in Mexico.

Table S16. Annual rates of winter habitat degradation between 1971 and 2012 in Oyamel fir-pine forest ecosystems, Mexico.