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Report

Optimal conservation of migratory monarch butterflies requires immediate international coordination

Highlights

- Coordinated tri-national plans are needed to restore monarch butterflies
- Habitat restoration in the central USA is the most crucial action to take
- Delayed restoration actions had a lower chance of achieving conservation targets

Authors

D.T. Tyler Flockhart, Sam Nicol, Iadine Chadès, Greg W. Mitchell, Tara G. Martin, Richard A. Fuller, D. Ryan Norris

Correspondence

dt.tyler.flockhart@gmail.com

In brief

Over a 5-year time span, Flockhart et al. show that the best strategy to recover declining eastern North American monarch butterflies involves immediate international collaboration and a primary focus on restoring breeding habitat in the central USA.

Flockhart et al., 2025, Current Biology *35*, 1–8
August 18, 2025
https://doi.org/10.1016/j.cub.2025.06.068

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Please cite this article in press as: Flockhart et al., Optimal conservation of migratory monarch butterflies requires immediate international coordination, Current Biology (2025), https://doi.org/10.1016/j.cub.2025.06.068

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Report

Optimal conservation of migratory monarch butterflies requires immediate international coordination

D.T. Tyler Flockhart,[1,7,*] Sam Nicol,[2] Iadine Chadès,[2] Greg W. Mitchell,[3,4] Tara G. Martin,[5] Richard A. Fuller,[6] and D. Ryan Norris[1]

[1]Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada
[2]CSIRO Environment, Dutton Park, QLD 4102, Australia
[3]Wildlife Research Division, Environment and Climate Change Canada, Ottawa, ON K1S 5B6, Canada
[4]Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada
[5]Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC V6T 1Z4, Canada
[6]School of the Environment, University of Queensland, Brisbane, QLD 4072, Australia
[7]Lead contact
*Correspondence: dt.tyler.flockhart@gmail.com
https://doi.org/10.1016/j.cub.2025.06.068

SUMMARY

The eastern North American monarch butterfly, known for its spectacular annual migration between Mexico, USA, and Canada, is currently the focus of intense conservation attention to minimize extinction risk and reach a conservation target of approximately 132 million individuals (equivalent to occupying 6 ha of overwintering habitat in Mexico).[1] Given that migratory eastern North American monarchs breed over successive breeding generations across a vast area,[1–6] reaching this conservation objective must account for the inherent uncertainties of undertaking conservation actions across space and time.[7–11] We integrated a density-dependent full-annual-cycle matrix population model with stochastic dynamic programming to identify the optimal sequence of conservation actions (restoring habitat in three different breeding regions or protecting habitat on the wintering grounds), spanning three countries, to reach each of three objectives: maximize population viability, meet the population target, and maximize population size. Using an annual budget of $30 million over 5 years, we find that a coordinated approach that would primarily focus on habitat restoration in the central USA would best help achieve each of the three recovery objectives. Importantly, monarchs had a higher chance of reaching each conservation objective following a strategy that was coordinated across all three nations and commenced immediately rather than be delayed. Our results provide quantitative evidence for the necessity of coordinated international efforts to conserve migratory species and a tool for decision-makers in Canada, USA, and Mexico to recover this iconic and highly threatened butterfly.

RESULTS

Migratory animals, moving across the globe in vast numbers, highlight incredible endurance and contribute vital nutrient transfer to ecosystems.[12–15] Despite significant conservation efforts, plans to protect migratory species often neglect the spatial and temporal connections of populations throughout their annual cycle[7,8]; conservation actions taken in one location may be ineffective if threats persist elsewhere along the migratory pathway.[9] Furthermore, the economic cost and rates of habitat change vary significantly across countries, making uniform conservation approaches challenging.[7,10,16] Decision science offers a valuable framework for prioritizing conservation actions to achieve specific objectives,[17,18] yet the benefits of coordinated international plans compared with uncoordinated efforts have not been thoroughly examined for migratory species, especially considering population dynamics and the costs of delayed action.[19–21] Integrating population dynamics with decision models can demonstrate the necessity of coordinated international strategies to maintain sustainable migratory wildlife populations globally. Eastern North American monarch butterfly (*Danaus plexippus*) populations have declined by approximately 80% in the last two decades[1] and are considered at risk or endangered in Mexico and Canada, respectively,[22,23] with a final listing decision delayed in the USA.[24] This decline is attributed to factors including loss of wintering habitat and breeding habitat, changes during autumn migration, and severe weather.[1,4,5,25–29] Evidence suggests milkweed loss is a primary driver, with an estimated 1.5 billion plants lost in parts of the USA since 1999.[1,5,6,25,26,30,31] However, the most cost-effective restoration strategy across the migratory flyway (USA, Canada, and Mexico) remains uncertain (Figure 1A); a robust, cost-effective plan is urgently needed to guide stakeholders in restoring monarch populations and preventing the loss of this unique migratory phenomenon.[1,2]

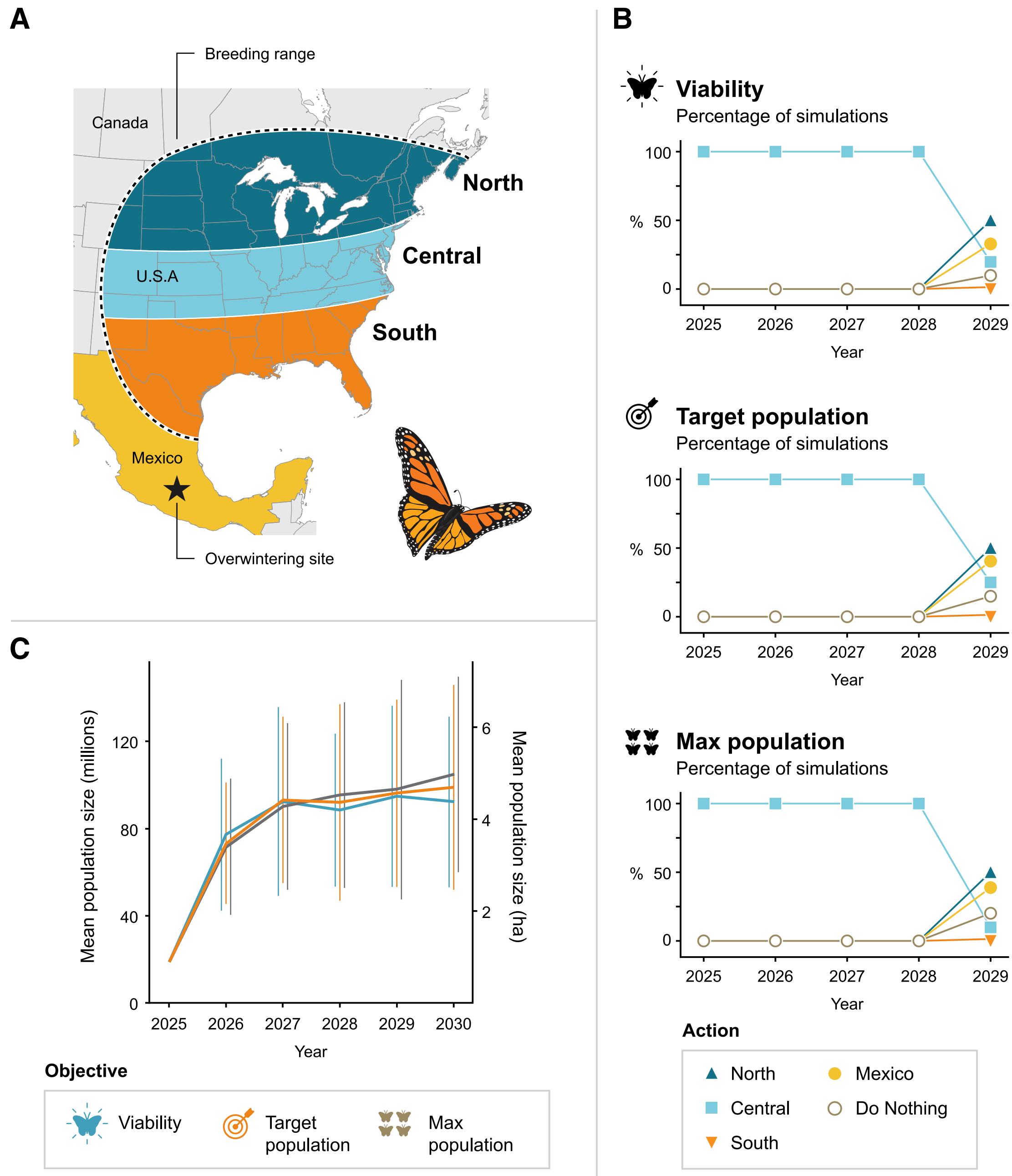

Figure 1. The optimal solution to restore eastern North American migratory monarch butterflies

(A) The spatial structure of the conservation decision model depicting the non-breeding grounds in Mexico (black star) and three breeding regions in the USA and Canada: South (orange), Central (light blue), and North (dark blue).

(B) The frequency of each action selected at each time step for the optimal solution to reach three conservation objectives: maximize population viability (top), reach the population target of 6 ha (middle), and maximize population size (bottom). There are five conservation actions that can be performed and one action is performed at each time step (1 year): protect forest in Mexico; restore milkweed in the South, Central, or North; or do nothing. The percentage of each action is how frequently that action was selected in 500 simulations for a coordinated trinational conservation plan.

(C) The predicted population size by year, following the optimal conservation solution for the three conservation objectives. Population size is depicted as both total abundance in millions of monarch butterflies (left axis) and the estimated surface area in ha of overwintering forest colonies occupied in Mexico (right axis). The predicted mean (vertical line is 1 standard deviation) population size of monarch butterflies under the optimal solution given the starting population size (0.9 ha) for each conservation objective.

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Table 1. The scenarios that compare different conservation models considered in the analysis of making optimal conservation decisions for the recovery of monarch butterflies

Scenario	Model	Description
The benefit of a coordinated trinational conservation plan	optimal decision	optimal coordinated trinational conservation where actions are taken in any country at each time step
	uncoordinated decision	uncoordinated trinational conservation where actions are taken by randomly choosing one region at each time step
	no action	no conservation actions are taken
The value of a coordinated trinational plan compared with individual national plans	optimal decision	optimal coordinated trinational conservation where actions are taken in any country at each time step
	Canada only	conservation actions taken in North region only, representative of conservation actions only taken in Canada
	Mexico only	conservation actions taken in non-breeding region only, representative of conservation actions only taken in Mexico
	USA only	conservation actions taken in South or Central regions only, representative of conservation actions only taken in USA
The cost of waiting to implement an optimal conservation plan	optimal decision	optimal coordinated trinational conservation starting 2025
	1-year delay	optimal coordinated trinational conservation starting in 2026
	2-year delay	optimal coordinated trinational conservation starting in 2027
	3-year delay	optimal coordinated trinational conservation starting in 2028

In this paper, we developed an optimal conservation strategy to restore monarch butterflies in eastern North America. To do this, we linked a full-annual-cycle population model that incorporated estimated rates of habitat loss on both the breeding and non-breeding grounds[26] with stochastic dynamic programming.[18] Our first goal was to estimate the financial investment necessary to restore monarch breeding and non-breeding habitat that has been lost over the past two decades. Our second goal was to develop an optimal strategy of habitat restoration actions across the annual cycle of the monarch (Figure 1A) under each of three conservation objectives: (1) maximize population viability, (2) maximize the probability of reaching the stated population target for monarch butterflies in eastern North America,[32,33] and (3) maximize population size. Our final goal was to assess the relative benefit of an immediate, coordinated, and optimal trinational conservation strategy to restore the eastern North America monarch population compared with an uncoordinated conservation plan and single-nation conservation efforts where only one country takes action while the other two countries take no actions or a delayed implementation of the optimal strategy (Table 1).

We estimated that an annual budget of $30 million for 5 years would be sufficient to restore habitat needed for monarch recovery. This budget would be expected to restore most (at a cost of $0.18/milkweed) or all ($0.09/milkweed) of the 1.5 billion milkweed plants that have been lost over the past three decades (Figure S1). The number of milkweeds restored in each region was based on the relative availability of public land in each region as a measure of the relative difficulty of implementing restoration activities (Tables S1 and S2). Given this projected constraint and a cost of $0.18 per milkweed, if all of the budget were allocated to one of the three breeding regions, it would translate to annual restorations of 86.5 million milkweeds in the South, 92.3 million in the Central region, or 166.7 million in the North. Similarly, if the same 5-year budget were allocated solely to Mexico, it would result in a 2.74% annual forest recovery rate that would combat continuing forest degradation and restore habitat that would provide the benefit of reducing mass mortality events (Figure S2).

Given these possible actions, the optimal conservation strategy for monarch conservation across North America to reach three conservation objectives (maximize population viability, meet the population target, or maximize population size) was to consistently take actions in the Central region for the first 4 years and the North region in the final year (Figure 1B). Greater uncertainty occurred in the final year of the simulation, when taking action in Mexico, taking no action, or taking action in the Central region all held some level of support (Figure 1B). Actions in the North were highest at the last time step, resulting in a short-term boost of the population size because it maximized the reproduction in the final breeding generation before the annual population survey occurred in Mexico in December. Investments in Mexico in the final time step would mitigate periodic extreme weather events that kill large numbers of monarchs, which may temporarily reduce the population below the population target of 6 ha. However, for any of the three objectives, few simulations indicated taking action in Mexico, suggesting the return on investment for halting forest cover loss was minimal compared with restoring milkweed on the breeding grounds (Figure 1B). The South region held almost no support as the best location to implement actions to reach any of the three objectives. Under these optimal strategies, the monarch population, on average, is expected to increase to about 5 ha by 2030, with the trajectory varying slightly depending on the specific objective (Figure 1C).

For all conservation objectives, a coordinated trinational conservation strategy—a schedule of which specific action is taken in a specific country at each year—had a higher probability of reaching the target population compared with both an uncoordinated trinational plan—an action is taken in a randomly selected country at each year—or taking no action (Figures 2A–2C). A coordinated trinational conservation strategy for monarchs resulted in higher population viability, higher population size, and a higher probability of achieving the target population compared

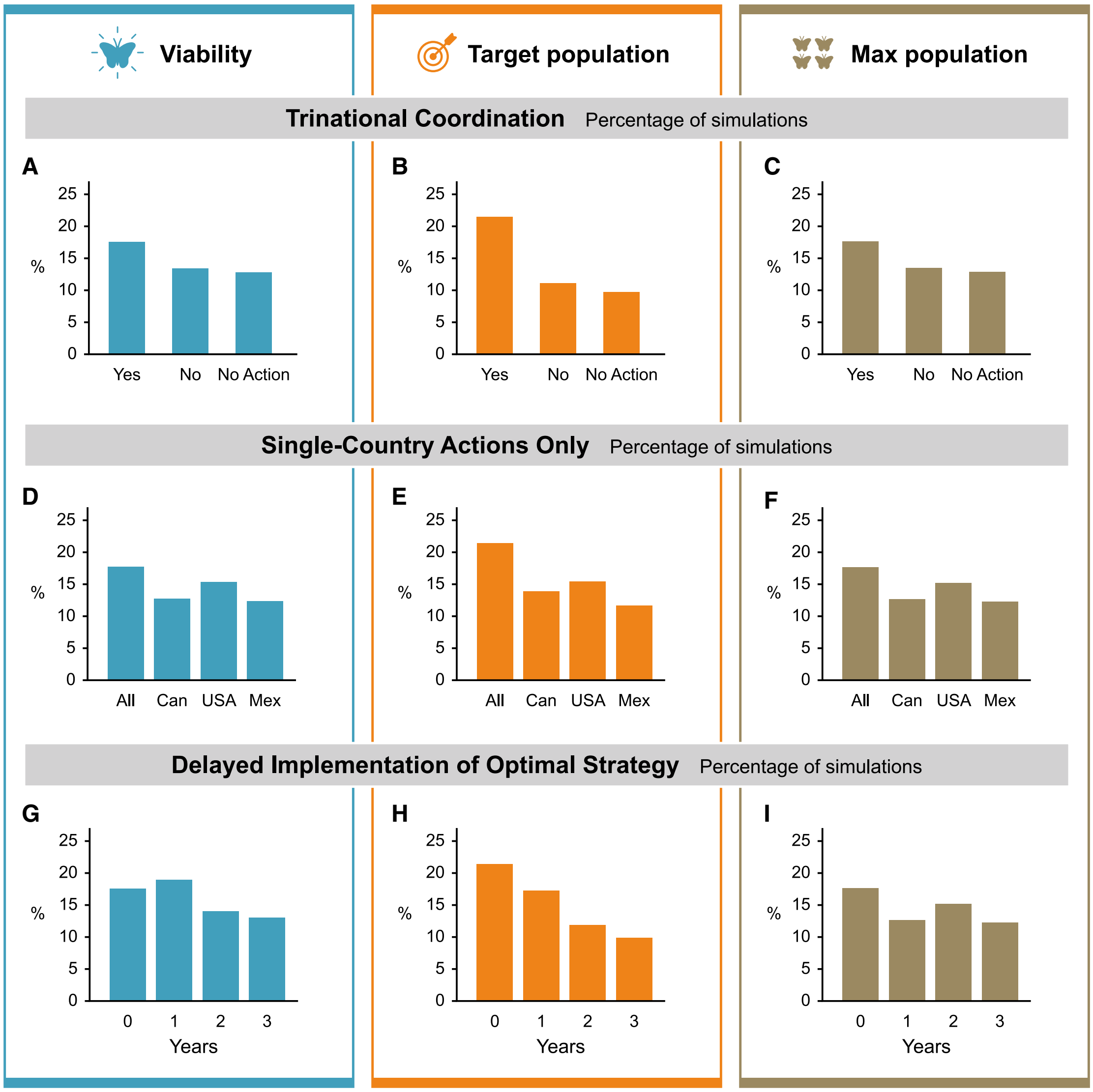

Figure 2. A coordinated and immediate trinational conservation plan is the best method to restore migratory monarch butterflies in eastern North America

(A–C) The proportion of the 500 simulations that resulted in reaching the population target of a coordinated trinational action plan (Yes), uncoordinated trinational action plan (No), and taking no action (No Action) for three conservation objectives: maximize population viability (left, blue banner), reach the population target of 6 ha (middle, orange banner), and maximize population size (right, brown banner).

(D–F) A coordinated trinational conservation plan is better than single-nation action plans to restore monarch butterflies in eastern North America. The proportion of 500 simulations that resulted in reaching the population target of a coordinated trinational action plan (All), action plans occurring only in Canada (Can), USA (USA), or Mexico (Mex) for each conservation objective.

(G–I) The cost of waiting to implement an optimal conservation strategy. The proportion of 500 simulations that resulted in reaching the population target of an optimal conservation plan enacted immediately (0) or delayed 1, 2, or 3 years for three conservation objectives.

with any single-nation conservation plan focused on conserving monarch butterflies (Figures 2D–2F and S5). An uncoordinated trinational plan generally had a better chance of achieving the population target compared with taking no action but had similar probabilities of the population being below the 5-year mean population size or extinction under all objectives (Figure S4). Finally, immediate implementation of an optimal conservation strategy was generally the best strategy to reach the population target of 6 ha (Figures 2G–2I). With the exception of the objective to maximize viability, where a 1-year delay was acceptable (Figure 2G), there was a sharp decline in the probability of the monarch population being above the population target if conservation efforts were delayed (Figures 2G–2I and S6).

DISCUSSION

Our results provide evidence that an immediate implementation of a coordinated trinational conservation strategy for monarchs is likely to have the highest probability of restoring monarch butterflies in eastern North America. Our work supports the notion that actions that restore milkweed on the breeding grounds are imperative for restoring monarchs[1,5,6,25,26,30,34] and that the best return on investment should involve focusing primarily on the Central region of the USA, followed by restoring habitat in the Northern region (northern USA and southern Canada). Investment in Mexico to combat ongoing forest loss and improve habitat beyond existing protections did not outweigh the benefits of actions on the breeding grounds for the 5-year time horizon of our study. This result does not imply that the forests on the wintering grounds should not be protected but, instead, suggests that, if the goal is to maximize recovery over a 5-year time horizon, money from all three countries should be invested in milkweed restoration during this short time frame. Indeed, a coordinated trinational strategy was superior to an uncoordinated trinational strategy with the same annual budget, as well as to any single nation conducting conservation actions alone. The probability of reaching the population target declined for each year in delaying implementation, emphasizing the need to act quickly.[21] The successful conservation of monarch butterflies in eastern North America is a shared responsibility among Canada, USA, and Mexico and our results suggest that cooperation among these nations will provide the best return-on-investment for the conservation of this iconic migratory insect.

Monarch butterflies in eastern North America had the highest probability of persistence following a coordinated conservation strategy between Canada, USA, and Mexico. Trinational strategies were superior to ad hoc approaches when investments were made randomly among the three countries using the same budget. The superiority of coordinated efforts may arise from the population dynamics that result due to migratory connectivity between—and habitat loss within—breeding and nonbreeding areas.[1] These same principles apply to habitat restoration or protection, whereby optimal actions taken in one location has impacts on population responses that lead to a higher probability of reaching management objectives[10] even when differences in costs between countries are substantial.[1,35]

Our results, and those of previous analyses for migratory animals,[7,10,35] assume that all countries are capable of cooperation and willing to cooperate to implement actions under a given conservation strategy. However, coordination is challenging, and countries often act independently when attempting to achieve conservation goals and legal obligations.[36] Furthermore, population changes arising from one portion of the annual cycle could be masked by habitat loss in another portion of the annual cycle,[37] and, as a result, strategic decision-makers may defer expensive conservation actions. In other words, countries could free-ride and multinational conservation situations are best considered game-theoretic, where strategic decisions (i.e., investments) depend on the perceived actions of other countries and probabilistic expectations of population change.[38] Underscoring the difficulties of multi-nation conservation planning, monarchs are currently afforded no legal protection in the USA,[24] listed as requiring special attention in Mexico,[22] and endangered in Canada.[23] Our results suggest that single-nation strategies are less effective than trinational strategies.[20,39,40] Therefore, in cases where the status of a species forces governments to fulfill their legal obligation to restore species at risk, a sound financial investment could involve transferring capacity or funding to another country; monarchs in eastern North America serve as an example.[11]

Our results provide an indication of the financial investments necessary by USA, Canada, and Mexico to restore monarchs to reach target populations. We estimated that approximately \$30 million (USD) annually over a 5-year period (\$150 million total) was necessary to have an approximately 80% chance of maintaining or increasing monarch population size above current levels and an approximately 20% chance of successfully reaching the monarch population target. A total restoration investment of \$150 million is far below the estimated public "valuation" of \$4.5–6.5 billion for the species in the USA alone.[34] Previous studies have estimated that more than 1.5 billion milkweed stems have been removed over the past 20 years due to land conversion and adoption of bio-agricultural technology that removes or reduces milkweed.[25,26,30,31] Our models suggest that the above probabilities of success could be achieved when restoring, on average, a total of about 369 million milkweed stems over the 5-year time horizon (Figure S1). Furthermore, two of our objectives indicated some support for not investing in the final year, meaning a total cost of \$120 million. It is important to note, however, that the precise per-milkweed restoration cost is not given with certainty and our total budget estimates are relative to the per-milkweed cost we estimated in this analysis. For instance, if the actual per-milkweed cost were \$1.80/milkweed instead of our estimate of \$0.18/milkweed, the estimated annual budget of \$30 million would necessarily scale to \$300 million per year, resulting in a total of \$1.5 billion over the 5-year period. Despite the uncertainty of the overall financial commitment required, even under an assumption of mass production and considering a range of costs for milkweed restoration (STAR Methods), restoring this many milkweed plants would require a large financial commitment over a relatively short period. Computational limitations constrained us to a 5-year time horizon and required assumptions about restoration activities being completely efficient and having immediate contributions to population growth. Inefficiencies in conservation actions, along with uncertainties in funding availability and better cost estimates of restoration activities, should be incorporated into future planning efforts because they could have material impacts on the probabilities of reaching conservation population targets.

Our study provides guidance on where and in what order investments should be made. To consider events across the annual cycle, we assumed that investment would result in a specific number of milkweed plants and that restoring those plants incurred increased costs (financial, effort, access, speed of implementation, etc.) in areas with less public lands. These assumptions do not take into account challenges associated with restoration activities across a range of landholders and landscape types.[31] Given our results, the next step would be to investigate how the approximate numbers of milkweeds would be restored in each region. For instance, restoration along rights of way has been touted as an approach to make quick gains for monarchs,[41,42] but roadways are managed differently by state and region, and public safety is paramount in decisions regarding habitat restoration or maintenance (e.g., mowing). These factors will be region specific and seasonally variable because monarchs breed over multiple generations through the spring and summer.[3] To obtain a realistic computational time for the model, we also assumed that successful milkweed restoration was not spatially or temporally dependent. However, milkweeds have a higher probability of use by monarchs in some habitats over others,[1,2,25,29,43] and survival of those eggs likely varies seasonally,[44] among landscape types[45] and across latitudes.[44]

Stochastic dynamic programming provides a powerful approach for determining best actions to conserve migratory animals by accounting for the consequences of current decisions made over time and across different geographic areas. The shift in the optimal action toward the end of the time horizon is a key indicator of the necessity for such a dynamic solution to conserve monarchs in eastern North America. The model prioritized conservation in the North in the final time step, suggesting that while restoration efforts in the Central region offered the most immediate gains in monarch production, the seemingly less-cost-effective action of milkweed restoration in the North region becomes crucial for achieving the conservation objectives over the entire planning horizon. In other words, restoration activity in the Central region accrues the most productive habitat to produce monarchs until near the end of the time horizon, and the dynamic framework reveals that continuing to focus solely on the Central region would likely be suboptimal in the long run. A longer time horizon might reveal a shift to actions outside the Central region, potentially indicating a saturation point where the benefits of further habitat restoration in the Central region begin to attenuate or a need to diversify risk away from the Central region to buffer against environmental stochasticity that could cause widespread reproductive failure.

It is important to recognize that other actions to promote monarch recovery exist beyond the conservation actions considered in our analysis.[31] Actions such as promoting flowering plants that monarchs use to fuel southward migration,[34] active pruning of non-native milkweeds that promote disease,[27] conversion of marginal agricultural land to conservation lands,[31] reduction in pesticides that would reduce direct mortality of larvae and promote restoration of milkweed,[46] and mowing milkweeds at optimal times[47] all have the potential to benefit monarchs. Furthermore, the financial commitments for some of these activities are lower than those of wide-scale milkweed restoration based on public land availability. Such nature-based solutions, therefore, have both the potential to engage diverse stakeholders to monarch restoration activities and at a potentially lower cost. Given the optimization approach we advocate, there are two constraints to considering these types of actions. First, we must be able to model a direct link to these actions and monarch vital rates. For example, we used milkweed restoration to reduce density-dependent larval mortality[44,48] and a model of estimated milkweed abundance over time across our study area.[26] Actions that enhance nectar availability or reduce disease prevalence, while likely important to monarch population ecology, do not yet have a direct empirical link to monarch vital rates. Furthermore, these relationships must be underpinned by a model that captures the current dynamics of the system and can account for nectar plant loss or gains over space and time. The second constraint that limits our ability to consider additional conservation actions is the need to balance model complexity, time horizon, and the state-space of the solution. Analyses that prioritize a subset of actions among a large suite[31] are beneficial because they identify regional solutions of high priority that can form a subset of efforts that might be applied across the distribution of the monarch. Further research that assesses how conservation actions directly influence monarch vital rates, the relative cost of those efforts, and the probability of successfully implementing those actions require different disciplines, such as ecology, economics, and sociology, to advance strategic solutions toward monarch butterfly conservation.

The restoration of milkweed in the USA Midwest is paramount to the immediate recovery of monarch butterflies in eastern North America.[6,25,26,30,31] Focus should now shift to how to achieve this scale of restoration required, the infrastructure needed, and the time necessary to achieve the mission. Although these details are being worked out, we should not delay, given the negative effects of delaying actions on reaching conservation goals for monarchs. Approaches such as ours that quantify the probability of reaching conservation objectives for monarchs and defining the best strategy to allocate scarce resources are a useful tool in recovery processes for threatened and endangered species. The approach we outline here is flexible and could be altered to address multiple hypotheses to explain monarch population decline,[1,5] the use of adaptive management in restoration activities,[18] and the uncertainty of observing a significant change in the metric used to determine conservation success.[49]

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to the lead author, Tyler Flockhart (dt.tyler.flockhart@gmail.com).

Materials availability

This study did not generate new materials.

Data and code availability

- This paper analyzes existing published and publicly available data that are accessible through the computer code at https://github.com/Warbler1/monarchSDP.git.
- All original code for the study is deposited on GitHub and is publicly available at https://github.com/Warbler1/monarchSDP.git.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

ACKNOWLEDGMENTS

D.T.T.F. was supported by a Liber Ero Fellowship. D.R.N. was supported by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada (NSERC). T.G.M. was supported by NSERC (2019-04535), Liber Ero Conservation Chair, and Laura and Reid Carter Fund. We appreciate the constructive comments of three reviewers that improved our manuscript.

AUTHOR CONTRIBUTIONS

D.T.T.F., S.N., I.C., and T.G.M. wrote the model code. D.T.T.F., G.W.M., R.A. F., S.N., and D.R.N. collected the data. All authors conceived and designed the models and wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2025.06.068.

Received: February 16, 2025
Revised: June 7, 2025
Accepted: June 25, 2025

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Please cite this article in press as: Flockhart et al., Optimal conservation of migratory monarch butterflies requires immediate international coordination, Current Biology (2025), https://doi.org/10.1016/j.cub.2025.06.068

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
Data and code to run optimization	This paper	https://github.com/Warbler1/monarchSDP.git

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Our study area encompassed the geographic range of migratory monarch butterflies in eastern North America including the non-breeding areas in central Mexico and breeding areas in eastern USA and Canada (Figure 1A). Each spring in April, monarchs migrate from dense overwintering colonies in the central highlands of Mexico to the southern breeding areas in Texas where they lay eggs on milkweeds, their obligate hostplants. These eggs develop into caterpillars and eclose, after which adults migrate north to lay eggs in the Central region and the North region over successive breeding generations.[3] In autumn, monarchs eclose in a reproductive diapause and migrate thousands of kilometers south to Mexico where they overwinter between November and March.[2]

METHOD DETAILS

We developed an optimal conservation strategy to restore monarch butterflies in eastern North America. To do this, we linked a full-annual-cycle population model that incorporated estimated rates of habitat loss on both the breeding and non-breeding grounds[26] with stochastic dynamic programming.[18] Our first goal was to compare scenarios to determine the financial investment necessary to restore monarch breeding and non-breeding habitat that has been lost over the past two decades. Our second goal was to develop an optimal strategy of habitat restoration actions across the annual cycle of the monarch under each of three conservation objectives: (a) maximize population viability, (b) maximize the probability of reaching the stated population target for monarch butterflies in eastern North America,[32,33] and (c) maximizing population size. Our final goal was to assess the relative benefit of an immediate co-ordinated optimal trinational conservation strategy to restore the eastern North America monarch population compared to an unco-ordinated trinational strategy, single-nation conservation efforts where only one country takes action while the other two countries take no actions, and delayed implementation of an optimal strategy.

Optimal decisions for monarch conservation

Making sequential optimal management decisions in the face of ecological uncertainty is best solved using stochastic dynamic programming.[18,50] Stochastic dynamic programming finds the sequence of conservation actions that maximize benefits (or minimize costs) to reach a conservation objective given the initial state of the system and assuming that the sequence of optimal actions is followed by the decision-maker.

There are several steps to our stochastic dynamic problem: define the conservation objective(s), define the state space, define the action space and estimate the necessary annual budget, define the time horizon, construct a state-action transition model that describes the effects of conservation actions taken on the state variables, define the utility function that quantifies the reward at each time step with respect to the conservation objectives, and finally find the optimal solution(s).[50]

Defining the state space

We define our system at time t using a vector of five states $X_t \in \{b_t, s_t, c_t, n_t, m_t\}$. b_t represents the annual population size of monarch butterflies as measured each December in Mexico. We represent b_t using the area of occupied habitat in Mexico at 1 ha intervals $b_t \in \{0, \ldots, 8\}$, where 8 ha was chosen as the upper limit since this is above the population target set by stakeholders. Because we were interested in calculating the optimal management strategy given an initial population size b_0, we define the initial state $x_0 = \{b_0, s_0, c_0, n_0, m_0\}$ where b_0 corresponds to the latest survey performed for monarchs[51] and starting habitat levels is based on a habitat model given the study period.[26]

The remaining state variables $\{s_t, c_t, n_t, m_t\}$ represent the number of conservation actions that have been taken in each of the regions used by monarchs during their migration, specifically restoration of milkweed in the South (s_t), Central (c_t) and North (n_t) regions, or protection of Oyamel fir (*Abies religiosa*) forest in Mexico (m_t). Only one of these actions can be implemented in each time step, so each of the action states can be applied up to T times, where T is the number of timesteps in the model. Here we set $T = 5$, so each of these state variables can take values in {0, 1,…,5}. We chose to track the management actions performed in each region rather than the actual milkweed habitat in each region because it is computationally advantageous to do so. An alternative (and equivalent) model could track the milkweed habitat in each region.

Defining the action space

In each timestep, an action can be implemented in one of the geographic regions, so the action space was defined as $A_t \in \{a_s, a_c, a_n, a_m, DN\}$, where $a_s, a_c, a_n, a_m \in \{0,1\}$ represent whether an action was taken in South, Central, North or Mexico. The action *DN* represents doing nothing. Actions are implemented in January, immediately after the annual population census,[51] and conservation actions are assumed to happen instantaneously.

Estimating the necessary budget

Estimating the necessary budget for monarch butterfly habitat restoration required a novel approach, as previous cost estimates for milkweed restoration and an overall annual budget for monarch recovery were unavailable. Our methods focused on restoring milkweeds in breeding grounds and conserving forest habitat in Mexico using simulations to identify the point where restoration efforts would outpace annual habitat losses that were previously estimated.[26] We considered annual budgets of \$0, \$1 million, \$10 million, \$30 million, and \$100 million (cumulatively \$0, \$5 million, \$50 million, \$150 million, and \$500 million over the 5-year study).

The cost of restoring milkweed to guide the recovery of monarchs in eastern North America have not previously been estimated or published. We therefore considered a range of estimated per-milkweed costs from \$0.02 to \$0.36. Our per-plant estimates were likely conservative, considering the potential for economies of scale in large-scale projects and diverse restoration methods, such as seed dispersal or planting greenhouse-germinated plugs. When no action is taken (annual budget \$0) there is a continuing decline of milkweed habitat while an annual budget of \$1 million per year for five years barely keeps pace with ongoing milkweed loss resulting in small net gains in milkweed abundance (Figure S1). There were net gains of milkweed over the study period at budgets greater than \$10 million per year for five years and a budget of approximately \$30 million per year for five years could restore most (at \$0.18/milkweed) or all (at \$0.09/milkweed) of the 1.5 billion milkweed plants that have been lost over the past three decades.[26,30,31] We therefore assumed that a cost of \$0.18 per plant and an annual budget of \$30 million would be sufficient to restore milkweed habitat needed for monarch recovery. The number of milkweeds restored in each region was based on the relative availability of public land in each region as a measure of the relative difficulty of implementation of milkweed restoration (Tables S1 and S2); the above estimate translated to annual restorations of 86.5 million milkweeds in the South, 92.3 million in the Central, or 166.7 million in the North (Figure S1).

Forest cover improves the survival of monarchs at the overwintering grounds as it provides cover from extreme weather events that can kill large number of monarchs.[26,28,29] For the overwintering grounds in Mexico, we considered similar annual budgets to determine the proportional forest recovery, aiming for a return to pre-1995 levels with the highest annual investment. In this case, conservation actions would restore 0%, 0.69%, 1.37%, 2.74%, or 5.48% forest cover at the five different budget amounts. We found that a budget of more than \$10 million/year is needed to result in a net benefit of restored forest cover. The exercise revealed 2.74% annual forest recovery (corresponding with an assumed annual budget of \$30 million) as a suitable restoration metric to combat continuing forest degradation (Figure S2) and provide a benefit of reducing mass mortality events in Mexico (Figure S2). Given the scenarios considered above, for our optimization model we assumed an action represents an annual investment of USD \$30 million into one of the geographic regions.

Defining the time horizon

Since the habitat area can change in each time step, the state space of the model increases at each time step, which limited the time horizon of the model. This increase to the decision space is referred to as the 'curse of dimensionality' in stochastic dynamic programming problems. To balance the need to represent a sufficiently long time series with the practicality of performing optimization over large state spaces, we set our time horizon (*T*) for decision-making to 5 years, from 2025 to 2029.

Defining the transition model

The transition model $P(X_{t+1}|X_t, A_t)$ defines the probability of transitioning from state X_t to state X_{t+1}, given that action A_t is implemented. Transitions for the state variables s_t, c_t, n_t, m_t were deterministic and simply record the number of actions taken in the respective region at a given time. For example, an action taken in the South (i.e. $A_t = (a_s, a_c, a_n, a_m, DN) = (1,0,0,0,0)$) increases the value of s_t by 1, i,e:

$$P(s_{t+1}|s_t, A_t = (1,0,0,0,0)) = \begin{cases} 1, \text{if } s_{t+1} = s_t + 1 \\ 0, \text{otherwise} \end{cases}$$

Transitions for variables c_t, n_t, m_t follow the same format. The 'Do Nothing' action ($A_t = (0,0,0,0,1)$) has no effect on variables s_t, c_t, n_t, m_t.

The transition for the population size variable $P(b_{t+1}|b_t, A_t)$ is computed using a stochastic and density-dependent matrix population model. The population model considers events at monthly intervals to capture recolonization of monarch butterflies across three breeding regions in Canada and the United States,[26] the autumn migration of butterflies between the breeding and non-breeding seasons,[52] and a single non-breeding region in the highlands of central Mexico[2] (Figure 1A). The original model[26] was updated with density-dependent larval survival rates[44] that better reflect survival during northward recolonization and to ensure reasonable limits to population growth through density-dependent feedbacks and adherence to an expected carrying capacity. The full code for the population model is available in Github.

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In practice, $P(b_{t+1}|X_t, A_t)$ was computed by simulating the population matrix model 5000 times for each of the possible actions that can be taken at time t. Note that $P(b_{t+1}|X_t, A_t)$ depends on all state variables, since the habitat restoration actions that have been taken in previous timesteps have a continuing effect and will influence the population size b_{t+1}. For T=5 timesteps, the matrix $P(b_{t+1}|X_t, A_t)$ is an 1890×9 matrix.

The full joint probability for the transition model is then: $P(X_{t+1}|X_t, A_t) = P(b_{t+1}|X_t, A_t) \prod_{\theta_t \in \{s_t, c_t, n_t, m_t\}} P(\theta_{t+1}|\theta_t, A_t)$.

Utility functions and management objectives

We used recent publications[53] and current ongoing management position statements[32,33,54] to define three conservation objectives: (a) maximize population viability, (b) maximize the probability of reaching the stated population target for monarch butterflies in eastern North America,[32,33,54] and (c) maximize population size.

The first objective was to maximize population viability (i.e. minimize quasi-extinction probability) of monarchs in eastern North America.[6,26,53] The utility function R_t used to express the first objective was the population viability at a given population size. The population viability follows an asymptotic curve (Figure S3) derived from quasi-extinction estimates for a stable population growth rate (i.e. λ=1) at several thresholds (0.01 ha, 0.05 ha, 0.15ha, and 0.25ha) for a 10-yr time horizon.[53] We used values from Semmens et al.[53] at the 0.25 ha threshold, subtracted the quasi-extinction estimates from 1 to derive viability estimates and fit a 4-parameter non-linear regression (Table S3) to the data to produce an estimate of monarch population viability, R_t, as

$$R_t = 1.005128 + \frac{-1.005208}{1 + \left(\frac{b_t}{0.7253921}\right)^{0.9924441}}$$

where b_t is the overwintering population in hectares at time t (Figure S3).

The second objective was to maximize the probability of reaching a population target of 6 ha endorsed by the US Department of Agriculture's Natural Resources Conservation Service[54] and by the government of Canada.[33] At the time, the 6-ha target was assumed to translate to approximately 225 million butterflies. A more recent estimate suggests 225 million individuals translate into approximately 10 ha.[55] We have taken the conservative approach and used 6 ha, or approximately 132 million butterflies, as the second management objective. The utility function R_t for reaching the population target is zero if the population at time t was below the target and 1 if the population was equal or above the target (Figure S3):

$$R_t = \begin{cases} 0, b_t < 6 \\ 1, b_t \geq 6 \end{cases}.$$

The third objective was to maximize population size and the utility function is simply the population size b_t in ha divided by the population target up to a maximum of 1 (Figure S3)

$$R_t = \begin{cases} b_t/6, b_t < 6 \\ 1, b_t \geq 6 \end{cases}.$$

The objective function for each of these objectives is to maximize the expected sum of rewards over the time horizon, i.e.:

$$max\left(\boldsymbol{E}\left[\sum_{t \in \{1,..,T\}}^{T} R(t)\right]\right)$$

Computing the optimal solution

Our model was a finite-time, non-stationary Markov decision process.[50] The expected value of a state at time t was described by the value function $V^*(X_t)$, which was computed backwards from the terminal timestep.[56]

$$V^*(X_T) = \max_{a \in A} (R(X_T, A_T))$$

$$\forall t \in \{0, T-1\}, V^*(X_t) = \max_{a} \left(R(X_t, A_t) + \sum_{s \in S_t} P(X_{t+1}|X_t, A_t) V^*(X_{t+1})\right)$$

The optimal action for each state at each timestep was the action which maximizes $V^*(X_t)$. The sequence of optimal actions was called the optimal policy, and was computed using:

$$\pi^*(X_t) = \underset{a \in A}{\operatorname{argmax}} V^*(X_t)$$

We solve this finite horizon stochastic dynamic problem using the backward iteration algorithm.[56]

All modeling was conducted in R[57] and computer code for all analyses are provided in a Github repository.

QUANTIFICATION AND STATISTICAL ANALYSIS

Optimal decisions for monarch butterflies

We used simulation to evaluate the consequences of making optimal decisions to reach each of our objectives under a variety of scenarios (Table 1). We started each simulation using the population estimate of 0.9 ha (∼19 million monarchs) measured in December 2023.[51] In each scenario, we considered 500 simulations to draw our inference and for each objective we tallied the outcome and present the proportions of the 500 simulations that resulted in a final population above the population target of 6 ha. In Figures S4–S6 we also show the proportion of the simulations that resulted in a final population above the 5-year mean population size of 2.2 ha[51] and above 1 ha.

First, we present the coordinated, trinational optimal decision plan that determined the optimal action strategy over the forthcoming five years given the stochastic population response to conservation actions; these results represent the current optimal conservation plan for monarchs in eastern North America, given current understanding of the population dynamics of monarchs and their expected response to management interventions. We show the percentage of the simulations that selected each conservation action in each year (Figures 2 and S4–S6). Since these simulations account for stochastic processes and dynamic population responses, we plot the estimated mean and standard error of the population sizes at each time step (Figure 1C).

Next, we determined the value of a coordinated trinational recovery strategy (where an action could be taken in any country and the best location is selected) compared to an uncoordinated trinational strategy (where an action could be taken in any country but which region was randomly selected) and to single-nation conservation plans (where only one country taking conservation action with the other two countries not taking any action), as well as the cost of waiting to implement an optimal conservation strategy with respect to our three objectives (Table 1). In the first scenario, we consider the benefit of a coordinated trinational conservation action strategy for monarchs, an uncoordinated trinational conservation action plan, and taking no action at all. The uncoordinated trinational action plan randomly selected one region to implement actions each year. In the second scenario, we consider the benefit of a coordinated trinational conservation action strategy for monarchs compared to single-nation action plans (Mexico only, Canada only [represented by conservation action taken in the North region only], and USA only [actions taken randomly in the South or Central region only]). The third scenario was to evaluate the cost of waiting to implement an optimal conservation strategy. Under this scenario, we consider the effects of waiting one, two, or three years before implementing an optimal conservation strategy compared to acting immediately.