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Anthropogenic Impacts on Mortality and Population Viability of the Monarch Butterfly

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Abstract

Monarch butterflies (*Danaus plexippus*) are familiar herbivores of milkweeds of the genus *Asclepias*, and most monarchs migrate each year to locate these host plants across North American ecosystems now dominated by agriculture. Eastern migrants overwinter in high-elevation forests in Mexico, and western monarchs overwinter in trees on the coast of California. Both populations face three primary threats to their viability: (a) loss of milkweed resources for larvae due to genetically modified crops, pesticides, and fertilizers; (b) loss of nectar resources from flowering plants; and (c) degraded overwintering forest habitats due to commercially motivated deforestation and other economic activities. Secondary threats to population viability include (d) climate change effects on milkweed host plants and the dynamics of breeding, overwintering, and migration; (e) the influence of invasive plants and natural enemies; (f) habitat fragmentation and coalescence that promote homogeneous, species-depleted landscapes; and (g) deliberate culture and release of monarchs and invasive milkweeds.



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1. INTRODUCTION

Fred Urquhart (164–166) began marking monarch butterflies (*Danaus plexippus*) in 1937 to find out what happens to them after they leave Ontario in southern Canada each September. In 1975, he discovered that monarch butterflies east of the Rocky Mountains fly to the Trans-Mexican Volcanic Belt of central Mexico, where they spend the winter tightly aggregated in oyamel fir trees (*Abies religiosa*) at elevations above 3,000 m (165, 166). Over the next 40 years, this discovery morphed into thriving citizen science initiatives (113) driven by interest in the biology of *D. plexippus*, which has been revealed by a wide range of scientists working on ecology, evolution, behavior, genetics, chemistry, physiology, cell biology, and disease dynamics (1, 18). Each year, between 100 million and 1 billion monarchs migrate from southern Canada and the United States east of the Rocky Mountains to aggregate tightly in central Mexico. Such a remarkable annual coalescence of almost an entire population prompted action to protect overwintering sites in Mexico and to monitor the size of the aggregations each winter because they may serve as an indicator of environmental threats across large spatial areas (20, 26). A similar but more diffuse pattern of migration occurs west of the Rocky Mountains, with overwintering in approximately 400 wooded locations along the coast of California (83, 118, 162).

Regular monitoring of overwintering colony areas in Mexico began in 1993, followed in 1997 by regular counts of monarchs at overwintering sites in California (**Figure 1**). These data show a steady and consistent decrease in overwintering numbers for monarch populations both east and west of the Rocky Mountains (**Figure 1**) (28, 133, 160). Given that monarch larvae are specialist herbivores of milkweeds, particularly of the genus *Asclepias*, and that most monarchs migrate each year to locate these host plants across North American ecosystems (**Figure 2**) now dominated by agriculture, monarch populations face three threats to their viability: (a) loss of milkweed resources for larvae due to genetically modified (GM) crops, pesticides, and fertilizers; (b) reduced nectar resources from flowering plants to fuel adult migration; and (c) degraded overwintering forest habitats due to commercially motivated deforestation and other economic activities. Secondary threats to monarch population viability include (d) climate change effects on the distribution and abundance of milkweed host plants and the dynamics of breeding, overwintering, and migration;

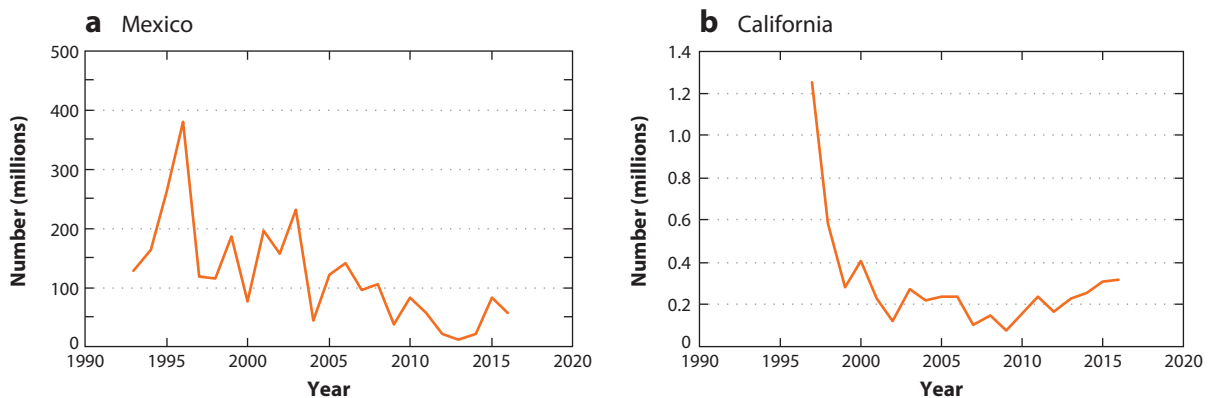


Figure 1

(a) Number of monarch butterflies (*Danaus plexippus*) (millions) overwintering in Mexico since the winter of 1993/1994, estimated as total occupied forest area [hectares (ha)] (133) in December multiplied by the estimated median density of 21.1 million/ha (34, 160, 173). (b) Number of monarch butterflies (millions) overwintering in California in December since the winter of 1997/1998 (from <http://www.westernmonarchcount.org/>) (118).

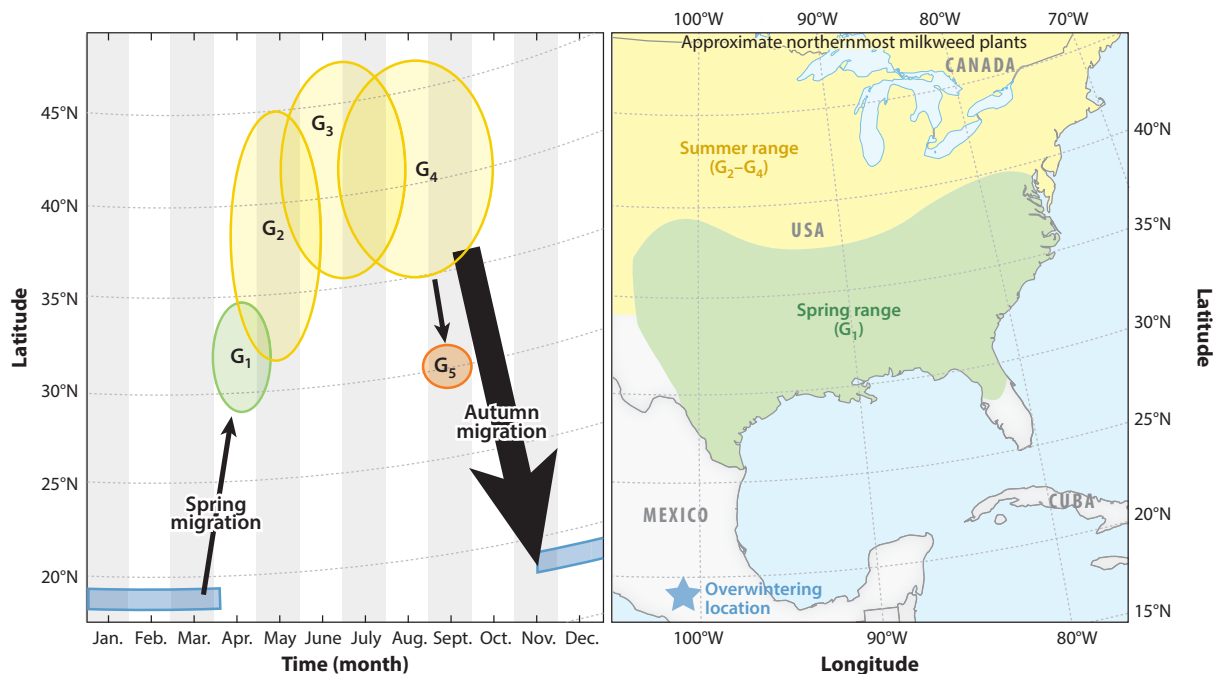


Figure 2

Distribution of monarch butterfly (*Danaus plexippus*) overwintering (starred location on the map) and five annual generations (G_1 – G_5) in eastern North America against latitude ($^{\circ}$ N) and time (month). Spring (G_1) and summer generation ranges (G_2 – G_4) are determined from patterns of monarch voltinism (97), cardenolide fingerprinting (99), and wing isotope ratios (58–60, 170), with recent evidence for G_5 in late summer in the southern United States (10, 138).

(e) the influence of invasive plants and natural enemies; (f) habitat fragmentation and coalescence that promote homogeneous, species-depleted landscapes; and (g) deliberate culture and release of monarchs and invasive milkweeds.

Monarch butterflies are partial migrants (40), as not all migrate (48, 171). Most of the population east of the Rocky Mountains shows clear annual migration and tight aggregation each winter in the mountains of central Mexico (**Figure 2**). West of the Rocky Mountains, monarch migratory and overwintering behaviors are more typical of the partial migration in monarchs elsewhere (48, 96, 171). Monarchs also occur throughout the Caribbean islands, in Central America, and in nonforested regions of northern South America, where they show similar movement behaviors with both migratory and nonmigratory life histories. The human introduction of milkweed host plants of monarch larvae enabled the nineteenth century range expansion of monarch butterflies across the Pacific Ocean to Hawaii, Samoa, Fiji, New Caledonia, New Zealand, and Australia (120, 167, 184, 185) and the more recent colonization across the Atlantic Ocean to the Canary Islands, southern Spain, Portugal, and Morocco (55, 120).

This movement across different spatial and temporal scales generates considerable overlap between monarchs and ecosystems affected by agriculture, forestry, and land-use patterns that generate habitat fragmentation and facilitate the establishment of invasive species. Migratory monarch populations link agricultural, forest, urban, rural, and natural ecosystems and provide an assay of performance through coalescence into aggregated overwintering locations in central Mexico (72, 115, 173). A similar but less understood pattern occurs in monarchs west of the Rocky Mountains (54).

Monarchs are familiar across North America because adults and larvae are conspicuously colored and easy to observe. This has generated considerable interest in monarchs as a learning tool and for citizen science activities that promote environmental awareness (113). Such interest culminated in a 2014 petition to protect monarch butterflies with US Endangered Species Act legislation and presidential action in 2015 to promote the health of pollinator networks (126).

Here, I review the evidence of anthropogenic impact on monarch butterflies to integrate information about threats to monarch mortality and viability as indicators of environmental stress over large spatial scales.

2. MILKWEED RESOURCES: LOSSES FROM GENETICALLY MODIFIED CROPS, PESTICIDES, AND FERTILIZERS

The abundance and migratory behavior of monarch butterflies both east and west of the Rocky Mountains are a product of the diversity and abundance of larval milkweed host plants of the genus *Asclepias*. Approximately 130 species occur throughout North America (57, 174). Postcolonial human activity such as deforestation and tillage practices (167) may have benefitted the highly modular common milkweed, *Asclepias syriaca*, and the showy milkweed, *A. speciosa*. Plowing may have increased their abundance in agroecosystems (98) before the use of effective herbicides to control weeds. However, precolonial habitat management by Native Americans may have also benefitted *Asclepias* diversity and abundance through agricultural clearing, bison management in grasslands, and the use of fire as a management tool (47).

North American agriculture has changed dramatically with the advent of GM crops to target two primary problems: losses to insect herbivores and interspecific competition with other plants (weeds). Each year, monarch butterflies traverse a North American landscape dominated by human activity, especially agricultural activity. After flying from the Transvolcanic-Guatemalan Conifer Forest in Mexico, eastern monarchs fly north each spring and use milkweed resources distributed across six biomes in the following order (132) (**Figure 2**): Gulf Coast thornscrub, Gulf Coast grassland, eastern deciduous and evergreen forest, semidesert grassland, Great Plains grassland, and temperate deciduous forest. Agriculture dominates the landscapes of the Great Plains grasslands and temperate deciduous forests, and extensive deforestation of temperate deciduous forests in the nineteenth century was suggested to increase milkweed abundance and hence monarch abundance (167). Cotton and wheat are the dominant crops in the Great Plains grasslands (and in eastern deciduous and evergreen forests), and both soybean and maize crops dominate eastern Great Plains grasslands and western temperate deciduous forests.

The area planted with maize in June 2016 increased by 7% to 38.08 million hectares (ha) (94.1 million acres) and was the third-largest planted area since 1944. In the same year, soybean increased by 1% to 33.87 million ha (83.7 million acres) and cotton increased by 17% to 4.05 million ha (10.0 million acres). With the inclusion of 20.56 million ha of wheat, this represents 15% of the area of all six biomes (132) that monarchs traverse each year east of the Rocky Mountains.

With the use of herbicide-tolerant (HT) crops, agriculture has shifted from conventional tillage to no-till management. Benefits include higher retention of water and organic material, less disturbed soil ecosystems, and reduced compaction and soil erosion (90). The life history of monarch butterflies in North America provides us an opportunity to use them as an indicator of human impact—the “canary in the cornfield” (20).

2.1. Effect of *Bt* Crops on Monarch Butterflies

In 1999, Losey et al. (95) showed in greenhouse experiments that pollen from GM maize plants expressing crystalloproteins from the soil bacterium *Bacillus thuringiensis* (*Bt*) was toxic to monarch

larvae; mortality increased by as much as 44%. Similarly, field experiments showed that *Bt* maize pollen deposited on potted plants is toxic to first-instar monarch larvae (84).

These results prompted a strong response from a wide range of constituencies that questioned the adequacy of risk assessment by the US Environmental Protection Agency (EPA). A controversial meeting arranged in November 1999 that concluded *Bt* maize had little effect on monarch butterflies prompted the EPA to request more research on the impact of *Bt* maize on monarchs (119) and to establish a Scientific Advisory Panel to review the evidence (109). By most scientific standards around the world, the response was hugely successful, with six peer-reviewed papers (76, 110, 122, 144, 149, 186) and a commentary (143) published in the *Proceedings of the National Academies of Science USA (PNAS)* in an expedited process to meet EPA regulatory deadlines.

The conclusion was that risk (R) to monarch butterflies is negligible because the product of probability of exposure (P_e) \times the probability of toxicity (P_t) is so low (144). For pollen-specific expression of *Bt* crystalloproteins in event *Bt176*, $R = 0.0038$, and for constitutively expressed events *Bt11* and *Mon810*, $R = 0.00012$ for the state of Iowa, with the highest estimate for P_e among 16 maize-growing states in the United States and 1 Canadian province. This value was then modified for Iowa and monarchs exposed to event *Mon810* with a different measure of P_e to give a risk of 0.0124 (50). Despite an increase in risk of more than two orders of magnitude, Dively et al.'s (50, p. 1124) conclusion remained that "it is likely that *Bt* corn will not affect the sustainability of monarch butterfly populations in North America."

Sadly, none of this risk assessment makes any sense at all unless it is put into the context of spatial and temporal variation in the life history of monarch butterflies exposed to these crops (109). No research has yet been conducted to illustrate the impact of additional mortality from *Bt* crops on the viability of exposed monarch populations as they move across the North American landscape each year. Part of the reason for this lack of understanding is that the *Bt* crop issue has been eclipsed by the use of herbicide-resistant GM crops and their impact on nontarget species. Another reason is the lack of larger-scale, multidimensional examinations of the impact of agricultural technologies on mobile species such as the monarch butterfly. All six *PNAS* papers asked proximate questions about exposure and toxicity to target a standard toxicological risk assessment procedure, but none of them put these questions into the ecological context of life table survivorship, key mortality factors that may or may not be density dependent, fecundity analyses across multiple annual generations, or the impact on migration and overwintering (Figure 2).

One consequence of this response to the impact of GM crops on monarch butterflies was the realization that agricultural fields in the midwestern United States contain large amounts of milkweeds and generate a large number of monarch butterflies each year (121, 123).

2.2. Effects on Milkweeds of Herbicides with Herbicide-Tolerant Crops

Across the regions of North America used by monarch butterflies, the adoption of GM crops such as maize, soybeans, and cotton has increased rapidly since 1996 (Figure 3). In 2016, between 80% and 95% of the area planted with these crops expressed *Bt* crystalloproteins, herbicide tolerance, or both as stacked constructs.

Since the adoption of HT crops, there are now 252 species of plants that are resistant to herbicides globally, with evolved resistance to 23 of the 26 known herbicide sites of action distributed among 161 different herbicides (75). HT weeds occur in 91 crops across 68 countries. While resistance to photosystem II (PSII) inhibitor herbicides such as atrazine began to appear in the early 1970s, resistance to 5-enolpyruvylshikimate-3-phosphate (EPSP) synthase inhibitors such as glyphosate has increased in concert with the increase in adoption of HT Roundup Ready maize, soybean, and cotton in the United States since they were approved for planting in the United

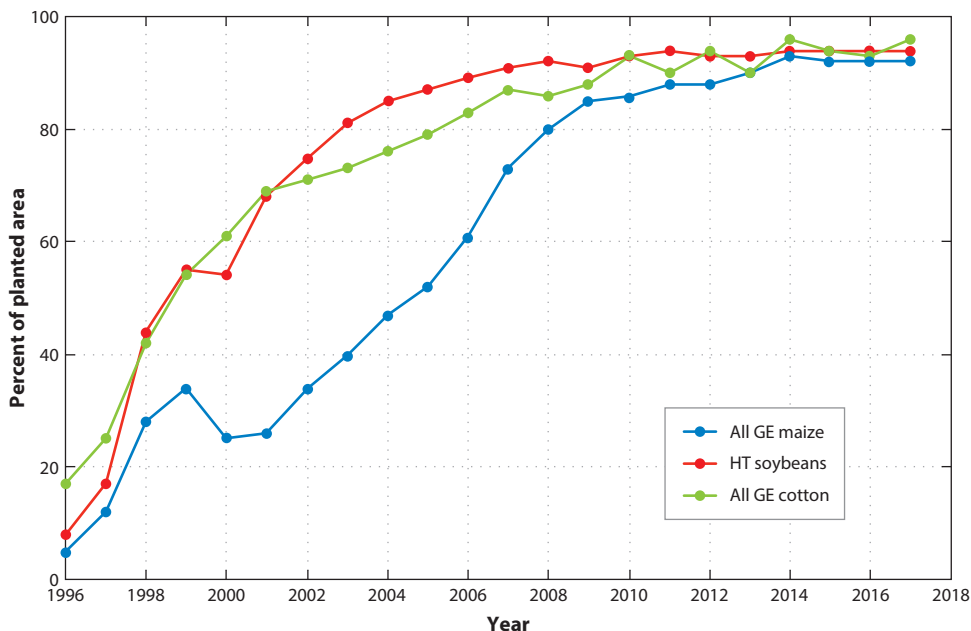


Figure 3

The percent of planted area of genetically engineered (GE) maize (corn), soybean, and cotton in the United States from 1996 to 2016. Data include the increasing trend for stacked constructs, especially *Bt* and HT expression. Data from the United States Department of Agriculture Economic Research Service (<https://www.ers.usda.gov/data-products/adoption-of-genetically-engineered-crops-in-the-us/recent-trends-in-ge-adoption/>), used with permission from Seth Wechsler. Abbreviations: *Bt*, plants that express *Bacillus thuringiensis* crystalloproteins; HT, herbicide tolerant.

States in 1996 (**Figure 3**) (12, 75). US farmers now apply approximately 1.0 kg/ha of glyphosate on all cultivated cropland, and this has generated new problems with the appearance of so-called superweeds such as waterhemp and Palmer amaranth (*Amaranthus* spp). Part of the reason for the proliferation of these superweeds is that herbicide use facilitates extensive no-till agriculture with some associated benefits that include higher-functioning soil ecosystems, carbon sequestration, and reduced management costs that are balanced by higher seed and herbicide costs. However, no-till land management also favors the life history of dioecious *Amaranthus* species (108), and waterhemp is now the first US weed to develop three-way multiple resistance to acetolactate synthase-, PSII-, and protoporphyrinogen oxidase-inhibiting herbicides in addition to resistance to glyphosate (an EPSP synthase inhibitor). Thus, the new generation of crops will incorporate multiple HT pathways and the use of both preemergence and postemergence herbicides to eliminate the economic costs of weed competition, and selection for resistance will become even more intense. It is relevant to point out that, at the same time that these technologies have been developed and deployed, US maize yields increased independently by 27% between 1984 and 2013 through increases in incident solar radiation known as solar brightening (161).

From 1999 to 2009, low densities of *A. syriaca* occurred in 51% of Iowa maize and soybean fields and dropped to 8% of similar fields, and the area occupied by *A. syriaca* within crop fields was reduced by approximately 90% (74). Widespread use of glyphosate-resistant maize and soybean and postemergence application of glyphosate were considered to cause the milkweed decline. Balance equations (151, 180) that reflect monarch life history (**Figure 2**) predict plant removal

could reduce lifetime potential fecundity of monarchs by approximately 30%. A common consequence of anthropogenic impact on metapopulation persistence is its reduction due to habitat fragmentation and removal of resources from the landscape matrix (151, 183).

North American habitats that generate monarchs from milkweeds include crop fields, pastures, old fields, roadsides, parks (local, state/provincial, and federal), backyards, and land set aside from farming in the Conservation Reserve Program. *A. syriaca* is the most abundant and widely distributed milkweed in these habitats across the northern United States east of the Dakotas and in southern Canada (98, 174), and it accounts for 92% of the monarch butterflies that overwinter in Mexico (98, 99). Approximately 50% of overwintering butterflies fed as larvae on milkweeds in the US midwestern states of Iowa, Illinois, Indiana, Kansas, Michigan, Minnesota, Missouri, Nebraska, North Dakota, South Dakota, Ohio, and Wisconsin (170), that is, habitats dominated by maize and soybean fields. Pleasants & Oberhauser (123) estimated that milkweeds have decreased in the Midwest by 58% between 1999 and 2010, coinciding with the increased use of glyphosate herbicide and the widespread adoption of GM herbicide-resistant maize and soybeans (141). Using data from their citizen science Monarch Larva Monitoring Project for monarch eggs per plant, Pleasants & Oberhauser (123) estimated an 81% decrease in monarch production in the Midwest from 1999 to 2010. The authors argue that the extensive loss of agricultural milkweeds is responsible for this decline and that there is a strong, significant relationship between monarch production in the Midwest and the size of the subsequent overwintering areas in Mexico. In 2012, Pleasants (121) corrected these estimates to a monarch decline of 88%. Overall, Pleasants (121) estimated that 98.7% of milkweeds were eliminated from agricultural fields with herbicide between 1999 and 2012. It has been estimated that 0.86 billion milkweed ramets have been lost from agroecosystems, with 1.34 billion ramets remaining for monarchs that require >1.8 billion more ramets to achieve viable overwintering densities in Mexico of 126.6 million butterflies (160).

An annual, spatially structured matrix model (59) predicts monarch population declines of 14% and a quasi-extinction probability of >5% below a viable threshold within a century and compares simulations for overwintering habitat loss, extreme weather events, and loss of milkweed habitat. Monarch abundance was more than four times more sensitive to milkweed loss than to the other two hypothesized causes of declines. A Bayesian multivariate, auto-regressive, state-space model subsequently estimated a more alarming quasi-extinction risk for the eastern population of North American monarch butterflies: 11–57% over 20 years (145).

Although we know that *A. syriaca* is declining dramatically in agroecosystems across North America, we do not know the fate of other milkweed species. Monarchs can use any of the approximately 130 species of *Asclepias* in North America (57, 174), and the impact of host plant choice by ovipositing females is largely unknown.

2.3. Influence of Pesticides on Monarch Butterflies

The most widely used insecticides in the world are neurotoxic neonicotinoids, such as imidacloprid, which are routinely applied as seed dressings to provide systemic, prophylactic protection to all plant tissues against arthropod pests (68). This includes their presence in nectar and pollen (68). Neonicotinoids spread from target plants because they are water soluble and spread in planter dust when seeds are sown. Not surprisingly, *A. syriaca* on the edges of maize fields in South Dakota had an average of 1.14 parts per billion (ppb) of the neonicotinoid clothianidin and a maximum of 4 ppb in a single ramet (117). Although toxicity assays revealed that clothianidin has an LC₅₀ of 15.63 ppb, negative, sublethal effects on weight and development time of first-instar monarch larvae occurred at 1 ppb, with significant effects at concentrations as low as 0.5 ppb. Imidacloprid added to soil in which the milkweed *A. curassavica* was translocated was concentrated in the flowers

to 6,030 ppb after a single treatment (88). Early-instar monarch larvae on untreated *A. curassavica* plants showed significantly higher survivorship than did larvae on plants given either one or two soil treatments with imidacloprid, and no larvae survived more than 14 days of exposure.

Approved barrier treatments for mosquito control with the synthetic pyrethroid permethrin were toxic to both larvae and adults of monarch butterflies associated with sprayed plants of *A. syriaca* in Minnesota (111). More than 95% of monarch larvae were killed at 50%, 10%, 5%, 2%, and 1% dilutions, and even 0.5% and 0.1% dilutions of the operational dose of permethrin significantly reduced larval survivorship compared with controls. Development times of larval survivors were increased, and the authors estimate that toxic effects will persist for at least 3 weeks after spraying.

In addition to these widely used pesticides, many preparations of different *Bt* strains are available for application against insect pests on agricultural, ornamental, and forestry products. DiPel is a widely available example of a *Bt* preparation, and Brower (17) warned against using it to spray 2,195 ha of oyamel fir forest against larvae of the geometrid moth *Evita hyalinaria blandaria* (148), which defoliates oyamel fir trees in the overwintering location of monarch butterflies in Mexico (148).

2.4. Ecosystem Eutrophication

Cascade strength through multiple trophic levels of a milkweed-based system was strongly affected by manipulated soil nutrients (104). Effects varied among 16 *Asclepias* species in ways that suggest the trade-offs between growth and differentiation in plants will be strongly influenced by cultural eutrophication.

High foliar nitrogen concentrations in the milkweed *A. curassavica* resulted in an interaction between nitrogen and leaf cardenolides that increased the toxicity of cardenolides and decreased growth rates of monarch larvae (157, 159). But this effect was not detected in two additional *Asclepias* species, *A. syriaca* and *A. incarnata*, with much lower leaf cardenolides, or from soil applications of phosphorus to all three species. In similar experiments with *A. curassavica* and nitrogen and phosphorus soil fertilizers (159), monarch larvae sequestered cardenolides less effectively from fertilized plants and showed lower growth rates and weights. In *A. syriaca*, increased nitrogen fertilizer caused phosphorus limitation in leaves, but not in monarch larvae (158). However, application of phosphorus fertilizer increased the production of latex in *A. syriaca* leaves, and it is well known that increased latex reduces monarch larval performance, especially for early-instar larvae (179, 181, 182). A subsequent study of six *Asclepias* species that included manipulations of arbuscular mycorrhizal fungi (AMF) found additional complex effects of nitrogen and phosphorus fertilizer application (156). Tolerance of milkweeds to monarch larval herbivory and both cardenolide and latex expression were affected by AMF treatments. Tolerance to herbivory also increased with leaf phosphorus, and both cardenolide and latex expression increase with leaf nitrogen.

3. NECTAR RESOURCES: LOSS OF RICHNESS AND ABUNDANCE

Monarch butterflies require flower nectar to generate the lipids that fuel flight, reproductive behavior, and successful overwintering. Nectar resources are especially important during migration; each autumn, monarch butterflies accumulate considerable fat stores from ingested nectar (4, 11, 22, 24, 30, 63, 64, 101). In November, monarchs arriving at overwintering sites in Mexico had a mean lipid mass of 133 mg, but by mid-March this had dropped to 56 mg—a loss of 58% during overwintering (4). By the time monarchs reached the southern United States in April, lipid mass had dropped to 26 mg. Although floral nectar is the only known precursor source of these lipids, it is surprising that we know little about the distribution, abundance, and diversity of the flower

resources used by monarchs across North America (22, 27, 136). The few field observations (22, 27, 136) indicate that migrating monarchs feed at autumn-flowering Asteraceae. Drought can influence nectar availability for monarchs. For example, irrigated *Liatris mucronata* flowers supported nectaring monarchs with 80 mg of lipid, whereas monarchs at flowers of drought-stressed *Verbesina virginica* had significantly less lipid at 40 mg (22).

In addition to the sugars ingested, adult monarchs also seek out some flower species as a source of pyrrolizidine alkaloids (PAs), which they sequester for both reproduction and defense (16, 66). PAs were found in monarchs overwintering in both California and Mexico (85, 150). In California, PA profiles altered once monarchs had access to the invasive, PA-producing asterid *Delairea odorata* (formerly *Senecio mikanioides*), which has invaded the coast of California from its native South Africa. The principal PA-containing plant families include Asteraceae, Boraginaceae, Apocynaceae, and Fabaceae, and the autumn-blooming species in the asterid tribe Eupatorieae may be especially valuable as sources of both nectar and PAs for monarchs (85).

Some evidence exists for a weak trade-off between lipid storage and immune defense against pathogens in migratory monarchs so that lipids decrease with increased phenoloxidase activity (140), although the relationship was not significant for monarchs infected with the specialist protozoan pathogen *Ophryocystis elektroscirrha* (*Oe*).

While monarchs have been decreasing in abundance across the North American landscape, so too have other pollinators been decreasing in abundance and diversity (31). Although the widespread use of herbicides in agroecosystems is likely to reduce both plant and pollinator abundance and species richness, other factors, such as fire suppression, also play important roles. Frequent, prescribed fires increased the abundance of nectar resources for monarch butterflies (136). During the autumn migration, 70% of 2,701 observations of monarch nectaring indicated that monarchs nectared on *Bidens aristosa*, with the remaining observations distributed among *Eupatorium serotinum*, *Solidago* spp., *Vernonia baldwinii*, and approximately 30 additional plant species. Significantly more monarchs were seen nectaring in plots that had been burned than in unburned controls, especially in the first year after a burn.

4. OVERWINTERING FOREST HABITAT: THREATS

Temperature and water availability are the most important environmental characteristics influenced by trees on which monarchs aggregate during winter. In Mexico, forest cover and a contiguous canopy are necessary to modify temperature extremes in the forests of oyamel fir, *Abies religiosa*, within which monarchs overwinter at elevations of approximately 3,000 m (3, 7, 19, 35, 37, 101, 165, 172). The closed oyamel fir canopy reduces temperature extremes, which is thought to be important for minimizing lipid use during overwintering so that monarchs do not waste lipids from unnecessary thermoregulatory behaviors (101). These benefits have been described as the umbrella and blanket effects of the closed canopy to reduce temperature fluctuations and the hot-water-bottle effect of heat stored in oyamel fir tree trunks (7, 29, 172). High-quality, intact, closed-canopy forests with mature trees ensure monarchs have sufficient lipid reserves to fuel remigration back to the southern United States in the spring. This fuel economy is especially important given that nectar sources in the mountains of central Mexico are scarce during monarch overwintering from November to March (172).

In Mexico, adiabatic cooling of air as it rises up the mountains to lower pressures condenses moisture on trees and butterfly bodies, making it available for consumption by monarchs. Monarch butterflies also fly to high-elevation streams near overwintering locations to ingest water. Similar processes occur in overwintering locations in California in which moisture from westerly wind systems laden with water from the Pacific Ocean condenses on overwintering trees (92, 93).

4.1. Mexico

Monarch butterflies overwintering in Mexico are protected within the Monarch Butterfly Biosphere Reserve (MBBR), located in the Trans-Mexican Volcanic Belt of mountains that straddle the states of Michoacán and México in central Mexico (128). Oyamel fir forests occur in the Trans-Mexican Volcanic Belt between elevations of 2,400 and 3,600 m at latitudes of 19–20°N, and existing forests are small remnants of more extensive forests lost to deforestation by humans (148). The MBBR is a World Heritage Site designated as a UNESCO Biosphere Reserve (163), and current Mexican environmental legislation defines a core zone of 13,551 ha surrounded by a buffer zone for a total reserve area of 56,259 ha.

Although part of the overwintering locations in Mexico have been protected since 1986, the combination of the complex social structure of the local *ejido* communities and the absence of adequate enforcement infrastructure resulted in an absence of sustainable forest management between 1920 and 2000 (128). Despite the existence of logging bans in the high-elevation oyamel fir forests, considerable illegal logging, some legal logging, forest fires, agricultural clearing, tree extraction for domestic uses, winter storm damage, and natural mortality of fir trees resulted in measurable forest loss and habitat degradation (78–80, 128). With the creation of the Monarch Butterfly Conservation Fund in 2002, illegal logging was reduced by compensating *ejidos* for lost earnings in the core MBBR zone (80, 128). However, between 1986 and 2012, 4,300 ha of protected oyamel fir forest were lost or altered, mostly from human activities, including 8% of the MBBR (128). Between 2001 and 2012, both large-scale and small-scale logging occurred throughout the MBBR, so that a total of 1,254 ha was deforested, leaving less than 10% of the canopy intact (169). A further 925 ha were degraded owing to reduced canopy cover, and 122 ha were influenced by climate. Of the total 2,179 ha of affected MBBR forest, 69% was caused by large-scale logging and 25% by small-scale logging, although efforts to enforce forest protection increased in effectiveness between 2007 and 2012 (169).

4.2. California

Monarch butterflies overwinter in coastal trees spanning 1,000 km from Mendocino County in Northern California to Baja California in northwestern Mexico. Monarchs spend the winter at more than 400 locations subject to a wide range of state, county, local, and private measures for their protection (83, 118). Despite some legislated and voluntary protection, overwintering monarch numbers are decreasing in California in concert with the decreases in Mexico (**Figure 1**).

There is substantial variation among the origins of monarchs at overwintering locations in California (175). Such variations in origin are consistent with the suggestion that monarchs in California are simply dispersing rather than migrating (171) and with the bimodal orientations of spring migration flights shown by marked monarchs from overwintering locations in California (105). Monarchs in the west may be using riparian corridors to navigate and move between overwintering resources on the coast and inland, elevated breeding resources that have milkweeds (48). These riparian corridors could ensure the availability of nectar resources during migration. The availability of water resources across seven western states as measured by the Palmer Drought Severity Index predicts monarch abundance patterns (153). Combining these data with temperature conditions and the phenology of milkweed host plants in these same states indicates that monarchs overwintering in California are not local recruits from coastal breeding habitats; instead, variation in moisture availability in central California predicts overwintering abundance.

Like oyamel fir forests in Mexico, overwintering habitats in California moderate temperature extremes and provide moisture for overwintering monarchs to prevent desiccation (39, 92, 93,

94). The low-elevation sites at 60–90 m face south, southwest, or west so that monarchs can bask effectively and benefit from warming through solar radiation (94). Winter flowers provide valuable nectar resources and moisture for overwintering monarchs and generate fuel for spring migration to find milkweed resources (150, 162). In California, monarchs roost on introduced blue gum eucalyptus (*Eucalyptus globulus*), native Monterey pine (*Pinus radiata*), and native Monterey cypress (*Hesperocyparis macrocarpa*) and less commonly on introduced red gum eucalyptus (*Eucalyptus camaldulensis*), native western sycamore (*Platanus racemosa*), native coast redwood (*Sequoia sempervirens*), and native coast live oak (*Quercus agrifolia*) (118). Researchers thought that monarchs in California prefer to overwinter on *Eucalyptus* species introduced from Australia because the trees have become so abundant, especially in Southern California (69), and because monarchs use eucalyptus at 75 % of overwintering sites in California (61). However, early observations demonstrate that monarchs overwintering in California aggregate on native conifers, especially Monterey pine (135), and recent observations show that monarchs aggregate significantly more than expected on native conifers when able to choose between native trees and *Eucalyptus* species (69). Thus, the prevalence of *Eucalyptus* in California is probably not a cause of the decrease in monarch numbers at overwintering locations.

The spectacle of clustered monarchs overwintering in Monterey pines at Pacific Grove resulted in early versions of ecotourism so that today two inns are located near the Monarch Grove Butterfly Sanctuary. The sanctuary was created in the mid-1990s to mitigate loss of overwintering habitat from economic development in Pacific Grove—a town that called itself Butterfly Town USA because monarchs once spent the winter there in large numbers. The high economic value of land along the coast of California suggests that a component of monarch population decline in California could be a negative outcome of land development. However, I can find no research on possible links between monarch overwintering and development, even though the Xerces Society has spent many years in California working to mitigate the loss of overwintering monarch habitat (83, 118).

5. CLIMATE CHANGE

By 2030, altered temperature and rainfall patterns are predicted to reduce overwintering forest areas in Mexico by 69% and could completely eliminate the oyamel fir ecosystem by the end of the century (128, 137). Climate change may also influence the severity of winter storms that cause substantial mortality to butterflies and fir trees during monarch overwintering in Mexico (25). In addition to having impacts on overwintering resources, climate change is also affecting other plant resources of monarchs. Within the genus *Asclepias*, the *Incarnata* clade is more likely than the *Syriaca* clade to respond to the effects of climate change by changing to a different defensive phenotype, because it shows less evolutionary inertia of defensive traits such as cardenolides (129).

Climate change effects are complex. For example, milder North American winter temperatures, in combination with planting of introduced milkweeds such as *A. curassavica* and early-spring growth of native species such as *A. perennis*, have increased year-round breeding in the southern United States (81). Winter-breeding monarchs have higher rates of infection by the protozoan pathogen *Oe* than migratory monarchs do, and it is thought that migration may be a mechanism for escaping such high parasite loads (5, 6). Resident, year-round-breeding monarchs in south Florida had the highest prevalence of *Oe*, followed by western monarchs in California, which fly shorter distances than eastern monarchs, which fly much longer distances to Mexico and have the lowest prevalence of *Oe* (5).

A Bayesian hierarchical analysis of 40 years of flight records across an elevational transect in Northern California and overwintering data were used to show negative population trends with

time (54). Declines were more pronounced during early-season spring breeding, but warmer temperatures and increased precipitation had positive effects. However, no relationship with dynamics was found for eastern monarchs and changing climatic conditions did not explain the decline in monarch overwintering numbers in California (**Figure 1**). Similarly, Zalucki et al. (178) found no evidence for an effect of climate on the decline of eastern monarch butterflies (**Figure 1**) using a CLIMEX model based on temperature and rainfall data. Their model could not address climate impacts on monarch mortality during spring and autumn migrations and at overwintering sites.

However, the year-to-year variation in monarch numbers from the six regions of eastern North America that generate monarchs does covary with climate on the basis of the Southern Oscillation Index and regional temperature and precipitation data (58). Temperature and precipitation influence larval development rates and host plant condition and are especially important in the US Midwest, which produces 38% of monarchs that overwinter in Mexico (58).

There are interactions between climate and monarch performance across its range in North America. A Poisson regression model (187) for spring monarch arrivals and host plant use in Texas and Ohio showed that both high spring rainfall and intermediate temperatures result in early monarch arrival in Texas and highest population growth in Ohio (141). Climate in Ohio does not influence the timing of arrival, but warmer summer temperatures tend to generate higher monarch abundance. These effects appear to be mediated by host plants such as *A. syriaca*, in which elevated temperatures increase, and water stress decreases, plant growth (43). However, across a latitudinal gradient in Wisconsin, more northern *A. syriaca* plants show larger growth responses to temperature and are more resistant to water stress than more southern plants. Both temperature and water stress, especially when combined, increased leaf nitrogen, which resulted in faster growth rates for monarch larvae.

5.1. Altered Spatial and Temporal Distributions of Milkweeds

The distributions of *Asclepias* milkweeds are expected to shift northward in North America under both moderate (1–3°C increase) and severe (2–6°C increase) climate change scenarios (91). Maximum entropy species distribution models predict that monarch summer-breeding areas will become less suitable for both milkweeds and monarchs under a climate change scenario. Thus, monarchs will expand their range northward while they migrate across less suitable habitats. Lemoine (91) predicts an especially dramatic northward shift for *A. viridis* under moderate climate change. Such a change might have a disproportionately large impact on the spring migration of monarch butterflies because they would have much farther to fly to reach this resource at a critical time when their fat resources to fuel flight are at their lowest.

5.2. Effects of Elevated CO₂

Experimentally elevated CO₂ increased the growth of five genotypes of *A. syriaca* and also both leaf toughness and latex expression (168). However, elevated CO₂ resulted in decreased leaf cardenolides that varied among *A. syriaca* genotypes, although cardenolide induction by monarch larvae was not affected.

5.3. Air Pollution

Both milkweeds and monarchs are affected by air pollutants such as ozone. Ozone concentration and exposure time influenced soluble carbohydrates, amino acids, cardenolides, and phenolics of the tropical milkweed, *A. curassavica* (15). Fifth-instar monarch larvae had higher growth rates and relative consumption rates on ozone-treated plants of both *A. curassavica* and *A. syriaca*, perhaps

because ozone increased amino acid concentrations in both plants (14). The milkweed *A. exaltata* is used as a sensitive bioindicator of ozone damage in the Great Smoky Mountains National Park in the southeastern United States, where 74–79% of observed plants showed evidence of ozone injury (41). It is not known what impact this injury might have on monarch larval herbivores under field conditions.

Nothing is known about the effects on monarchs of other important air pollutants such as NO_x and SO_x compounds or volatile organic compounds and acidic precipitation, although one should expect monarchs, milkweeds, and nectar resources to be affected.

5.4. Changes to Abiotic and Biotic Cues Used by Monarchs for Migration

Data on the degree-day accumulation for development by eggs, each larval instar, and pupae to produce monarch adults, as well as the degree days required for egg maturation in adult females (176, 177), have been used extensively in niche modeling exercises for monarch generations in North America (42, 153, 184, 185, 178) and fit the spatial distribution of voltinism patterns described for monarch generations (42, 97) (**Figure 2**). However, the measured degree-day development was based on monarchs in Australia that tend to be nonmigratory. Thus, it is reasonable to ask whether these physiological development times are representative of migratory monarchs in North America and whether there might be evolutionary shifts in degree-day accumulations through the monarch life history that are influenced by climate change or by variation in physiological performance among milkweed host plants (106). We know that monarch larval performances vary among different species of *Asclepias* host plants (53, 89, 142) and that monarch larvae can increase development rates by basking to achieve higher degree-day accumulations (130, 146).

As monarchs progress through their annual life-history cycle (**Figure 2**), they occupy the same niche that shifts spatially and temporally across North American landscapes during breeding. However, the niche changes during migration and overwintering, and these changes are triggered by both abiotic and biotic cues, such as day length, temperature, and both larval and adult access to host plants (10). Breeding niches are projected to move northward under climate change scenarios over the next 50 years, especially at the northern extent of the current range (10). Successful spatial shifts, from the perspective of monarch population viability, will require that milkweed host plants also track changing conditions in a similar manner (91).

Warming trends may even have disastrous effects on monarch orientation during migration. Recent research has shown that cold temperatures trigger the reversal of an antenna-dependent, time-compensated sun compass (71). Thus, without exposure to cold temperatures, autumn migrants use a time-compensated, sun compass to navigate south to overwintering sites in Mexico. This compass is necessarily reversed when monarchs are exposed to cold overwintering temperatures, so that spring migrants fly north. Perhaps monarchs can compensate for temperature changes by supplementing their temperature-dependent sun compass with their magnetic compass (70).

Monarch butterflies respond to photoperiod, temperature, and the availability of milkweed host plants, synchronizing their physiological status with the requirements of overwintering, migration, and breeding (67). These physiological states are controlled by hormones (8, 77) so that monarchs reduce trade-off conflicts between reproduction and directed flight during migration, or between lipid accumulation and use during migration and overwintering. Overwintering monarch females from Mexico that were exposed to milkweed at increasing day lengths showed significantly higher ovarian development than did monarchs given access to milkweeds at constant day length. Ovaries matured significantly faster in females given access to both males and milkweeds than in females given only milkweeds or only males, compared with control females with access to neither males nor milkweeds (67). These experiments suggest that altered temperature regimes across North

America in combination with altered phenologies of milkweeds and the presence of nonnative milkweeds will affect the physiology and dynamics of monarch migration.

6. INFLUENCE OF INVASIVE PLANTS AND NATURAL ENEMIES

Monarchs increased their range across the Pacific Ocean in the nineteenth century and across the Atlantic Ocean in the twentieth century owing to the introduction of milkweeds by humans into most of the larger islands of the Pacific and into islands in the Atlantic and into Europe and North Africa. Seeds of *A. syriaca* were sent from Canada to France and then grown by Jacques-Philippe Cornut and described in 1635 (62). Linnaeus named the plant *A. syriaca* in 1753 because Cornut had linked the plant with a dogbane from Asia Minor (*A. cornuti* is a synonym for *A. syriaca*).

6.1. Potential Host Plant Invaders

The most common invasive milkweeds in North America are *A. curassavica* from South America, Central America, and the Caribbean (9) and the swallow-wort vines *Vincetoxicum rossicum* and *V. nigrum* from Europe and farther east (38). Common invasive milkweeds around the world include *A. curassavica*, *Gomphocarpus fruticosus*, and *G. physocarpus* from southern Africa (174), and *Calotropis procera* and *C. gigantea* from India and Africa (103).

Woodson's (174, p. 60) descriptions of *A. curassavica* as herbaceous annuals, as an "almost ubiquitous waif of the tropics and subtropics of the Americas," and as "blooming sporadically throughout the year" describe the problem with this milkweed quite nicely. *A. curassavica* is easy to grow from seed and cuttings, flowers constantly, and is the go-to milkweed for rearing monarchs. Flowering plants are attractive to monarchs, and when autumn migrants encounter the plant in the southern United States, they break reproductive diapause, stop migrating, and reproduce (9, 138, 139). Monarchs in southern Florida are able to breed year-round and do not migrate because *A. curassavica* has invaded, and monarchs prefer it to native milkweeds (86, 96). This reproductive activity that occurs in the southern United States in the autumn when monarchs encounter *A. curassavica* partly explains the fifth autumn generation of monarchs in the south (Figure 2). However, this generation is also explained by evidence for an autumn resurgence of native milkweeds that reflush in the south after hot summer temperatures (32) and by the abundance of native *A. perennis* in the wetlands of Florida, Georgia, Mississippi, Louisiana, and Texas. Similar effects can be achieved farther north by mowing senescent *A. syriaca* in late summer to attract monarch oviposition on new ramets (2).

Although use of *A. curassavica* as a food resource by monarch larvae benefits monarchs by reducing the intensity and virulence of *Oe* infections (46), this milkweed is now thought to cause an increase in the prevalence of *Oe* because it breaks reproductive diapause and halts migratory behavior (138, 139). The medicinal benefit of *A. curassavica* against *Oe* has been used to justify the cultivation of *A. curassavica* in frost-free regions of the southern United States to benefit monarchs. However, more recent research shows that although monarchs reared on *A. curassavica* have the highest tolerance for *Oe* spore load, compared with monarchs reared on 10 native *Asclepias* species, monarchs reared on the California milkweed *A. erosa* had the highest resistance to *Oe* infections (152).

Migration allows monarch butterflies to escape density-dependent effects of attack by *Oe* through migratory culling of infected individuals, migratory escape from regions of high pathogen prevalence, and migratory allopatry, in which infected adults can be spatially separated from susceptible larvae (139). Warmer winters in the southern United States allow *A. curassavica* to be cultivated as an ornamental, which favors year-round breeding in monarchs and loss of the disease-related benefits of migration in both eastern (138) and western (139) populations.

The swallow-worts *V. nigrum* and *V. rossicum* invaded North America from Europe in 1854 and 1897, respectively, and spread extensively across the continent after deforestation. The plants are thought to act as sinks for monarch eggs. For example, even in the presence of preferred host plants such as *A. syriaca*, monarchs on Rhode Island chose to lay 11–22% of their eggs on *Vincetoxicum* plants, though all their larvae died (38). Similar results were obtained in New York with much the same experimental design (49), but in this case the threat to monarchs of a nonviable egg sink was considered less important than aggressive interference competition from these plants to displace native *A. syriaca*.

Monarchs in Australia and Spain use the introduced milkweeds *A. curassavica*, *G. fruticosus*, and *G. physocarpus* (55, 176, 177). In the Caribbean, most monarchs use the introduced milkweeds *C. procera* and *C. gigantea*, although *A. nivea* may be an important native milkweed involved in elevational migrations, especially in the Greater Antilles (51). Thus, we could argue that introduced milkweeds have benefitted monarchs in a broad sense and generated a global range expansion (167).

6.2. Novel Natural Enemies

In Hawaii, two introduced species of bulbuls (*Pycnonotus jocosus* and *P. cafer*) do not appear deterred by sequestered cardenolides in adult monarchs and select against typically aposematic orange monarchs in favor of a more cryptic white morph (154). Once the white morph increased in frequency, the two bird species changed their behavior to prey on conspicuous monarch larvae feeding on the introduced milkweed *C. gigantea*. The inability of the birds to discriminate between the adult morphs as larvae decreased the frequency of the white morph from 8% to 1.7% (155).

Monarchs that overwinter in Mexico are preyed on in large numbers by birds that either migrate to Mexico from the western United States or are endemic to Mexico and do not encounter eastern monarchs during the summer. Thus, black-backed orioles (*Icterus abeillei*), black-headed grosbeaks (*Pheucticus melanocephalus*), and Steller's jays (*Cyanocitta stelleri*), as well as black-eared mice (*Peromyscus melanotis*), all feed extensively on monarchs aggregated at overwintering sites in Mexico and use novel feeding behaviors to reduce or avoid the impact of sequestered defensive cardenolides (21, 36, 56, 65).

Several species of invasive or deliberately introduced natural enemies also attack monarch eggs, larvae, and adults. Multicolored Asian lady beetles, *Harmonia axyridis*, were introduced into North America to control soybean aphids (*Aphis glycines*) and now pose a significant source of mortality for monarch larvae feeding on milkweeds, especially those in or near soybean fields (87). In Texas, imported fire ants, *Solenopsis invicta*, were responsible for 100% mortality of monarch larvae on the milkweeds *A. asperula* and *A. oenotheroides*, when compared with monarchs in fire ant exclosures (33). Fire ants have spread throughout the southern United States since their introduction in the 1920s and now represent a significant mortality factor for monarch immatures. In the northern United States, invasive, social paper wasps, *Polistes dominula*, prey on monarch larvae (131). The larval host plant had an influence on the number of monarch larvae taken by the wasps, and the wasps showed a preference for palatable prey and for monarch larvae from low-cardenolide plants. Chinese mantids, *Tenodera sinensis*, feed on monarch larvae, from which they remove the gut before consuming remaining tissue (127). In addition to these introduced natural enemies, monarch immatures are subject to mortality from a wide range of predators and parasitoids used for biological control of insect pests, such as tachinid flies, chrysopid lacewings, and pentatomid bugs (114).

7. HABITAT FRAGMENTATION AND COALESCENCE

Habitat fragmentation and coalescence read like an oxymoron, but the two processes occur simultaneously across the North American landscape and elsewhere. Contiguous habitats are fragmented

by resource use, agriculture, and urbanization, and industrial agriculture coalesces mosaics of crop fields into monocultures that exclude almost all biodiversity owing to the use of herbicides and other pesticides. This results in the homogeneous habitat matrix, largely devoid of milkweeds, over which monarchs migrate to find their milkweed resources (180). But this matrix is intersected with roads that link among rural, suburban, and urban human activities, and roads pose both problems and solutions for monarch butterflies.

Peak mortality of monarch butterflies in central Illinois due to road traffic coincided with late-summer breeding and the onset of their autumn migration from August 25 to October 19 in 1998 (13, 102). Road traffic killed 1,824 butterflies along 13 transects, and from these numbers it was estimated that 20 million butterflies and 500,000 monarchs are killed along roads in Illinois each week. These roadside verges were of value to monarchs because they included the presence of both milkweed host plants (*Asclepias verticillata*) and various nectar resources (e.g., Asteraceae, *Trifolium* spp., and Apiaceae).

In addition to direct mortality from road traffic, roads generate problems for monarchs and their resources from the application of road salt in winter. In Michigan roadside habitats, road salt accumulated more in poorly drained, clay soils than in sandy soils and resulted in high mortality of both *A. syriaca* and native nectar sources used by monarch butterflies (73). Road salt runoff also increases sodium concentrations in leaves of *A. syriaca* growing alongside roads (2,065 ppm) compared with control plants growing in a prairie (62 ppm) (147). Although survivorship of monarch larvae was significantly higher on prairie *A. syriaca* than on roadside *A. syriaca*, roadside plants resulted in significantly higher tissue sodium concentrations in both male and female monarchs than prairie plants did. Because sodium concentrations are low in milkweed leaves in prairie habitat, augmentation of this micronutrient from road salt benefits monarchs with increased muscle mass in males and larger eyes in females (147). The implications of these effects are not known.

8. DELIBERATE CULTURE AND RELEASE OF MONARCHS AND MILKWEEDS

Monarch butterflies are commonly released at weddings and other events (107). Although considerable information is available about the culture of monarchs on milkweeds and risks from pathogens such as *Oe*, these released butterflies likely harbor *Oe* spores. On the basis of warnings by Brower et al. (23), the U.S. Department of Agriculture does not permit transfers of monarchs between eastern and western populations partly owing to concerns posed by *Oe* but also because the ecologies and behaviors of the released butterflies are likely to be disrupted. Released butterflies are fed mostly *A. curassavica* as larvae, and the consequences of these releases are unknown.

9. RECENT INTERPRETATIONS OF MONARCH POPULATION VIABILITY

On the basis of comparisons between 22 years of citizen science records from four monitoring programs in North America and declining monarch overwintering numbers in Mexico (Figure 1), Inamine et al. (82) conclude that monarchs are not limited by milkweeds. Instead, they argue that problems encountered during both autumn and spring migrations, including lack of nectar resources, habitat fragmentation, and degrading overwintering habitat, are more likely responsible for declining numbers. Their analysis was based on the North American Butterfly Association (NABA) citizen science counts of monarchs and data collected on monarch movements at two funnel points in Cape May Point, New Jersey, and Peninsula Point, Michigan (see also 44, 45, 134). The conclusions of these analyses, namely that milkweeds had no effect on monarch

abundance and that a disconnect exists between summer breeding and overwintering, have been questioned (124, 125, 151). Citizen science data cannot address changes in spatially explicit densities, especially when the NABA data are supplemented with data from monitoring programs (such as Cape May and Peninsula Point) that are spatially irrelevant to 95% of eastern monarchs to the north or east of regions where milkweeds are expected to be lost to herbicide use (124, 151). Cleaning the habitat matrix through herbicide-induced loss of milkweeds is predicted to reduce monarch egg-laying by as much as 30% because spatial changes to metapopulation structure generate increased costs of reproduction (183). Pleasants et al. (125) use counts of monarch eggs per milkweed ramet, corrected for changes in monarch densities between agricultural and nonagricultural habitats in response to removal of milkweeds by herbicides to show that corrected summer monarch counts do decline with time in concert with declines in overwintering monarch numbers in Mexico. Thus, they find support for the milkweed limitation hypothesis and offer evidence against changes in mortality during autumn migration. Dyer & Forister (52) support the significance of negative density dependence with their use of discrete Ricker equations to model the effect of losing milkweed in agricultural habitats. Aggregative responses by monarchs to milkweed patches and by natural enemies to monarch larvae will be increased with the widespread use of herbicides that kill milkweeds to generate higher interpatch intervals. These effects are expected to increase mortality and reduce fecundity. They also explain erroneous interpretations of monarch breeding density in eastern North America (44, 82, 134, 160).

10. CONCLUSION

Monarch butterfly populations both east and west of the Rocky Mountains have declined (**Figure 1**), and this decline appears to be accelerating (82). The declines are associated with dramatic losses of milkweed resources in and near agricultural fields to which herbicides are applied. These losses have accelerated in concert with increased use of herbicides and GM crops modified to express herbicide tolerance. While these losses have occurred, overwintering habitats in Mexico and California have been affected by human economic activity both directly from tree removal and indirectly from the effects of anthropogenic climate change. In fact, climate change poses the greatest threat to the MBBR in Mexico because oyamel fir on which monarchs spend the winter is predicted to be eliminated from the entire reserve by 2090 (137). Such changes to overwintering forests occurred long ago in California with the introduction of invasive *Eucalyptus* species and land development along the coast, especially in wooded locations that supported monarch butterflies. Monarch overwintering in Pacific Grove, California (Butterfly Town, USA), is a ghost of its former self because motels were built among the overwintering trees along the coast. However, monarchs in California and elsewhere around the world have adapted and overwinter successfully in *Eucalyptus* species (93, 94, 162). This may happen in Mexico where alternative overwintering species include *Pinus pseudostrobus* and possibly rare *Picea martinezii* with a very restricted distribution north of the MBBR (137). If monarch overwintering is to persist in Mexico, these species will need augmentation in the MBBR, or the MBBR might even have to move to suitable habitats on volcanoes such as Nevado de Toluca or Popocatepetl to the southeast if monarchs move their overwintering locations (137).

Despite the doubt that has been cast on the milkweed limitation hypothesis (44, 45, 82, 134), there is no doubt that both monarchs and milkweeds are declining. The doubt was generated from the use of citizen science data that are not designed to be collected in a manner that addresses the viability of monarch populations. However, in the absence of more rigorous, large-scale alternatives, these are the best data we have. But there is much information that we do not have, especially for the partitioning of additional anthropogenically generated mortality among life-history stages.

We need rigorous, spatially explicit life table data for monarchs collected across North America for the most ecologically relevant milkweed host plant species (52). Such data would have resolved the *Bt* maize controversy with an analysis of the impact of additional immature mortality from exposure to *Bt* maize pollen. Instead, we have a proximate conclusion of minimal risk based on a traditional risk assessment protocol that cannot be interpreted as it stands (109, 144). Such a conclusion is meaningless in terms of monarch viability. Risk for this highly mobile species has to be put into the context of a complex life history across relevant time and space for both eastern and western populations of monarchs in North America.

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