

REVIEW

Monarchs in decline: a collateral landscape-level effect of modern agriculture

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Abstract We review the postulated threatening processes that may have affected the decline in the eastern population of the monarch butterfly, *Danaus plexippus* L. (Lepidoptera: Nymphalidae), in North America. Although there are likely multiple contributing factors, such as climate and resource-related effects on breeding, migrating, and overwintering populations, the key landscape-level change appears to be associated with the widespread use of genetically modified herbicide resistant crops that have rapidly come to dominate the extensive core summer breeding range. We dismiss misinterpretations of the apparent lack of population change in summer adult count data as logically flawed. Glyphosate-tolerant soybean and maize have enabled the extensive use of this herbicide, generating widespread losses of milkweed (*Asclepias* spp.), the only host plants for monarch larvae. Modeling studies that simulate lifetime realized fecundity at a landscape scale, direct counts of milkweeds, and extensive citizen science data across the breeding range suggest that a herbicide-induced, landscape-level reduction in milkweed has precipitated the decline in monarchs. A recovery will likely require a monumental effort for the re-establishment of milkweed resources at a commensurate landscape scale.

Key words *Asclepias*; citizen science; conservation; *Danaus plexippus*; migration; transgenic GM crops

Introduction

Of all insect species that have been studied, the population ecology of the eastern North American monarch butterfly, *Danaus plexippus* L., is unique, because virtually the entire population of adults emerging in the late summer migrates to, and overwinters in, a very restricted area: 12 mountain massifs in an area less than 30 km by 60 km in the neovolcanic highlands of central Mexico (Brower,

1985, 1995; Calvert & Brower, 1986; Brower *et al.*, 2002; Slayback *et al.*, 2007). The overwintered survivors migrate back to the Gulf Coast States, and establish a new spring generation. That generation continues the journey north across the eastern United States and into southern Canada, re-establishing the summer breeding range (Cockrell *et al.*, 1993; Malcolm *et al.*, 1993). Three or 4 more generations are produced across an area of 2.6 million km² before the southerly fall migration (Borkin, 1982; Malcolm *et al.*, 1987). The monarch migration has been considered an endangered phenomenon for a quarter of a century (Brower & Malcolm, 1991).

The overwintering population in Mexico coalesces on predominately oyamel fir, *Abies religiosa*, at estimated densities ranging from 6.9 to 60.9 million monarchs per ha

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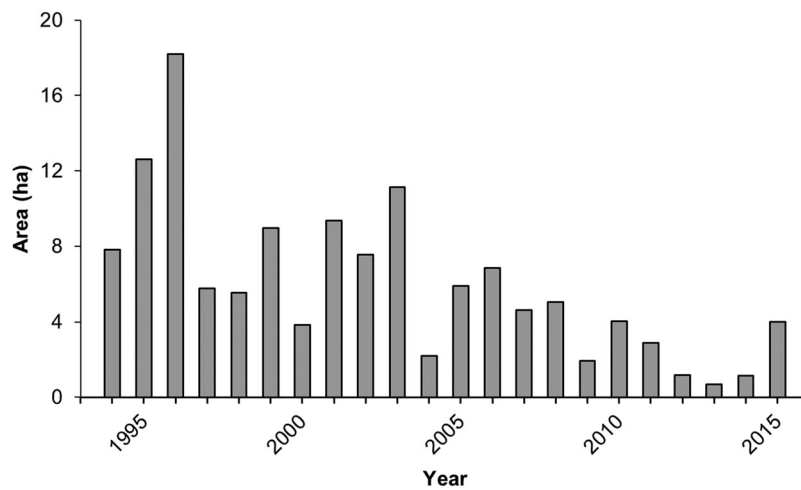


Fig. 1 Area of forest occupied by overwintering monarchs recorded in Mexico from 1994–1995 to 2015–2016 (data from Rendón-Salinas *et al.*, 2015).

(Brower *et al.*, 2004; Calvert, 2004a). The total population size has been estimated by measuring the area occupied by the overwintering butterflies in a consistent fashion since 1994 (Rendón-Salinas *et al.*, 2015). Although density estimates within colonies vary (Williams & Brower, 2016), and the area occupied fluctuates greatly from year to year, the Mexican overwintering area shows a consistent and significant decline (Fig. 1; Brower *et al.*, 2012). This led to a petition to list the species as threatened (Center for Biological Diversity, Center for Food Safety, Xerces Society, & Brower, L.P., 2014), and calls to formulate recovery plans. Unless these plans and actions actually address the threatening processes (*sensu* Caughley, 1994) that are leading to population decline, they could be a waste of time and effort. In fact, a recent population viability analysis (Semmens *et al.*, 2016) suggests a substantial risk of drastically reduced population levels that may lead to the demise of the migratory phenomenon.

Here we summarize threats to monarchs, as well as various views and interpretations of monarch population dynamics and citizen science data. We focus on the role of landscape-level changes wrought by the widespread planting of genetically modified herbicide resistant plants as the most likely driver. Amelioration of the threats to monarchs is likely to require the massive re-establishment of milkweed resources, a truly grand challenge.

What are the threatening processes?

The following is a balance equation for the size of the overwintering population in Mexico from 1 year, $G_{W,i}$, to

the next, $G_{W,i+1}$, as a product of 4 key ecological processes:

$$G_{W,i+1} = G_{W,i} \times OWS_i \times JN_i \times (G_1 : G_5)_i \times JS_i, \quad (1)$$

where OWS_i is the proportion that survives the winter, JN_i is the proportion that survives the journey north in the spring, $(G_1 : G_5)_i$ is both breeding “success” and survival or population change/increase over 4–5 generations produced in the spring–summer period, and JS_i is the proportion of the population that survives the journey south in the autumn (see also Yakubu *et al.*, 2004). We use this equation to ask, what may have precipitated a sustained decline in monarch numbers in Mexico (Fig. 1)?

Threats that may be responsible for the decline have been identified for each of the key processes (see also Inamine *et al.*, 2016). These include logging in, and adjacent to, forested overwintering sites (Brower *et al.*, 2002, 2009, 2016); widespread agricultural use of herbicides and increased areas farmed with glyphosate-tolerant crops that have reduced the abundance of milkweeds, *Asclepias* spp. throughout much of the core summer breeding areas (Zalucki & Lammers, 2010; Pleasants & Oberhauser 2012; Pleasants, 2015); widespread use of neonicotinoid insecticides (Pecenka & Lundgren, 2015); possibly *Bt* maize (Losey *et al.*, 1999; Jesse & Obrycki, 2000, 2004); introduced nonnative predators (Koch *et al.*, 2005); possibly reduced nectar availability for fall migrants due to changing land-use and agricultural practices and increasingly frequent droughts (Brower *et al.*, 2006); and the general impact of climate change on monarchs and the ecosystems across which they move during their annual migration (e.g., Oberhauser & Petersen, 2003; Batalden

et al., 2007; Sutherst *et al.*, 2011; Lemoine, 2015; Nail & Oberhauser, 2015; Ramírez *et al.*, 2015; Zalucki *et al.*, 2015).

Overwintering survival

Brower and colleagues (2008, 2009) have argued for the importance of intact mature forest stands in Mexico for overwinter survival, as both the forests and their altitude provide the microclimatic conditions that enable monarchs to survive the winter. Large oyamel trees and intact forest act as a “blanket,” “hot water bottle,” and “umbrella,” ameliorating the effects of adverse winter conditions (Anderson & Brower, 1996; Williams & Brower, 2015). Colonies generally form in arroyos near streams on densely forested sites at elevations of approximately 2900–3300 m, usually on southwest-facing slopes (Slayback *et al.*, 2007). The dense canopy and mature trees protect the butterflies from precipitation and extreme temperatures, enable the butterflies to maintain a state of reproductive diapause, keeping them warm enough to avoid freezing, but cool enough that their lipid reserves are not depleted (Brower *et al.*, 2012; Williams & Brower, 2015). However, even with these protections, rain during winter storms followed by freezing conditions can be devastating to the population and occasionally causes up to 80% mortality (Brower *et al.*, 2004).

The importance of the overwintering sites and their condition was recognized by a decree from the Mexican federal government in 1980 that declared all overwintering areas protected (DOF, 1980) and later by the establishment of a special conservation zone (DOF, 1986). This protected area (the Monarch Butterfly Biosphere Reserve) was further expanded in 2000 (DOF, 2000). Although periodic episodes of illegal logging continue (Vidal *et al.*, 2013; Brower *et al.*, 2016), the fact that the rapid decline of monarchs over the last decade has happened after deforestation rates slowed greatly (Vidal *et al.*, 2013) means that it is unlikely that deterioration of forests can be the sole cause of the sustained reduction in population size.

Effects of climate change on overwintering survival

Global warming may affect the timing of arrival and leaving at the wintering sites. If it does, we would expect that migrants would either arrive later, leave sooner, or both. There is currently no indication that the arrival or departure of the monarchs to/from their overwintering sites has shifted. If anything, monarchs are being sighted later in the Southern United States in spring (Howard & Davis, 2015). Climate change is also predicted to make the

overwintering sites and microclimates within these sites less suitable for both monarchs and the fir trees on which they overwinter (Oberhauser & Petersen, 2003; Ramírez *et al.*, 2015). In addition, more frequent rainfall events followed by freezing conditions can result in severe negative impacts on monarchs, such as in March 2016 (Brower *et al.*, 2016). Analysis of storm frequency in Mexico to date suggests that although negative effects are likely, they are not precipitous, frequent, or rapid enough to account for the sustained decline in monarchs (Barve *et al.*, 2012; Zalucki *et al.*, 2015). However, the low numbers of the current populations could make the impacts of such storms more threatening, if storms result in the population reaching an unviable size (Semmens *et al.*, 2016). If the suitability of overwintering sites changes heterogeneously in space and time, monarchs may be able to move between overwintering areas if conditions are locally unsuitable to minimize energy expenditure, maintain diapause, and increase chances of survival (Mexico: Masters *et al.*, 1988; California: Urquhart *et al.*, 1965; Leong *et al.*, 1991; Frey *et al.*, 1992; Griffiths, 2014; Australia: James, 1993).

Migration success: journeys north and south

Measuring mortality during migration is complicated (Flockhart *et al.*, 2015; Oberhauser *et al.*, 2016) and it has been suggested that deteriorating landscapes, fewer nectar plants at critical times and locations, and the diminishing numbers of roosting sites have reduced the numbers arriving in Mexico in the fall (e.g., Brower *et al.*, 2006). If this were the case, we would expect monarchs arriving in Mexico to be in generally poorer condition as measured by lipid reserves. This does not seem to be the case. Monarchs arriving in Mexico have high lipid reserves, indicating that they accumulate sufficient fuel for migration and overwintering (Masters *et al.*, 1988; Alonso-Mejía *et al.*, 1997; Brower *et al.*, 2006, 2015). There is no evidence either, that monarchs arriving in Mexico have lower fat reserves than in the past (Brower *et al.*, 2015). Low lipid reserves could also negatively affect survival during the spring migration into the southern United States, but this hypothesis has yet to be investigated.

Effects of climate change on migration success

Climate and local weather can have dramatic effects on migration. Widespread drought can affect the availability of nectar (Brower *et al.*, 2006, 2015), and if climate change-driven drought consistently affects large portions of the migratory pathways, it could have population-level impacts. However, even after migrating

through drought-stricken Texas in autumn 2011, monarchs appeared to compensate for low nectar availability in 1 region as they moved southward through Mexico (Brower *et al.*, 2015). While persistent drought could definitely affect migratory and breeding success, there is no evidence, other than a superficial analysis (see below) of summer count data (Inamine *et al.*, 2016), that this has driven the current decline. Additionally, storms can blow monarchs off course (Brower, 1995), with some even ending up in Europe (Fernández Haeger *et al.*, 2015), although such events are unlikely to have population-level impacts. These effects tend to be localized, and are unlikely to lead to sustained declines.

Summer breeding success

Effects of climate change on breeding success

There does not seem to be a directional climate change signal affecting monarch summer breeding success, although summer conditions can affect local populations (Zipkin *et al.*, 2012; Saunders *et al.*, 2016) and a changing climate may shift the suitable summer range northward (Batalden *et al.*, 2007). Using a CLIMEX model that estimates the seasonal distribution of the abundance of monarch butterflies anywhere in the world, Zalucki *et al.* (2015) estimated the effect of climate on long-term monarch population dynamics in North America. They used daily maximum and minimum temperatures and rainfall from 1970 to 2010 for 25 locations that cover the breeding range across eastern North America to generate a series of abundance indices. Although there is considerable variation in the population indices over this period, climate variables were not useful in predicting or detecting trends in monarch breeding populations. However, climate impacts on mortality during spring and autumn migrations, and at overwintering sites cannot be ruled out (see above). Similarly, indirect effects of climate change mediated by resource quality and availability may also have effects on monarch populations and also cannot be ruled out (Zalucki & Rochester, 2004).

Agriculture and GM crops—collateral effects at a landscape scale

When Losey *et al.* (1999) first suggested that genetically modified (GM) *Bt* maize pollen could have a negative impact on monarch larvae feeding on milkweed in the Midwest Corn Belt, the paper was met with a mixed response (Hodgson, 1999; Niiler, 1999; Shelton & Roush, 1999; Brower, 2001). Subsequent work showed there

was little measurable mortality of early instar monarch larvae due to pollen from most maize transformation events (e.g., Hellmich *et al.*, 2001; Stanley-Horn *et al.*, 2001). Even the worst case scenario was predicted to have negligible negative effects because the industry-accepted standard for calculating risk, $R = P_t \times P_e$ (EPA, 1998; where R is risk, P_t is the toxic effect, and P_e is the probability of exposure), gave a low value for R (Sears *et al.*, 2001). Subsequently, Dively *et al.* (2004) measured a toxic effect, P_t , comparable to Losey *et al.* (1999) and others (Jesse & Obrycki, 2000, 2004), but R was still “small” because P_e , the probability of exposure, was low (Sears *et al.*, 2001). Perhaps the most relevant outcome of this research, in terms of understanding the potential impacts of changing agricultural practices on monarchs, was an appreciation of the amount of milkweeds in row crop fields (primarily soybeans and maize) and monarchs’ widespread use of these milkweeds (Oberhauser *et al.*, 2001).

Due to the advent of glyphosate resistant (“Round-Up Ready®”) maize and soybean, global use of glyphosate has risen approximately 15 fold since 1996 (Benbrook, 2016). Glyphosate has become the most widespread and intensively used herbicide in the United States, where agricultural use in 2014 totaled 113.4 million kg, enough to apply approximately 1 kg on every hectare of U.S.-cultivated cropland (Benbrook, 2016). Glyphosate-tolerant or herbicide resistant (HR) maize and soybeans now dominate production, accounting for over 90% of the total area planted for each crop; the total area planted in both crops is approximately 66 million ha (USDA NASS, 2015). As a result, the “common milkweed,” *Asclepias syriaca*, that was once abundant in the Midwest, has become much less abundant (see below). Consequently, the risk of monarch exposure to pollen containing *Bt* toxin has become truly vanishingly small because milkweeds have been eliminated from the pollen shadow of *Bt*-expressing crops.

Along with glyphosate resistant crops came a concomitant increase in the prophylactic use of systemic insecticides to protect the investment in expensive GM seed technology. The use of neonicotinoids in U.S. agriculture mirrors the use of glyphosate; both have escalated dramatically. For example, use of imidacloprid, a neonicotinoid commonly applied to soybean crops via seed coatings and broadcast sprays, rose from ~100 000 kg in 2000 to ~900 000 kg in 2013 (USGS, 2016). Again, the potential adverse effects of low-level exposure to neonicotinoid on immature monarchs (Pecenka & Lundgren, 2015) are probably small, simply because there are so few milkweeds in agricultural fields. Nevertheless, there may well be additional effects of these systemic insecticides

on larval and adult monarchs feeding on contaminated milkweeds and nectar due to pesticide drift from adjacent agricultural fields.

How would such a landscape-level decline in milkweed resources impact monarch summer breeding success? Essentially, the carrying capacity, K , or milkweed biomass (*sensu* Dempster, 1983) has drastically declined. Standard population theory based on the logistic equation would suggest a resulting population decline.

A realistic model for monarchs in North America might be spatially explicit and represent the landscape as a mixture of breeding and nonbreeding habitats in a Geographic Information System framework (e.g., Feddeman *et al.*, 2004; Zalucki & Rochester, 2004) linked by explicit models of movement and egg laying. None exists at present, but there are models that suggest how milkweed decline can impact egg laying. Published field studies based on citizen science data also show a decline in monarch breeding success. We summarize these findings here and outline key research questions that need to be addressed if the decline is to be understood, arrested, and reversed.

Monarch movement and egg laying

Soybean and maize crops genetically modified to be resistant to glyphosate now dominate the monarch butterflies' summer breeding range in North America. As a consequence, milkweed abundance has declined dramatically. *A. syriaca* was a common "weed" of Midwestern cropland (Hartzler & Buhler, 2000; Oberhauser *et al.*, 2001) and southern Canada (Frick *et al.*, 1990). Early surveys of northern Michigan, for example, found milkweed in 10% of the cropland and in 1 surveyed county, at an average density of approximately 27 000 stems/ha (Timmons, 1946). In Iowa, common milkweed was abundant, occurring in over 5 million ha in the 1980s (Cramer & Burnside, 1980). In 1999, *A. syriaca* was detected in 51% of Iowa maize and soybean fields, but in only 8% of the fields during 2009, over a 6 fold reduction (Hartzler, 2010). The mean milkweed density in fields where milkweed was present also declined to approximately one tenth, from 52 to just 5 occupied square meters per hectare (Hartzler, 2010). The declining number of fields with milkweed, and the reduced density where it was found, translate to an estimated 97% decline in agricultural milkweed density in Iowa from 1999 to 2009, with 99% of the milkweed present in maize and soybean fields in 1999 eliminated by 2013 (Pleasant, 2015). Pleasant and Oberhauser (2012) recorded declining milkweed populations in 7 fields surveyed over a 9-year period. Of roughly 1 000 milkweed stems at the start of the survey in 2000, none remained

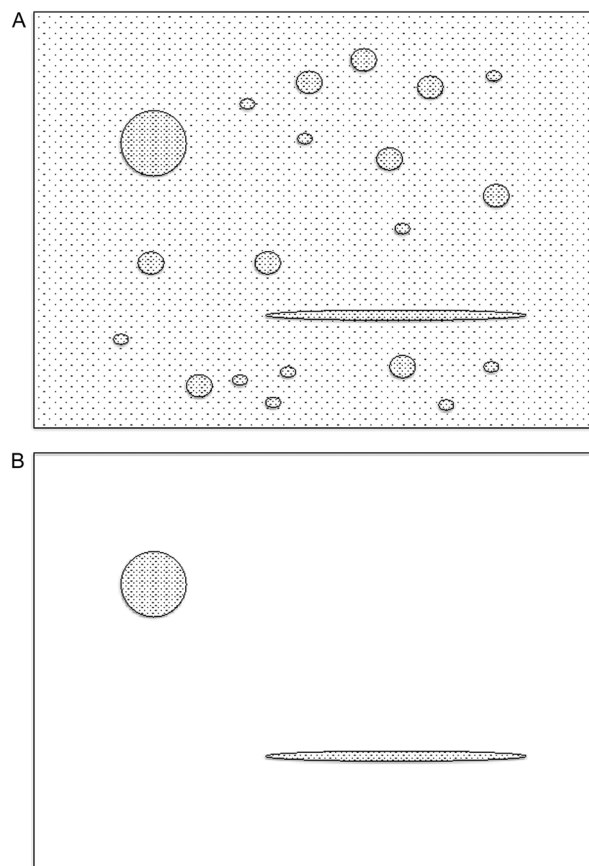


Fig. 2 Stylized representations of milkweed habitat for monarchs in landscape preherbicide-resistant GM crops. There is a large milkweed patch in an old field, a long thin patch along a roadway, small patches in agricultural fields, and background low density of milkweed in the matrix (A). Post GM crops and glyphosate use, the matrix is almost completely empty, small patches are absent, and only the road and old field remain with a 95% reduction in milkweed numbers (B).

by 2009 (Pleasant, 2015). Milkweed has been effectively extirpated in the monarchs' core breeding range and the landscape has been dramatically transformed (Fig. 2).

Spatially implicit (Zalucki & Lammers, 2010) and spatially explicit individual-based (Zalucki, 1983) models exist to describe host seeking behavior over the lifetime of a monarch butterfly, in which host plants both aggregated in patches and scattered across the wider landscape are utilized for egg laying (Zalucki *et al.*, 2016). In the explicit model, we examined the simulated movement distances and spatial population distribution (eggs laid) as a result of different movement rules; we varied directionality or tendency to fly in straight lines, perceptive distance or the ability of monarchs to find milkweed, their tendency to leave habitat patches, and landscape configuration

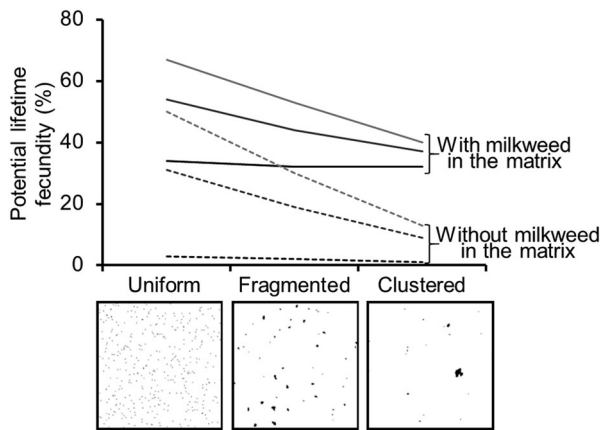


Fig. 3 Potential lifetime fecundity of a monarch butterfly in 3 hypothetical landscapes with a 1% milkweed cover but in patches of uniform, fragmented or clustered distribution. Solid lines: milkweed present in the matrix between patches; dashed lines: no milkweed in the matrix. The 3 lines in descending order for each matrix type indicate 3 levels of patch habitat preference (1, 0.5, and 0.1). A lower habitat preference means butterflies are more likely to leave a patch. Data on lifetime fecundity are from Zalucki *et al.* (2016) and are the means of simulations varying perceptive distance, movement step length and directionality or tendency to fly in straight lines. See Zalucki *et al.* (2016) for further details.

(how milkweed is distributed). Both models of monarch movement and searching indicated how cleaning up the habitat matrix (i.e., the eradication of milkweeds in cropland with glyphosate) and changing habitat configurations at a landscape scale could affect individual movement behaviors and the emergent property of number of eggs laid (the birth term in the population model) (Fig. 3). Our models suggest that elimination of low-density milkweed in the matrix (i.e., cropland) has reduced egg laying by 30%–90%. The models also suggest that the spatial arrangement of milkweed habitat at a landscape scale can affect monarch success. Realized fecundity was affected by how habitat units are arranged, as well as habitat preference (Fig. 3). The greater the number of habitat patch units, and the more evenly or uniformly spaced, the more likely they were to be encountered and utilized (percentage eggs laid is always higher, Fig. 3). Clustered landscapes, in which milkweed occurred in larger, fewer “fragments,” resulted in the lowest realized fecundity (Fig. 3). Relative habitat preference was also important. The preference parameter is best interpreted as a likelihood of leaving a patch (Zalucki *et al.*, 2016). High relative preference values led to agents concentrating eggs in patches of hosts, and increased fecundity. However, monarchs appear to ignore boundaries (Ries & Debinski,

2001) and milkweed patch edges (Zalucki & Kitching, 1982c) and most likely have low preference levels. The models also point to effective amelioration strategies (see below).

In summary, cropland once harbored low-density milkweeds that are essential to monarchs realizing their egg laying potential. Although high-density patches of milkweed in old fields and conservation areas continue to be important for mating and egg laying (see e.g., Zalucki, 1993), most monarchs are travelling between patches in which, in the past, they could utilize low-density milkweed in the (matrix) space between these patches (Zalucki & Kitching, 1982a,c; Zalucki *et al.*, 2016). Larval survival was, on average, better on these low-density plants compared to plants within dense patches (Zalucki, 1981; Zalucki & Kitching, 1982b; Oberhauser *et al.*, 2001). However, the matrix of North American agricultural landscapes is now effectively empty of the resources that once supported diverse ecosystem services, including monarch butterflies. This landscape-level change has been rapid and directional. It is likely that monarchs’ opportunity for realizing their potential fecundity has been substantially reduced and, importantly, that their population has shifted to the remnant milkweed where citizen scientists likely undertake counts.

The misinterpretation of NABA seasonal and migration counts

The North American Butterfly Association (NABA) coordinates butterfly counts in Canada, Mexico, and the United States (NABA, 2016). To participate in these counts, teams of at least 4 volunteers compile lists of all butterflies observed within 15-mile diameter count circles over a 24-h period. The location and total number of the count circles and the sites sampled within each count circle may change from year to year based on the volunteers’ preferences. One effect of this sampling protocol is that volunteers avoid sampling areas where they expect to see few butterflies, such as urban areas and conventionally farmed fields, with the effect of maximizing the quantity and diversity of butterflies observed. Some authors, summarized in Davis and Dyer (2015) and the more recent effort by Inamine *et al.* (2016), have suggested that summer breeding numbers have not changed because seasonal butterfly count data have not indicated a decline, and they therefore conclude that the decline in Mexico is due to other threats such as those present during migration or at the overwintering sites. However, this argument defies a simple logic test. For example, if we had 10 count circles with 10 butterflies each, but we then lost 9 count circles

(e.g., lost agricultural milkweed) and found that the remaining area still had 10 butterflies, this does not mean the population has not declined! In fact, it has declined by 90%. Only if the counts had gone up to 100 at the remaining site would this logic suffice. Pleasants *et al.* (2016) show that the spatially biased citizen count data, if properly analyzed by taking into account the decline and shifting distribution of milkweed, does, in fact, show a decline in population size (see below). Ries *et al.* (2015) also make use of NABA and Illinois Butterfly Monitoring Network data, but are much more circumspect in drawing conclusions from spatially biased samples.

The other fallacious argument concerns counts of migrants at 2 so-called funnel sites, Cape May, NJ and Peninsula Point, MI; the interpretation being that because counts at these sites these have not declined, threats to monarch summer breeding are not the cause of the population decline. However, neither site is likely indicative of fall migration across the monarchs' summer range, given their locations at the edges of the species summer range. The former, Cape May, may be indicative of the far Northeastern states and the latter, Peninsula Point, of parts of Canada. These represent approximately 5%–10% of the range at best and are outside the desolation wrought by glyphosate (see Pleasants *et al.*, 2016 for a more extensive critique).

Citizen science data: population dynamics and habitat productivity

Long-term datasets of the density of immature monarchs, such as those of the Monarch Larva Monitoring Project (MLMP, 2016), can help to document changes in breeding success and also suggest habitat creation targets. In this project, citizen science volunteers monitor sites with milkweed on a weekly basis, counting the number of eggs and larvae (identified to stadium) observed on a known number of identified milkweed plants. Volunteers also report characteristics of each site, such as the surrounding area (rural to urban) and the type of site (e.g., roadside, garden, natural area, etc.), allowing comparisons of the relative productivity of different types of sites.

Two recent publications used MLMP data from 1997 to 2014 to summarize temporal patterns and site characteristics related to egg densities (Stenoien *et al.*, 2015a) and larval survival (Nail *et al.*, 2015a). Both egg densities and survival were highly variable in space and time. Nevertheless, the hypothesis that realized fecundity has declined in parallel with the decline in the overwintering population was supported by a piecewise linear regression, which showed a strong negative effect of year

on egg densities from 2007 to 2014 (Stenoien *et al.*, 2015a). MLMP volunteers only monitor sites containing milkweeds, but since the advent of HR crops, there are fewer sites with milkweeds on the landscape. Therefore, finding a pattern of constant egg densities across the duration of the MLMP dataset would have suggested an overall population decline. Instead, egg densities within these remaining patches were found to be declining over the most recent 7 years, suggesting that per capita realized fecundity has declined to a point where many of the remaining sites are found by fewer or no females as the overall population has declined, corroborating the findings from the spatial models mentioned earlier. Furthermore, the hypothesis that glyphosate applications to HR maize and soy fields have indirectly led to the decline in monarch populations was supported by the usefulness of annual HR crop acreage as a predictor in a linear model of the area occupied by overwintering monarchs, compared to models that ignored HR crop acreage (Stenoien *et al.*, 2015a).

The analysis by Nail *et al.* (2015a) offered insights into the survival of immature monarchs from egg to fifth instar. Causes of immature monarch mortality include abiotic factors such as temperature (Zalucki, 1982; York & Oberhauser, 2002; Nail *et al.*, 2015b) and insecticides (Oberhauser *et al.*, 2006, 2009), as well as biotic factors including resource quality and availability (Malcolm, 1995; Malcolm & Zalucki, 1996; Zalucki & Lammers, 2010), disease (Altizer & Oberhauser, 1999), and natural enemies (Calvert, 2004b; Oberhauser *et al.*, 2015; Stenoien *et al.*, 2015b; McCoshum *et al.*, 2016). Mean summer survival of monarchs from egg to adulthood was estimated to be 5.8% in the North Central United States. Interestingly, despite high year-to-year variation, when accounting for site-to-site variation, overall survival from egg to fifth instar has declined over time. Unlike egg density, however, the negative effect of year was evident across the entirety of the MLMP dataset. It is unclear what is causing the apparent decline in immature survival. Overall, larval competition should not be a factor, as overall egg densities declined over the study period. Possible explanations include increased mortality due to disease, or predators and parasitoids, though there is currently no evidence supporting either hypothesis. Unlike yearly HR crop acreage, the inclusion of yearly survival estimates did not improve a regression model of the area occupied by monarchs overwintering in Mexico. Thus, survival rates do not appear to be driving the population fluctuations observed at the overwintering sites, at least not in a straightforward way. One final conservation-related takeaway message from this analysis was that it takes, on average, ~28.5 milkweed ramets to produce 1 migratory monarch butterfly

from the North Central United States. This number was generated by taking the inverse of the product of weekly mean egg density, mean egg to fifth instar survival, mean fifth instar to adult survival, and the approximate number of weeks in the sampling period that leads to the generation of migratory adults.

These analyses also addressed whether certain site characteristics are correlated with increased or decreased monarch egg density and survival. When controlling for other factors, natural areas tended to have the lowest egg densities while gardens tended to have the highest egg densities out of the sites enrolled in the MLMP (roadsides, crop and noncrop-based agricultural areas, all possibly supporting monarchs, are not enrolled). An important finding for monarch conservation was that monarch egg densities and survival are negatively correlated, such that sites with fewer milkweed plants tended to lead to more eggs per plant, yet lower larval survival; see also Zalucki and Kitching (1982a,c) and Zalucki and Suzuki (1987). No site characteristics in the analysis negatively or positively predicted both egg density and survival, suggesting that none of the site characteristics studied have consistently high or low monarch production. Instead, the most consistent predictor of survival across all site types seems to be egg density, suggesting strong density dependence.

Taken together, these studies lead to context-dependent habitat restoration suggestions. If there were no effect of egg density on survival, it would be wise to focus on restoration of those areas correlated with the highest egg densities. However, the negative correlation between egg density and survival suggests that density dependent effects, perhaps including resource competition, predation, parasitism, and disease limit survival as egg densities increase. Laboratory work has shown density dependent effects due to cannibalism (Brower, 1961) and what was likely intraspecific competition (Flockhart *et al.*, 2012). Because of this apparent density dependence that is consistent across the range of sites analyzed, it seems there is no clear “best” or “worst” habitat type. Still, some areas may be better investments than others (Oberhauser *et al.*, 2016). For example, the North Central United States should be prioritized over the Northeastern United States because egg densities are consistently higher there, while survival estimates are similar between regions. Additionally, research using stable isotopes has led to the conclusion that the majority of the overwintering monarchs originate from the Corn Belt (Wassenaar & Hobson, 1998). Finally, a greater proportion of tagged butterflies released from the North Central United States are recovered in the Mexican overwintering colonies than tagged butterflies from coastal areas of the eastern United States (Orley Taylor, personal communication). Among

monarchs originating from east of the Appalachian Mountains in Virginia, tagged individuals from coastal sites were approximately 8 times less likely to be recovered in Mexico compared to tagged individuals from inland sites (Brindza *et al.*, 2008). We lack survival data from the Southern United States to make any strong conclusions, but this region provides essential breeding habitat on the spring migration north (Knight *et al.*, 1999), essential nectar resources on the fall migration south, and sometimes supports monarch reproduction during late summer (Baum & Sharber, 2012; Batalden & Oberhauser, 2015), so the creation and maintenance of habitats in this region are essential for population persistence.

We currently lack data on several variables that would help us better understand the effects of land use and landscape factors on habitat suitability for monarch reproduction and survival. First, we lack reliable estimates of milkweed densities within patches and in the “matrix.” While milkweed densities in agricultural areas (e.g., Hartzler & Buhler, 2000; John Pleasants, unpublished data) and along roadsides (Kasten *et al.*, unpublished data) have been estimated, densities within other habitats such as natural areas are currently not well known. As a result, we cannot estimate the relative contributions of these habitat types on a per-area basis. Second, determining the total acreage of different relevant habitat types, and their potential to contribute to monarch habitat, is not straightforward but deserves more attention (Wayne Thogmartin, personal communication). Finally, we do not fully understand the importance of milkweed distribution (patchiness) within a site nor the importance of the proximity, size, or connectivity of patches for monarch oviposition or survival. A better understanding of these variables would greatly inform future models of monarch movement, egg laying and population dynamics.

Bringing back the monarch—a possible way forward

The widespread use of HR crops has been driven by the increased yields afforded by these technologies, but a consequence of the removal of “weeds” from the agricultural landscape is the concomitant reduction of native plants and the insect communities they support. We have focused on the effects on the monarch butterfly, a particularly charismatic herbivorous insect that relies on native milkweeds, but similar negative effects have likely occurred for other insect herbivores, pollinators, predators, and parasitoids as well. Because agricultural practices are unlikely to change dramatically in the near future, there are only a few options to promote or bring back milkweed

in the matrix between remaining habitats in the agricultural areas that comprise the vast majority of monarchs' historical breeding range. These options are to establish more milkweed (1) along roadways, (2) between fields as "nature strips" or "prairie strips," and (3) through Conservation Reserve Program (CRP) or similar programs that incentivize taking marginal crop lands out of production and planting, instead, natural habitats that include milkweeds. Based on the models of monarch egg-laying behavior and citizen science data, these plantings may be most effective if done as a mixture of dense and low-density plantings of locally native milkweed species.

To design appropriate amelioration strategies will require an analysis of how current actual landscapes affect monarch egg laying. Our modeling work has been based on hypothetical landscape configurations (Zalucki et al., 2016). To better understand these issues, recording and mapping the geographic distribution of milkweed and nectar resources at a landscape scale relevant to monarchs (at least 300–400 km² in extent) and in a number of areas (at least 4–5) representative of the monarchs' summer range across North America is essential. This area estimate represents the average birth to death distance flown by a nonmigratory female monarch (Zalucki, 1983; Zalucki et al., 2016), and the number of sites is suggested for purposes of statistical power. These digitized resource maps can be used as input to our movement model (Zalucki et al., 2016). The simulated output (egg distribution) can be compared to observed egg distribution and the model refined and calibrated if needed. The model can then be used to optimize planting strategies: where to add milkweed and nectar sources (e.g., along roadsides or in nature strips integrated into cropland) to maximize the number of eggs laid. Given that resources are scarce, planting needs to be targeted. Should milkweed patches (of various sizes) be established in well-spaced focal clusters, or more uniformly distributed? Should low-density planting be along field margins, roads, or fewer bigger patches? The empirical evidence needed to answer these questions is limited, but current models suggest that uniform distribution of patches on landscapes would be best (Fig. 3). Convincing farmers to accept milkweed along margins will require active engagement. As has been shown in Europe, North America, and Australia, so called "nature strips" and remnant patches of native vegetation can be a valuable asset to the farming system as a whole, by providing both pollination and biological control services (e.g., Schellhorn et al., 2008, 2014, 2015; MacFadyen et al., 2015; Parry et al., 2015). The Monarch Joint Venture (MJV, 2016) and various state-based programs have been initiated to address the return of the monarch (e.g., in Iowa [<http://monarch.ent.iastate.edu/>]).

Additionally, the Monarch Conservation Science Partnership, a consortium of federal and state agencies and monarch biologists, is working to ensure strategic approaches to this huge problem, based on sound science to address real threats.

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Disclosure

The authors declare that they have no conflict of interests.

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