



# Grassland disturbance increases monarch butterfly oviposition and decreases arthropod predator abundance

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## ABSTRACT

Many species of conservation concern depend on disturbance to create or maintain suitable habitat. We evaluated effects of disturbance on the eastern migratory monarch butterfly (*Danaus plexippus* L.), which has declined markedly in recent decades, primarily attributed to the loss of milkweed host plants from annual crop fields in the US Midwest. Currently, remaining milkweeds in this region primarily occur in perennial grasslands, where disturbance is infrequent, predatory arthropods are abundant, and seasonal patterns of plant phenology differ from crop fields. In a two-year study in Michigan, USA, we applied three treatments to 23 patches of common milkweed (*Asclepias syriaca* L.); one-third of each patch was left undisturbed, while the remaining thirds were mowed in either mid-June or mid-July, respectively, and allowed to regenerate. We subsequently measured effects on monarch oviposition, predator abundance, survival of sentinel eggs and larvae, and tested how milkweed phenology and aphid colonization—both of which are reset by disturbance—structure predation risk for immature monarchs. Monarchs laid more eggs on regenerating versus undisturbed stems under both mowing regimes. Predators were strongly suppressed by mowing treatments, requiring 2–4 weeks to recolonize milkweed after disturbance, and were more abundant on flowering or aphid-infested stems. We found no significant differences in monarch egg/larval survival, although it tended to be higher in mowed plots. Overall, monarchs laid more eggs on regenerating stems where their offspring may also experience enemy-free space. Future work should focus on testing grassland disturbance as a management tool to improve productivity of existing monarch breeding habitat.

## 1. Introduction

Disturbance is a ubiquitous process that shapes terrestrial ecosystems. Many organisms are adapted to early-successional environments, or to the spatial heterogeneity produced by disturbance, and consequently depend on it to create or maintain their habitat (Sousa, 1984). Recovery efforts for several rare butterfly species have hinged on whether natural disturbances are reinstated (Thomas, 1980; Schultz and Crone, 1998; Thomas et al., 2009; Schultz and Crone, 2015; Schultz et al., 2011; Dunwiddie et al., 2016), and lessons from these rare species may help us understand and reverse the declines of other more common insects (Haddad, 2018). Matters may be more complicated in human-dominated landscapes, where natural disturbance regimes are replaced by anthropogenic ones and species of conservation concern can come to depend on human-caused disturbance (e.g., Tälle et al., 2016; Douda et al., 2017). Achieving conservation goals for these organisms may be particularly challenging, since disturbance patterns tend to be optimized for economic productivity rather than conservation objectives.

The monarch butterfly (*Danaus plexippus* L., Nymphalidae) is one organism fitting this description. The monarch is an iconic North American insect which inspires awe due to its aesthetic appeal, complex interactions with milkweed host plants, and long-distance migrations (Gustafsson et al., 2015). The Eastern migratory population breeds throughout the eastern United States and Canada, where landscapes are dominated by annual row-crop agriculture and its accompanying disturbance regimes. Each fall the butterflies travel thousands of kilometers to overwintering sites in Mexico. Recent evidence suggests the migratory phenomenon is threatened (Brower et al., 2012; Vidal and Rendón-Salinas, 2014) as overwintering populations in Mexico declined > 80% from the 1990s to 2014 (Semmens et al., 2016). As a result, monarchs are currently under review for listing under the US Endangered Species Act (Center for Biological Diversity, 2014).

Threats to monarch populations are as diverse as the landscapes they occupy, and include logging of critical overwintering habitat in Mexico, increased prevalence of pathogens, reduced availability of adult nectar resources, increased exposure to insecticides, and climate

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change (see reviews by Inamine et al., 2016; Stenoien et al., 2018; Thogmartin et al., 2017b). However, while it remains controversial, the most important contributor to the recent decline appears to be the loss of host plants and summer breeding habitat in the US Midwest (Pleasants and Oberhauser, 2013; Flockhart et al., 2013, 2015; Oberhauser et al., 2017; Stenoien et al., 2018; Thogmartin et al., 2017b; Marini and Zalucki, 2017). Around half of monarchs that arrive in Mexico for overwintering originate in the Midwest corn belt (Wassenaar and Hobson, 1998). In this region they use several milkweeds (Apocynaceae) as oviposition and larval hosts (Pocius et al., 2018; Pocius et al., 2017; Zaya et al., 2017). However, the most abundant and commonly used species is common milkweed, *Asclepias syriaca* L. It has been estimated that 92% of monarchs that reach Mexico from the Midwest used this species as a larval host (Malcolm et al., 1993).

Common milkweed (hereafter ‘milkweed’) is a native perennial which has long been considered an agricultural weed. Until relatively recently, it was abundant in corn and soybean fields that dominate midwestern landscapes. Mechanical control of milkweed was mostly ineffective; milkweed is a hardy perennial that survives agricultural disturbances like plowing, disking and cultivation. Furthermore, these methods break up milkweed roots and spread them to new areas (Bhowmik and Bandeen, 1976). As a result, common milkweed was once abundant in crop field interiors, and ~4 times more monarch eggs occurred on milkweed growing in crop vs. non-crop habitats (Oberhauser et al., 2001). However, since the late 1990s > 90% of corn and soybean production has shifted to herbicide-resistant varieties. Fields are now sprayed with broad-spectrum herbicides which have largely eliminated milkweeds from crop field interiors (Hartzler, 2010). Given the extensive footprint of agriculture, it is estimated that around 40% of milkweeds have been lost from the Midwest (Pleasants, 2017; Pleasants et al., 2017), and in these landscapes female monarchs frequently do not find enough resources to maximize fecundity (Zalucki et al., 2016; Grant et al., 2018).

In response to the loss of milkweed, recent research has focused on how to augment populations in the USA, including calls to restore 1.3–1.6 billion additional stems in the Midwest (Pleasants, 2017; Thogmartin et al., 2017a). However, a recent analysis suggests that even if all nonagricultural sectors (e.g. transportation rights of way, urban/suburban parks etc.) maximized the planting of milkweed in available habitats, it would still require conversion of half of all marginal agricultural lands to seminatural habitat to stabilize monarch populations at conservation goals (Thogmartin et al., 2017a). While replacing marginal farmland in the Midwest with grassland could bring about ecological benefits (Werling et al., 2014; Landis et al., 2018), these lands also serve other economic uses (Landis, 2017) and this magnitude of change is unlikely to occur on the time scale required to stabilize the overwintering monarch population. Therefore, finding ways to enhance suitability of existing monarch habitat could be key to preserving the migratory phenomenon.

Despite their loss from crop fields, milkweeds remain relatively common in the Midwest and are typically found in perennial grassland habitats like field margins and ditches, transportation and utility rights-of-way, planted grasslands, oldfields, wetlands, parks, and nature preserves (Thogmartin et al., 2017a). Importantly, however, monarch habitat in these perennial grasslands differs strongly from that in crop fields.

First, grasslands differ from crop fields in terms of host plant quality: agricultural lands are high-nutrient environments with frequent disturbances during the growing season (tillage, mowing, grazing, etc.) that may reset milkweed phenology and provide monarchs with attractive and suitable milkweed stems. Monarchs prefer to lay eggs on younger vegetative stems (Bergström et al., 1994; Urquhart, 1987), and younger plant tissues are in general more nutritious to herbivorous insects (Slansky, 1993). However, if left undisturbed, milkweed stems in the upper Midwest can flower as early as mid-June and may leave the

last 2–3 generations of monarchs with relatively fewer suitable options for oviposition. This is further evidenced by observations that in late summer monarch eggs and larvae are abundant on milkweeds that regenerate following mowing events (Marsh, 1888; Borkin, 1982; Fischer et al., 2015; Alcock et al., 2016).

Second, predation pressure on monarch eggs and larvae is likely to be much higher in grasslands than in crop fields. Grasslands harbor diverse and abundant communities of predatory arthropods (Werling et al., 2014) which result in consistently higher predation rates than in associated annual crops (Werling et al., 2011). It is well known that only a small fraction of monarch eggs reach adulthood, in large part due to predation. For example, in a Wisconsin old-field, sentinel monarch eggs had only a 2% survival rate after 7 days, and at times ants removed all eggs and larvae from individual plants (Pryby, 2004). Similarly, in a Minnesota restored prairie, ca. 20% of eggs survived to become larvae, < 10% reached 2nd instar, and < 2% reached third instar, with the lowest survival on plants harboring spiders or aphids (De Anda and Oberhauser, 2015). In addition to ants and spiders, reported predators of monarch eggs and larvae include lady beetles, cockroaches, mantids, assassin bugs, predatory wasps, and lacewing larvae (Oberhauser et al., 2015).

Previous observational studies have described monarchs favoring regenerating milkweed stems (Marsh, 1888; Borkin, 1982; Fischer et al., 2015; Alcock et al., 2016), but to our knowledge no study has experimentally manipulated disturbance to document its effects on monarch oviposition, predators, or survival. Therefore, we designed an experiment to test the effects of disturbance, in the form of strategically-timed mowing, on monarch butterflies and their arthropod predator community. We hypothesized that disturbance in grasslands during the growing season would benefit monarchs by providing them with preferred phenologic stages of host plants for oviposition as well as enemy-free space. We tested several predictions: First, we expected monarchs would lay more eggs in milkweeds that regenerate after disturbance. Second, we expected disturbance to reduce the number of predatory arthropods on regenerating stems. We also asked how the timing of disturbance affected these two variables. Finally, we expected survival of sentinel eggs and larvae to increase after disturbance.

We also tested for multi-trophic processes that are influenced by disturbance and could structure predation risk for monarchs. Previous work has shown that monarch egg and larval survival can be lower on milkweed stems that are flowering (De Anda and Oberhauser, 2015), which could be because floral resources attract predators. Therefore, we predicted that flowering stems in our study would harbor more predatory arthropods than neighboring ones in pre-flowering stages. Finally, as aphids are common on milkweeds, and their abundance appears to negatively correlate with monarch egg and larval survival (Pryby, 2004; De Anda and Oberhauser, 2015), we expected that, like flowering stems, those with aphid colonies would attract larger numbers of predators.

## 2. Methods

### 2.1. Experimental setup

This study took place in patches of common milkweed (hereafter referred to as sites) located in and around East Lansing, MI, USA. Each site contained at least 100 milkweed stems, and ranged in area from ca. 40–200 m<sup>2</sup>. We sampled 8 sites in 2017 and 15 in 2018 (Fig. S1.1, Table S1.1). Sites were located in old-fields, agricultural field margins, road or rail rights-of-way, and in one case, an un-mowed suburban lawn. Non-milkweed vegetation within each site was dominated by cool-season grasses (e.g., *Bromus inermis*, *Elymus repens*, *Festuca rubra*, *Phalaris arundinacea*, *Phleum pratense*, *Poa* spp.), with the most abundant sub-dominant forbs and legumes being *Lotus corniculatus*, *Cirsium arvense*, and *Solidago* spp.

We divided each site into three plots of approximately equal area,

with each plot containing at least 30 milkweed stems, and randomly assigned them to one of three treatments. One plot was mowed in mid-June, one in mid-July, and one was left undisturbed. Plots were mowed using gasoline-powered trimmers equipped with brush blades (Stihl™ chisel tooth circular saw blade 4112\_713\_4203), with all vegetation in a plot cut to a height of 5–20 cm (height varied due to the arcing motion with which hand-held trimmers are operated). Thus, some milkweed stems were cut above their lowest node and regrew from axillary buds, while others were cut below the first node and regenerated from buds below ground. The June mowing treatment occurred on June 13–14 in 2017, and June 11–13 in 2018. The July treatment occurred on July 12–13 in 2017, and July 16–17 in 2018. We began sampling in mowed plots when they had produced at least five regenerating stems, which usually took between 1 and 3 weeks depending on the site and year.

## 2.2. Sampling protocol

We collected data weekly, beginning the third week of June in both years. Sampling continued until the fourth week of August in 2017 and the first week of September in 2018. Milkweeds in our region typically emerge in May; we did not sample in May because during this period nearly all stems are newly growing, and oviposition rates are often very low as only a few monarchs have arrived in the region. We sampled 30 stems per plot in 2017, and 20 per plot in 2018. In each plot a single stem was selected randomly, then data were collected from it and its four closest neighbors. Then a new stem was selected, and the process repeated until the required number of stems in each plot had been sampled. If < 20 (or 30 in 2017) stems had regenerated in a plot, all stems were sampled. Before mowing each plot we used the same sampling method to estimate the number of monarch eggs and larvae present to document the direct mortality incurred by this form of disturbance. We recorded the total number of stems in each plot, as well as the number of fruits they produced, at the end of the season.

When sampling each stem we recorded its phenologic stage (vegetative, budding, flowering, or post-flowering). Next, all surfaces of the stem were searched for invertebrates. To assess oviposition we recorded the number of monarch eggs and first instar larvae; since eggs require 2–3 days to hatch and larvae remain in the first instar for 2–3 days, we assumed that all individuals we counted resulted from oviposition within the previous week, i.e., since our last sampling. We also recorded whether aphids were present on each stem, and recorded all predatory arthropods. We categorized arthropods as monarch predators based on established literature (see Table S2.1), on no-choice trials we conducted (Hermann et al., in review), or if they belonged to an overwhelmingly predatory taxonomic group. The full list of predators we considered, with justifications, can be found in Supplement S2.

## 2.3. Testing for differences in survival

In 2018, we deployed sentinel eggs and first-instar larvae to test for differences in their survival among the three treatments. They were harvested from wild-caught monarchs which we kept in colony and allowed to oviposit on common milkweed. After mowing in June, we deployed eggs and larvae on June 25–26 (eggs), July 3 (eggs), July 5–6 (first instars), and July 13 (first instars). After mowing in July, we deployed eggs and first instars in all three plots on August 14 and August 24. In each case our assessment of survival was based on a single egg and/or neonate deployed in each plot, except on July 3 we deployed two eggs in each plot (but still treated the survival rate in each plot as a single replicate). In total, we made 120 assessments of survival across two treatments in each of the 15 sites after mowing in June, and 154 assessments across the three treatments after mowing in July. On the August 14 deployment, we omitted three sites, and on August 24 we omitted two, because milkweed in July-mowed plots had not yet regemerged.

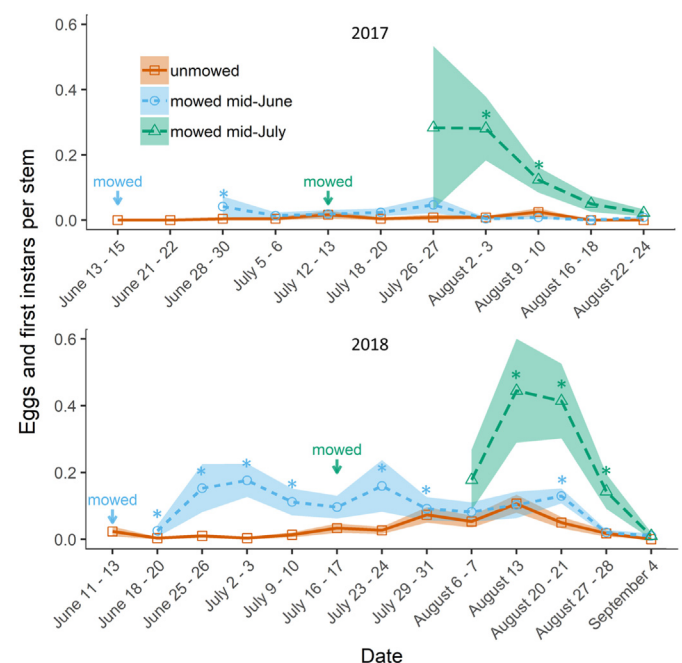
When deploying eggs or larvae we selected a phenologically-

representative milkweed stem close to the center of each plot and placed the individual on a leaf directly below the apex, mimicking natural oviposition behavior (Zalucki and Kitching, 1982). We attached eggs to leaf undersides using tiny amounts of Elmer's™ glue, but placed larvae on leaves' apical surface so they could establish without falling off the plant. We measured survival 48 h, 72 h, or 96 h after deployment; this time interval differed between deployments but was always consistent across the treatments we tested. We have observed that first and second instar larvae do not typically disperse from their natal stem, and thus during a < 96 h period a larva will remain and feed on a stem where it is placed unless predated. Depending on weather conditions, some eggs hatched after deployment, in which case we assessed survival of the resulting neonates.

## 2.4. Statistical analysis

All analyses took place in R 3.4.4 (R Development Core Team, 2018). Data from the two years of the study were analyzed separately. Within each year we partitioned the data into two sampling periods: the first period occurred during milkweed regeneration after mowing in June, and thus consisted of comparisons between June-mowed plots and undisturbed controls. The second period began in early August when stems were regenerating after mowing in July, such that all three treatments could be compared. Weekly data from each plot were compiled and treated as replicates. In the first few weeks after disturbance some plots had produced new stems before others, leading to unbalanced sample size between treatments. When sample sizes were extremely unbalanced we excluded these weeks from analysis, but show all means and standard errors in Fig. 1, noting the weeks for which statistical tests were not performed.

First, we tested whether our disturbance treatments influenced monarch oviposition. Since there were several instances in which no eggs were found in a plot, we used zero-inflated generalized linear



**Fig. 1.** Monarchs laid more eggs on milkweed stems regenerating after disturbance. Points represent mean numbers of eggs and first instars recorded per milkweed stem; shaded areas represent SEM. Asterisks show significant pairwise contrasts within each week, indicating when a given treatment differed from the undisturbed control. Data from July-mowed plots on July 26–27 in 2017 and August 6–7 in 2018 were excluded from analysis because less than half of them had produced regenerating stems leading to unbalanced sample sizes.

mixed models (GLMMs) with Poisson distributions, using the *glmmTMB* package (Brooks et al., 2017). We modeled the number of eggs laid in each plot as a function of mowing treatment, week, and the interaction between these two terms, plus a random effect for site. The number of stems sampled was included as an offset variable since fewer stems were sometimes sampled in the weeks immediately after disturbance. To determine if overall effects of disturbance were significant, we used likelihood ratio tests to compare the full model to a null model that was identical except that it lacked the term for treatment. When likelihood ratio tests indicated a significant effect, we calculated pairwise differences between treatments within each week using estimated marginal means with the *emmeans* package (Lenth, 2016). Our statistical approach was designed to detect differences in oviposition between stem samples in each treatment, but a different approach would be needed to estimate the absolute number of eggs laid at landscape scales, because disturbance influences milkweed stem density and availability throughout the summer. Therefore, we also estimated the total number of eggs laid in each plot each week, accounting for the number of stems that were present. We include results and discussion of this analysis in Supplement S3.

Next we tested for effects of disturbance on predator abundance. We quantified predator abundances (number per stem) using linear mixed models (LMMs) in the *lme4* package (Bates et al., 2015), again using likelihood ratio tests to compare full models with terms for treatment, week, their interaction, and a random effect for site, to null models without the treatment effect. Predator abundance was square-root transformed prior to analysis. Pairwise contrasts were conducted in the same manner as for oviposition. Since regenerating milkweed stems were smaller on average than those left undisturbed, we also repeated this analysis with predator abundance standardized by the number of nodes on each stem (Results in Supplement S2).

We tested for differences in survival of sentinel eggs and first instars using binomial GLMMs. We grouped replicates from either before or after the July-mowed milkweeds regenerated, as in previous analyses. Models included disturbance treatment, trial date, and life stage of the deployed individual (egg vs. first instar) as fixed effects and site as a random effect; model selection was conducted in the same manner as described above, comparing a full model including treatment to a null model without it.

Finally, we tested for effects of plant phenologic stage and aphid presence on predator abundance. In both cases we restricted the analysis to focus on undisturbed plots to avoid confounding plant phenologic stage with other factors. Predator numbers were square root transformed. To test whether predator abundance depended on milkweed phenologic stage, we compared the numbers of predators on stems that were vegetative, budding, flowering, or post-flowering. Since not all stages were represented in all weeks, for this analysis we averaged the number of predators found on stems of each phenologic stage across all weeks when that phenologic stage was present. We then compared models with terms for plant phenologic stage (fixed effect) and site (random effect) to those containing only the random effect using likelihood ratio tests followed with pairwise contrasts. Finally, we tested for similar effects of aphid presence on predator abundance. Since aphids were present in all weeks of the study, we built an LMM with aphid presence/absence, week, and their interactions as fixed effects, and site as a random effect. We compared this model to a null model that was equivalent except that it lacked the term for aphid presence/absence.

### 3. Results

#### 3.1. Oviposition

Monarchs generally laid more eggs on regenerating stems than on those that were left intact (Fig. 1, Table 1). In 2017, mowing in June produced a modest but significant increase in the number of eggs laid

**Table 1**

Results of likelihood-ratio tests to detect whether disturbance treatments affected monarch oviposition and arthropod predator abundance. In each case we compared a model including terms for disturbance treatment, week, their interaction, and a random effect for site to a null model that was equivalent but lacked the term for disturbance treatment. The column for time period partitions the data into two groups: early summer, when we compared June-mowed plots to undisturbed controls, and late summer, following disturbance in July, when we compared effects of all three treatments. Results of pairwise contrasts from these models are included in Figs. 1 and 2.

Response	Year	Time period	$\chi^2_{[df]}$	<i>p</i>
Monarch oviposition	2017	Early	14.85 <sub>[5]</sub>	0.011
		Late	88.77 <sub>[8]</sub>	< 0.001
	2018	Early	84.78 <sub>[8]</sub>	< 0.001
		Late	429.13 <sub>[8]</sub>	< 0.001
Predator abundance	2017	Early	35.12 <sub>[5]</sub>	< 0.001
		Late	58.42 <sub>[8]</sub>	< 0.001
	2018	Early	77.91 <sub>[8]</sub>	< 0.001
		Late	78.19 <sub>[8]</sub>	< 0.001

per stem during the first month of regeneration after disturbance, and stems that regenerated after July mowing received large increases in oviposition. For example, during the first week of August we recorded only two eggs laid on undisturbed milkweeds, but 60 in those that had been mowed in July (raw counts summed across the eight sites). In 2018, oviposition rates were much higher in June-mowed plots relative to undisturbed controls, with significant differences during six weeks from late June to the end of July, and during one week in August. As in 2017, stems regenerating after July mowing were especially attractive to ovipositing monarchs: on August 13 and August 20–21 we found nearly one egg for every two regenerating milkweed stems, mean ( $\pm$  SEM) 0.43 ( $\pm$  0.06) eggs or first instars per stem, compared to 0.08 ( $\pm$  0.01) per stem in control plots and 0.12 ( $\pm$  0.02) in those that were disturbed in June.

#### 3.2. Predator abundance

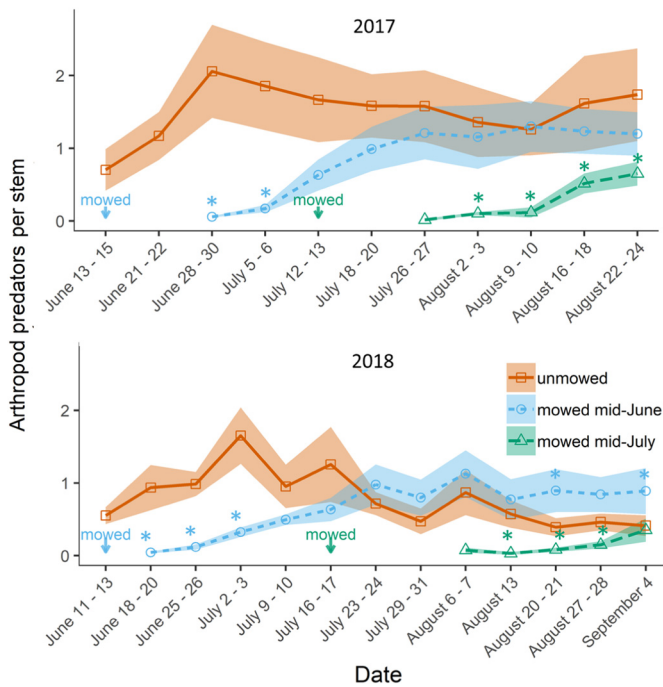
Predators were common on milkweed stems. In undisturbed plots we observed (mean  $\pm$  SE) 1.08  $\pm$  0.03 predatory arthropods per stem (calculated at a per-stem level across all sites, weeks, and both years). Of these observations, 69% were ants, 16% were arachnids, 6% were beetles, 3% were true bugs, and the remainder a variety of other taxa, including lacewings, earwigs, and tree crickets.

Mowing reduced predator abundance on regenerating milkweeds, with predators almost entirely absent in the weeks immediately after mowing and requiring 2–4 weeks to recolonize milkweed stems after they re-emerged (Fig. 2, Table 1). In 2017, there were significantly less predators after mowing in June during two weeks (June 28–30, July 5–6), while predators were significantly reduced for the remainder of the summer after mowing in July. In 2018, predators were suppressed significantly for the first three weeks of milkweed regeneration after mowing in June, and after July mowing they remained significantly reduced until the beginning of September. Also, during late summer 2018 the numbers of predators on June-mowed milkweeds significantly exceeded those on their undisturbed counterparts during two weeks of the study. Effects of disturbance on predators were similar when we standardized predator abundance by plant size (Supplement S4).

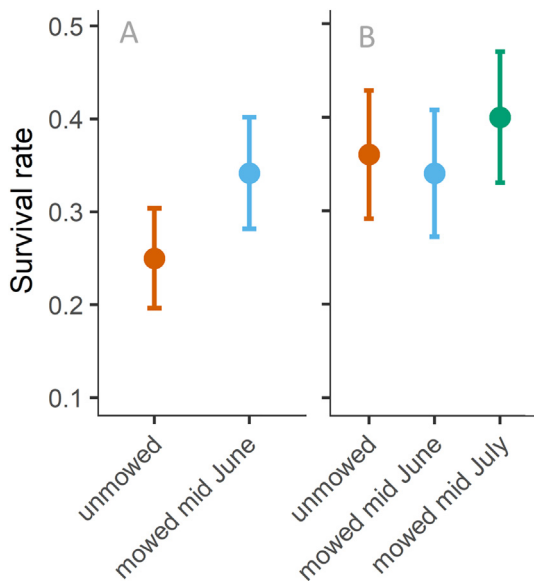
#### 3.3. Egg and larval survival

We did not detect significant differences in survival among disturbance treatments (Fig. 3). In the weeks after June mowing, average survival of eggs and first instars was variable, but averaged (mean  $\pm$  SE) 34.17%  $\pm$  6.00 in mowed plots compared to 25.00%  $\pm$  5.38 in undisturbed plots ( $\chi^2_{[1]} = 1.60$ ,  $p = 0.206$ ). Similarly, later in the summer, July-mowed plots had slightly higher survival on average,



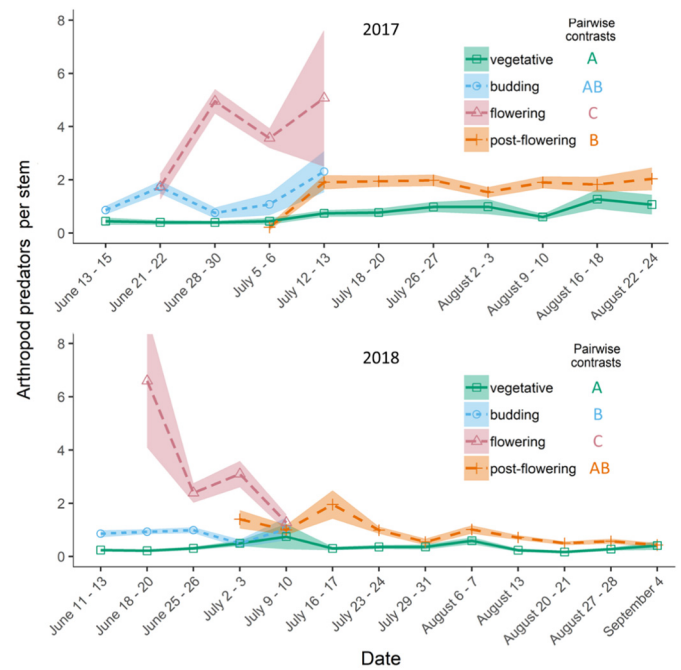


**Fig. 2.** We found less predatory arthropods on milkweed stems that were regenerating after disturbance. Points represent the mean number of predators per milkweed stem, and shaded areas denote the SEM. Asterisks show significant pairwise contrasts within each week, indicating when a given treatment differed from the undisturbed control. Data from July-mowed plots on July 26–27 in 2017 and August 6–7 in 2018 were excluded from analysis because less than half of them had produced regenerating stems leading to unbalanced sample sizes.



**Fig. 3.** Survival of sentinel eggs and first-instar larvae deployed in each treatment. Panel A shows mean ( $\pm$  SEM) survival of eggs and neonates deployed on June 25–26, July 3, July 5–6, and July 13, when milkweed stems were regenerating after disturbance in June. Panel B shows average ( $\pm$  SEM) survival of eggs and neonates deployed in all three treatments on August 14 and 24, when stems were regenerating after disturbance in July.

although the difference was smaller ( $40.00\% \pm 7.00$  compared to  $36.00\% \pm 6.86$  in undisturbed plots;  $\chi^2_{[2]} = 0.44$ ,  $p = 0.801$ ). Direct mortality due to the disturbance itself was minimal: in 2017, across the 8 sites we found no individuals prior to mowing in June and three eggs

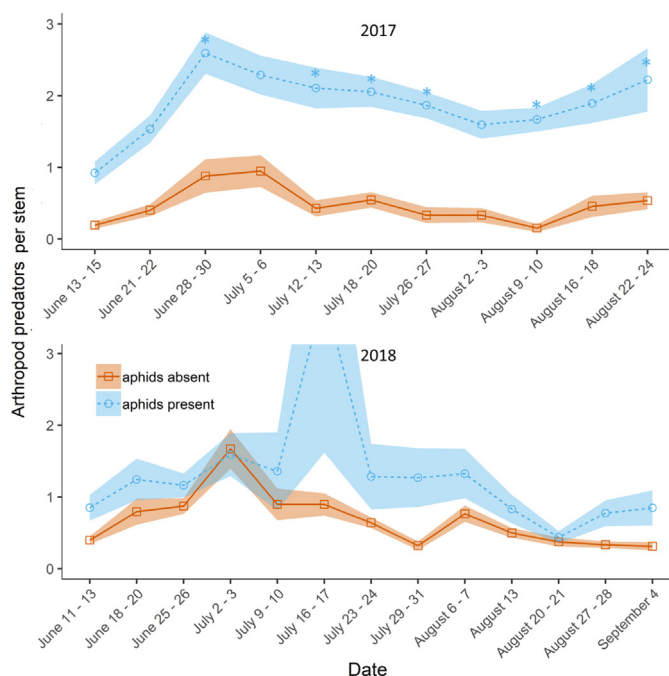


**Fig. 4.** Milkweed phenology influenced arthropod predator abundance. Points represent the mean number of predators per milkweed stem each week, and shaded areas denote the SEM. Since each phenologic stage was represented on only a subset of the weeks of the study, we show pairwise contrasts between stages compiled across the entire season, indicated on the legend in each panel. Phenologic stages not sharing a letter differed significantly. This figure includes data from undisturbed plots only. We omit data points for weeks when  $< 10$  stems of a given phenologic stage were present.

before mowing in July; in 2018, across the 15 sites we found 4 eggs and one larva before mowing in June, and 3 eggs and one larva before mowing in July.

### 3.4. Effects of plant phenology and aphids on predators

Plant phenology was an important predictor of arthropod predator abundance (for 2017,  $\chi^2_{[3]} = 26.00$ ,  $p < 0.01$ ; for 2018,  $\chi^2_{[3]} = 49.95$ ,  $p < 0.01$ ; Fig. 4). In both years, predators were most abundant on milkweed stems that were flowering; on average, flowering stems contained 6.03 times the number of predators as those that were vegetative or budding (raw predator counts, summed across weeks of bloom period, averaged across sites and years). Vegetative stems had fewer predators than more advanced phenologic stages in both years; in 2017 they hosted significantly less than flowering or post-flowering stems (but not less than budding stems); in 2018 they contained less predators than flowering or budding stems (but not significantly less than post-flowering stems). Aphid presence was also a strong predictor of predator abundance (Fig. 5). Averaging across all weeks and both years of the study, stems with aphids contained 3.92 times more predators than stems without aphids. This effect was stronger in 2017 ( $\chi^2_{[1]} = 57.28$ ,  $p < 0.01$ ); in 2018, while there tended to be more predators on aphid-infested stems the overall effect was not significant ( $\chi^2_{[1]} = 10.83$ ,  $p = 0.62$ ). We observed three common aphid species; *Myzocallis asclepiadis*, *Aphis asclepiadis*, and *Aphis nerii*. *Myzocallis asclepiadis* occurred at low levels throughout the summer, usually on leaf undersides. We observed scattered outbreaks of *A. asclepiadis*, mostly in June and July. Finally, we observed large colonies of *A. nerii* which were increasingly prevalent in late summer. The latter two species were tended by ants, but we also observed ladybeetles and lacewing larvae feeding on aphids.



**Fig. 5.** Arthropod predator abundance was higher on stems with aphids. Points represent the mean number of predators per milkweed stem each week, and shaded areas denote the SEM. Asterisks indicate weeks when differences were significant. The plot for 2018 crops out one data point with mean ( $\pm$  SEM) 3.81 ( $\pm$  2.18) on July 16–17. This figure shows data from undisturbed plots only.

#### 4. Discussion

We found evidence that disturbance to grasslands during the growing season increases monarch oviposition and provides a window of time when arthropod predators are less abundant. During some weeks, regenerating stems received more eggs by a factor of 5, 10, or more over those left undisturbed (Fig. 1). Predators were suppressed significantly for as many as four weeks after the milkweed stems re-emerged; this window of time could allow monarchs to hatch and complete the larval stage, or at least reach later larval instars, before the predator community recovers. We did not detect significant differences in survival of eggs and larvae we deployed (Fig. 3). However, in general, survival tended to be higher after disturbance, and we found no evidence that disturbance results in decreased survival. Survival among undisturbed milkweed stems was generally higher later in the summer (Fig. 3A vs. B); we are unsure of why this occurred, but it could be because predator abundance declined in these plots as the summer progressed (Fig. 2).

Importantly, even if egg and larval survival are unaffected by disturbance, conservation objectives could be met simply by increasing individuals' realized fecundity. Most female monarchs die before laying their full complement of eggs (Oberhauser, 1997), suggesting they are limited not by the number of eggs they contain, but rather by time and their ability to find suitable oviposition sites. In intensified agricultural landscapes, this ability has likely diminished (Zalucki et al., 2016; Grant et al., 2018). A recent model (Oberhauser et al., 2017) suggests that increasing fecundity and survival by 2% in the Midwest, or increasing fecundity alone by 4%, would stabilize the overwintering population. While we did not track individual adult monarchs, it seems likely that regenerating milkweeds in our study increased butterflies' realized fecundity. Actual predictions of egg production at landscape scales will need to account for direct mortality due to disturbance, and the opportunity cost associated with the time required for stem regeneration. While our study was not focused explicitly on this question, our data give preliminary evidence that the benefits of disturbance

outweigh the costs (see Supplement S3).

Follow-up studies could examine changes in monarch fecundity in more detail by recording not just the numbers of eggs laid in disturbed vs. undisturbed milkweed patches, but also testing for differences in visitation rates by female monarchs. Future work could also test effects of disturbance on other milkweed species, which are likely respond differently. We note that we treated the unmowed fraction of each milkweed patch as a control in this study, but since milkweed is clonal, defense traits of stems in the undisturbed plots could have been inadvertently affected by disturbance to neighboring areas. Finally, while we interpret weekly counts of monarch eggs as an indication of oviposition frequency, they actually reflect the combined effect of both oviposition and removal rates by predators. Therefore some of the differences we detected could be due to differential predation pressure among the disturbance treatments.

We note that in 2017, predators tended to accumulate on milkweed stems throughout the season, recolonizing over the course of several weeks if plots were disturbed. In contrast, in 2018 predators initially accumulated, but in unmowed plots appeared to diminish as the summer progressed. We suspect this was due to drought, which caused some of the undisturbed stems to senesce relatively quickly; the study area received 26 mm precipitation in July, compared to 70 mm averaged over the previous 5 years (EnviroWeather, 2018). In late July 2018, predators became more abundant on stems that regenerated after June mowing than on control plants. We suspect this was because undisturbed stems had begun to senesce at this time, while June-mowed stems were flowering which likely attracted predators. Mowing in June resulted in more oviposition in 2018 than it did in 2017. This could be because of improved replication in 2018 ( $n = 15$  vs.  $n = 8$ ), or because monarchs were generally more abundant in our area in 2018 (MLMP, 2018). It could also simply indicate that effects of disturbance timing vary inter-annually, with earlier disturbance more beneficial to monarchs in some years than in others.

Interactions between plants, herbivores and predators often involve complex indirect effects (Price et al., 1980), and the extent to which disturbance structures these types of interactions is mostly unexplored. In our study, predator abundance was strongly influenced by plant phenology and by the presence of aphids. Flowering milkweed stems were especially attractive to predators, and budding or post-flowering stems also tended to have more predators than vegetative stems. We noticed multiple predator taxa colonized budding inflorescences, especially spiders and plant bugs (*Plagiognathus* sp., Miridae), which we have observed feeding on monarch eggs (unpublished data). When stems flowered, they were often heavily colonized by nectaring ants. Similarly, aphid colonies on milkweed stems were often tended by ants, and exploited by a variety of other predators, particularly lady beetles and lacewing larvae. It seems likely that increased predator prevalence should result in more predation risk to monarch eggs and larvae, since predation rates on these life stages are generally high (Prysbay, 2004; De Anda and Oberhauser, 2015). However, in our study we did not test this link explicitly. Future work should more directly examine effects of predator abundance and community composition on predation risk to monarchs.

For strategically-timed cutting to be adopted as a management strategy for monarchs, potential benefits and drawbacks will need to be assessed. Impacts on other organisms will need to be considered carefully; for example, such disturbance could either disrupt or attenuate the availability of floral resources to pollinating insects (Meyer et al., 2017) and depending on its timing could impact ground-nesting birds (Frawley and Best, 1991). It is possible that regenerating milkweeds will attract ovipositing monarchs but then result in decreased survival for some other reason, forming an ecological trap (Battin, 2004). In this study our tests of egg and neonate survival provided no evidence of an ecological trap (Fig. 3), but further work is needed to explore this possibility, especially since we detected strong effects on oviposition and this at times resulted in relatively high densities of eggs and larvae.

Possible mechanisms for ecological traps in this system could include density dependent predation or parasitism, or increases in the transmission rate or virulence of pathogens such as the protozoan *Ophryocystis elektroscirrha* (Altizer and Oberhauser, 1999). Additionally, adult monarchs that emerge in the fall are in reproductive diapause as they migrate south. Diapause induction is largely a function of day length and temperature, but it can also be influenced by diet quality (Hunter and McNeil, 1997). Evidence thus far is mixed as to whether milkweed nutritional quality influences diapause in monarchs (Goehring and Oberhauser, 2002), and further study is needed to ensure that monarchs feeding on regenerating milkweeds in late summer or early fall still receive appropriate diapause cues. Finally, future work should measure effects of disturbance on milkweed defenses like cardenolides and latex, both of which can influence monarch fitness (Zalucki et al., 2001; Rasmann et al., 2009).

It is well known that large amounts of monarch breeding habitat have been eliminated from crop fields in the US Midwest (Flockhart et al., 2013, 2015; Oberhauser et al., 2017; Stenoien et al., 2018; Thogmartin et al., 2017b). However, in addition to habitat loss per se, monarchs have also undergone a habitat shift away from milkweed in crop fields and towards perennial grasslands where remaining milkweed stems are currently found. Monarchs may have historically benefitted from the frequent disturbances associated with annual agriculture, and our study suggests targeted growing-season disturbance in perennial grasslands could enhance habitat quality for monarch butterflies by providing phenologically-attractive host plants and the potential for enemy-free space. Habitat management efforts that include targeted grassland disturbance should be considered as a strategy to maximize monarch fecundity and immature survival.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.03.007>.

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