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Monarch butterfly host plant (milkweed Asclepias spp.) abundance varies by habitat type across 98 prairies

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Abstract

The decline in migratory monarch butterflies (*Danaus plexippus*) over the past 20 years has been attributed to several drivers, including loss of their host plants (milkweeds *Asclepias spp.)*. This has sparked widespread interest in milkweed ecology and restoration. We developed a model on environmental and habitat type variables to predict milkweed abundance by sampling 93 prairie plantings (47 conservation plantings and 46 roadsides) and five unplowed prairie remnants throughout the state of Iowa, U.S.A. Milkweeds were censused in 10-25 random locations within each site, and data on plant diversity, age of planting, soil characteristics, and management were tested as predictors of abundance. Milkweed densities of all species combined were highest in remnant prairies (8,705 stems/ha), intermediate in roadside plantings (1,274 stems/ha), and lowest in conservation plantings (212 stems/ha). Most milkweeds were common milkweeds *Asclepias syriaca*, which were more abundant in roadside than conservation plantings. Remnants contained the most milkweed species. Total milkweed and common milkweed abundance were both predicted by higher soil pH, a more linear site shape, and lower soil bulk density across restorations. Our results indicate that common milkweed is maintained by disturbance, and establishes readily in rural roadside habitat. Remnants are important as reservoirs for multiple milkweed species and should be protected.

Keywords

Monarch, Danaus plexippus, Milkweeds, Asclepias, Restoration, Soil pH

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Monarch butterfly host plant (milkweed *Asclepias* spp.) abundance varies by habitat type across 98 prairies

Running Head: Milkweed abundance in prairie habitats

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ABSTRACT

The decline in migratory monarch butterflies (*Danaus plexippus*) over the past 20 years has been attributed to several drivers, including loss of their host plants (milkweeds *Asclepias spp.)*. This has sparked widespread interest in milkweed ecology and restoration. We developed a model on environmental and habitat type variables to predict milkweed abundance by sampling 93 prairie plantings (47 conservation plantings and 46 roadsides) and five unplowed prairie remnants throughout the state of Iowa, U.S.A. Milkweeds were censused in 10-25 random locations within each site, and data on plant diversity, age of planting, soil characteristics, and management were tested as predictors of abundance. Milkweed densities of all species combined were highest in remnant prairies (8,705 stems/ha), intermediate in roadside plantings (1,274 stems/ha), and lowest in conservation plantings (212 stems/ha). Most milkweeds were common milkweeds *Asclepias syriaca*, which were more abundant in roadside than conservation plantings. Remnants contained the most milkweed species. Total milkweed and common milkweed abundance were both predicted by higher soil pH, a more linear site shape, and lower soil bulk density across restorations. Our results indicate that common milkweed is maintained by disturbance, and establishes readily in rural roadside habitat. Remnants are important as reservoirs for multiple milkweed species and should be protected.

Keywords: Monarch, *Danaus plexippus*, Milkweeds, *Asclepias*, Restoration, Soil pH,

Implications:

- Common milkweed (*Asclepias syriaca*) was the most common host plant species of the charismatic monarch butterfly in restorations. Abundance was associated with factors related to disturbance, suggesting that disturbance may be useful for increasing milkweed abundance.
- Unplowed remnant prairies in preserves provide the best habitat for all host plant species, and they should be located and protected whenever possible. However, the area of remnant prairies is much smaller than restored prairies.
- The most economically feasible strategy for establishing the conservation goal of an additional 1.6 million milkweed stems in the Midwestern US may be to establish milkweeds in rural roadside habitat.

INTRODUCTION

Monarch butterfly (*Danaus plexippus*) populations are in decline across North America (Vidal & Rendón-Salinas 2014). Two populations occur in North America: the eastern population east of the Rocky Mountains (the focus of this paper), and a smaller one along the west coast (Brower 1995). The eastern monarch butterfly population has a unique migratory behavior, travelling from their breeding range in central to northeastern USA down to a single overwintering site in the mountains of central Mexico (Brower 1995). Stable isotope studies have indicated that the source of the individuals in the Mexican overwintering site is primarily from the Midwest (Wassenaar & Hobson 1998, Flockhart et al. 2017). The size of the migratory population declined drastically between 1993 and 2013 (Vidal & Rendón-Salinas 2014), and recent data indicate that the population covered only 2.5 ha of the overwintering site in 2017-18, representing a 56% decline from the 24-year average of 5.7 ha (Monarchwatch.org).

Monarch caterpillars are host specific on multiple milkweed (primarily *Asclepias* in the family *Asclepiadoideae*) species (Brower 1969, Brower et al. 1984, Endress & Bruyns 2000). Within Iowa, there are 17 species of *Asclepias* milkweeds, plus the vining milkweed *Cynanchum leave* (Eilers and Roosa 1994). Oviposition and larval survival studies have examined whether monarchs select and survive preferentially on certain milkweed species. An early study found that pupation length, fecundity, and fertility did not differ among monarchs feeding on one of four different species of milkweed (Erickson 1973). Ladner & Altizer (2005) found evidence for oviposition preference across four host plant species, but monarchs utilized all four species examined at least to some extent. Similarly, a study of nine milkweed species found that monarchs laid eggs on all species, with evidence of oviposition preference for *A.incarnata* (swamp milkweed) and *A. syriaca* (common milkweed) (Pocius et al. 2018). Monarch larvae survived on all nine species (Pocius et al. 2017*a,b*). Taken together, these studies indicate that, although there is monarch preference for certain milkweed species, monarchs can utilize all milkweed species, and the abundance of all species should be considered in host plant studies.

Due to the obligate relationship between monarchs and milkweeds, the recent drastic decline in milkweed abundance in Midwestern agricultural land has been proposed as a driver of monarch population declines (Hartzler 2010), i.e., the "milkweed limitation hypothesis" (MLH) (Pleasants and Oberhauser 2013; Flockhart et al 2015; Pleasants et al. 2017). Since the inception of glyphosate resistant crops, the spraying of glyphosate has led to a large decline in milkweeds in crop fields (Hartzler 2010; Pleasants & Oberhauser 2013). This reduction in milkweeds means that the non-cropped areas in the Midwest are becoming increasingly important in supporting monarchs. Several other mechanisms have been proposed as contributing factors to monarch decline, including loss of nectar habitat, forest loss in the overwintering sites in Mexico, reduced nectar sources during fall in the southern USA, and mortality during migration (Inamine et al. 2016, Pleasants et al. 2017, Agrawal & Inamine 2018).

In 2014, a USA presidential memorandum on pollinator health called for an increase in the migratory eastern population to approximately 225 million butterflies, or 6 ha of cover at the overwintering grounds in Mexico by 2020 (Pollinator Health Task Force 2015). The Midwest currently has ~1.3 billion milkweed stems, supporting 3.2 hectares in Mexico (Pleasants et al. 2017). In order to reach the federal goal of 6 hectares, an estimated 1.6 billion new milkweed stems need to be established in the Midwestern U.S. (Thogmartin et al. 2017b). Because of the ubiquity of glyphosate resistant crops in the Midwestern USA, most of these stems will have to be re-established in non-cropped areas (e.g. grasslands, pastures, suburban areas) embedded within agricultural landscapes (Thogmartin et al. 2017a). However, it is poorly known which species thrive in these habitats, how abundant they are, and what habitat factors predict their abundance, the objectives of the current study. We present estimates of milkweed densities in three types of non-crop habitat: roadside prairie plantings, non-roadside prairie restorations, and unplowed prairie remnants. Our goal was to estimate milkweed stem densities in these areas and investigate which site-level factors including soil characteristics, and land management practices, best predict their abundance across habitats.

Milkweeds produce numerous small seeds that disperse widely and have very high germination (Morse and Schmitt 1985), suggesting they are favored by disturbance. Common milkweed is abundant in areas with plowing or other disturbances (Evetts & Burnside 1972) including roads, fencerows, and cleared fields (Bhowmik & Bandeen 1976). Based on this, we predicted that common milkweeds would be most abundant in areas with frequent disturbances. Extending this prediction to our measured variables, we predicted that linear areas with greater edge effects, and sites established more recently would have higher milkweed densities. These variables are associated with having greater colonization and persistence opportunities. Common land management practices including disturbance from mowing and burning may also favor milkweed establishment.

We test the following hypotheses: 1) milkweed abundances will vary across habitat types (roadside plantings, conservation plantings, and unplowed remnants), 2) milkweed abundances will decrease with time since planting, and 3) milkweed abundances will be higher in linear, fertile, and more frequently disturbed sites (e.g., from mowing or burning). We tested these hypotheses by sampling 98 prairie plantings (47 conservation plantings and 46 roadsides) and 5 unplowed remnant prairies across Iowa (Figure 1).

METHODS

SITE SELECTION

We collected data on milkweed abundances throughout the state of Iowa in 93 prairie plantings and 5 remnants. The 93 planted prairie restorations were selected randomly from plantings conducted by the Iowa Department of Natural Resources, other governmental agencies, and the Department of Transportation. Planted prairies were classified as either roadside restorations or "conservation" plantings. Conservation plantings were treated as a different category from roadsides because they were typically less linear in shape than roadsides and were not near a road (Table S2). Roadside plantings were found along gravel and paved roads, and were typically linear in shape. We sampled a total of 47 conservation plantings and 46 roadsides. For roadsides, we randomly selected 12 counties found within each quadrant of Iowa and then randomly selected sites within each county. This resulted in a range of site ages and soil characteristics. All 93 sites were seeded with prairie grass and forb species. Common milkweed (*Asclepias syriaca*) was very rarely seeded (n = 3). Most sites had at least one species of milkweed in the mix, usually either butterfly (*Asclepias tuberosa*) (n = 41), or swamp milkweed (*Asclepias incarnata)*(n = 42). Remnant prairies were defined as sites that were never plowed or over-seeded, and were dominated by native plant species. Four remnants were protected in the Iowa State Preserve system (Doolittle, Cayler, Liska-Stanek, and Marietta) and one was protected locally (Iowa State University's Anderson-Dyas Prairie) (Wilsey et al. 2005).

SAMPLING DESIGN

All sampling was conducted during the month of July during 2015 and 2016. At each site, we censused milkweeds, sampled the overall plant community, and collected soil cores. We located 10-25 sampling locations within each site by following a randomly determined compass direction in each site, or by walking haphazardly through linear habitats. Quadrat tosses were made at randomly chosen distances between plots, with at least 5 m between locations, and plants were sampled exactly where the quadrat landed. At each location sampled, we estimated all milkweed stems in a 3.14 m^2 round plot (1 m radius). We also collected plant species composition data as part of a larger study using point intercept sampling. At each location, a pin was dropped at the four corners of a 20 x 50 cm quadrat, and all plant species present were noted. Species present but not hit were assigned 0.5 hits. Plant community data will be presented in detail in another manuscript, but here we incorporate site level measures of plant diversity and proportion exotic biomass as predictors of milkweed abundance.

Environmental data were collected to test for predictors of milkweed abundance. We collected three soil cores to 10 cm depth (diameter = 1.75 cm). Soil samples were then analyzed for soil pH, bulk density (g/cm^3), and organic matter (Hendershot 1993). Organic matter was estimated with a muffle furnace by placing soil samples in the oven at 375° C for an hour, and then 600° C for 6 hours (Karam 1993). Age of planting was obtained from site managers.

To account for variation in the shape of sites, we calculated the fractal dimension as an indicator of how linear or square the site is with the following equation:

$$\text{Fractal dimension} = \frac{2ln(\frac{\text{perimeter}}{4})}{ln(\text{area})}$$

This measure increases with the linearity of the site, where a line has fractal dimension of two and a square has fractal dimension of one. Thus, more linear habitats have a higher ratio of perimeter to area and have a higher fractal dimension. Site dimensions were calculated using tools in ESRI ArcMaps. After site selection and sampling, we contacted the land managers and obtained information about site age, management history (i.e., mowing and burning regimes), and seed mix used.

STATISTICAL ANALYSES

We tested each hypothesis separately for both total milkweed stem density, and common milkweed stem density alone at the site level using generalized linear models with a negative binomial distribution and a log-link function (Proc GENMOD in SAS 9.4, Littell et al. 2002). Non-normal distributions were used to model milkweed abundance because many sampled sites had no milkweed present. All models included *ln* area sampled as a covariate.

We initially tested generalized linear models using a Poisson distribution, but this distribution did not fit the data well for total (deviance = 16.5), or common milkweed density (deviance = 13.5). The over dispersion in milkweed counts was likely due to the fact that they are rhizomatous plants, and can grow many stems per genet. The negative binomial distribution fit data well for both total milkweed density (deviance = 1.2) and for common milkweed alone (deviance = 1.1).

To test the hypothesis that milkweed density will vary among habitats, we used *a priori* contrasts to test whether 1) milkweed abundances differed between remnants and prairie restoration plantings (conservation plantings and roadsides combined), 2) between conservation plantings and roadsides, and 3) between seeded and unseeded restorations. To test whether milkweed density changed with time since planting, we did a separate generalized linear model with linear and quadratic terms for site age including all predictor variables listed below as covariates. Data on site age was not available for 7 of the 93 restorations, so the remaining 86 were used. Sites varied in age from 1 to 26 years since planting, with an average age of 10 years. The age range was similar between the roadside and conservation restorations, but the conservation areas were older on average (mean of 12.5 years) than roadsides (mean of 7.6 years). Partial (Type III) sums of squares were used to evaluate significance.

We tested whether milkweed stem density was related to environmental and management variables with a model that included soil pH, bulk density, and organic matter, and plant diversity (the exponent of Shannon's index ($e^{H'}$) as a measure of nectar plant diversity. Fractal dimension ($r = 0.61$, $P < 0.001$) and proportion exotic species ($r = 0.39$, $P < 0.001$) were correlated with pH, so only pH was included to prevent problems with inter-correlation. All other predictor variables had low intercorrelations. Management variables included mowing and burning regime categories. Mowing was categorized as: 1) none (*n* = 34), 2) early-establishment mowing (mowing only during years one and two, *n* = 31), 3) "other mowing" including spot mowing, haying, or mowing after the first 2 years (*n* = 20), or 4) unknown (*n* = 8). Burn frequency was classified as none, once, multiple times, or unknown. Size of plantings averaged 5.4 ha and ranged from 0.14 to 61 ha. Shannon's species diversity ($e^{H'}$) spanned from very low diversity sites with 1.2 species equivalents, to very diverse restorations with 25.6 species equivalents. Mowing and burning categories were treated as fixed effects in models. Partial (Type III) sums of squares were used to evaluate significance.

RESULTS

We found milkweeds at 65 of the 93 restored sites (70%, Fig. 2). Milkweed densities varied significantly among habitats (Table 1). Common milkweed was the most commonly sampled milkweed species (59 of 65 sites), but other milkweeds were present, especially in remnant areas. Other milkweed species sampled were butterfly weed *A. tuberosa*, whorled *A. verticillata*, and Sullivant's *A. sullivantii* milkweed. All of these species are clonally growing perennials, in which individual stems (ramets) are connected belowground as genets. We estimated stem densities instead of genet densities to align our numbers to restoration stem targets (Tables 1 and 2).

ALL MILKWEED SPECIES COMBINED

Milkweeds were much more abundant in remnant prairies when all species were considered together (Fig. 2B). The density of all milkweed species was significantly higher in remnants (median 8,705 stems/ha) than restored prairies (median 425 stems/ha) (χ^2= 9.86; p = 0.002) (Fig. 2B, Fig. S1). Within restorations, milkweed density was higher in roadsides than conservation areas, with 1,274 vs. 212 stems/ha respectively (χ^2 = 11.58; p =0.001). Total milkweed stem density was not significantly higher in sites that received milkweed seed (531 stems/ha; n=57) than those that did not (425 stems/ha; n=9)(χ^2=2.63; p =0.1050).

Total stem density was strongly correlated with soil variables and weakly correlated with site age. It was positively related to soil pH (χ^2= 12.68; p =0.0004; Fig 3A) and negatively related to soil bulk density (χ^2= 5.48; p =0.0192; Fig 3C). Soil pH was higher in roadsides than restoration areas, but bulk density was similar among habitat types (Table S2). Milkweed density changed significantly with site age with slightly higher densities at intermediate ages. (Fig. S2A, linear χ^2= 5.63; p =0.0177; quadratic χ^2= 4.83; p =0.0279). No other management or environmental variables were significant (Table S1).

COMMON MILKWEED

Common milkweed was more common in roadsides (Fig. 2A) than in conservation plantings, with median stem densities of 1,062 vs. 127 stems/ha in roadsides and conservation plantings, respectively (χ^2=8.98; p =0.0027). Common milkweed was not significantly different between remnants and restored prairies (χ^2= 0.07; p =0.7901). Similar to total counts, common milkweed density was not significantly different in areas where it was planted than those where it was not, with median 0, and 319 stems/ha respectively (χ^2=1.98; p =0.1590), although sample sizes were small with n = 3 seeded sites compared to 63 not seeded with common milkweed.

Common milkweed density also varied with soil variables, being strongly positively related to soil pH (χ^2=9.98; p =0.0016; Fig. 3B), and negatively with bulk density (χ^2=4.50; p =0.0338; Fig. 3D). Common milkweeds did not vary significantly with site age (Fig. S2B, linear χ^2=1.79; p =0.1807; quadratic χ^2=1.73; p =0.1885). No other variables were significant predictors (Table S1).

DISCUSSION

Declines in milkweed abundance throughout the Midwestern United States have been implicated as an important driver of monarch butterfly population collapse and quasi extinction risk (Semmens et al. 2016). Efforts to increase milkweed stems will rely on information about where milkweeds are currently located, and how to manage land to promote milkweed abundance and persistence (Pleasants 2017). Previous work has documented milkweed densities in several Midwestern habitats, but here we filled in the remaining gaps, and report densities for prairie remnants, restored prairies, and planted roadsides in Iowa (Table 2). The strength of this study is that we present data from 93 prairie plantings and five remnants throughout Iowa, covering a large portion of the central tallgrass prairie region. We assume Iowa is representative of the Midwestern breeding land and reflects similar milkweed densities in habitats across the range. We found that common milkweeds were most common in planted roadsides, and in areas with high soil pH and low bulk density. All milkweed species combined were most abundant in remnant prairies. The planted roadsides we sampled had considerably higher milkweed densities than the conservation areas.

Most milkweeds sampled were common milkweed, which was present at 59 of the 65 restorations (91%) where milkweeds were detected. Common milkweed accounted for 77% of all stems sampled at restored sites, but only 11% at remnants, representing a combined 62%. Among all restorations, we also found *A. tuberosa*, *A. incarnata*, and *A. verticillata*. Among the 5 remnants sampled, we found the four species previously mentioned, as well as *A. sullivantii* and *A. amplexicaulis*. All of these species are potential host plants for monarchs, but this relationship has not been tested for *A. amplexicaulis* explicitly (Pocius et al. 2017). As these other milkweed species are much more common in remnants, future studies should address how they differ from common milkweed in their habitat preferences and response to management practices. The greater number of milkweed species in remnants indicates their value as reservoirs for milkweed species and they should continue to be protected for their value to monarch butterflies. Diversity of milkweed host plants may be an important feature of habitat for monarchs as it may provide more phenological diversity throughout the breeding season (Kaul et al. 1991) or in the case one species fails, having other milkweeds present may help maintain their habitat value for monarchs.

We expected common milkweed density to be highest in younger or medium aged plantings, associated with establishment disturbance, and found some evidence to support this. We found a quadratic relationship between total milkweed density and age after accounting for site management and soil characteristics, where middle-aged planted prairies had more milkweeds. However, this relationship was weaker than relationships with other variables (Fig. S2A).

Consistent with our predictions, we found higher milkweed densities in prairies with higher forb diversity. Zaya et al. (2017) found that milkweeds were more common in species diverse areas in Illinois. When all milkweed species were combined, remnant areas had the highest densities of milkweeds. This effect was weak, but indicates that prairie habitats with more nectar producing plants are also better habitats for milkweeds.

We compared milkweed densities in our sampled habitats to previous estimates from other land uses in the literature (Table 2), including unplanted roadsides, Conservation Reserve Program plantings (CRP), and agricultural habitat (Kasten et al. 2016; Pleasants and Oberhauser 2013; and Pleasants 2017). Estimates of hectares of Iowa roadsides were estimated by Mark Masteller (personal communication), and hectares for remnant areas were from Samson & Knopf

(1994), and Wilsey et al. (2005). Planted prairie area was calculated as the sum of planted areas at National Wildlife refuges, Department of Natural Resource lands and county conservation areas (Karen Viste-Sparkman and Thomas Hazelton personal communications). Our estimates of stem density in planted roadsides were about 80 times higher than previous estimates for unplanted roadsides (Table 2). Milkweed densities may be higher in planted than unplanted roadsides due to the disturbances associated with seeding during establishment. Common milkweed is weedy, and we found that variables related to disturbance were positively correlated with their abundance. Despite this much higher density, they only contributed around five times as many total milkweed stems as unplanted roads due to their smaller coverage in Iowa (Table 2.). We found that restored conservation plantings have about twice the density of a previous estimate for CRP land. However, CRP makes up the largest portion of any habitat type, accounting for over half of the milkweed stems in the state. Agricultural cropland has the lowest density of milkweeds of any habitat surveyed to date, so it contributes very little to the total milkweed stem estimate, despite the extremely high proportion of cropland in the Midwest.

Remnants in Iowa have by far the highest density estimates of any habitat type. Despite being extremely rare on the landscape, we estimate that remnants have about a fifth of the total milkweed stems in the state.

Our results indicate that roadsides could be excellent habitat for new milkweed plantings. We found that planted roadside habitats have orders-of-magnitude higher densities of common milkweed than unplanted roads (Table 2). Because most of the milkweed in restored prairies is common milkweed, roadsides offer a great opportunity for establishing large populations of this monarch butterfly host species. Previous work indicated that planting roadsides with prairie species provides value to rare butterflies due to increased flowering plant species richness (Ries et al. 2001). Increasing larval host-plant density could enhance the value of roadside habitat for monarch butterflies, as long as densities are below saturation levels (Kasten et al. 2016), as most of our densities are here.

Our roadsides differed from previous studies in that they were primarily rural and not urban. McKenna et al (2001) found high Lepidoptera mortality in roadsides near a Midwestern city, especially near roads with high traffic rates. They suggested that traffic is a major form of mortality, which suggests some roadsides may be poor habitat for monarchs. However, in their study, country roads, which are more similar to our rural roadsides, had little to no mortality. Based on this, we suggest that roadsides in rural areas might make the best habitat for milkweed establishment. Future plantings of common milkweeds in rural roadside habitats may be an effective way of establishing these important host plants.

The strong correlation between milkweed density and soil pH needs to be studied further. Soil pH was higher in roadsides than conservation areas, and this may be the primary mechanism explaining the higher milkweed densities we found in roadsides. The relationship between milkweed density and pH could be explained by three different mechanisms, and further work is needed to test among these possibilities. The relationship between milkweeds and soil pH could be a direct cause and effect relationship. If this is so, then fertilizing fields could be leading to greater acidity as NH_3 is nitrified to NO_3^-. Fertilizing fields without liming leads to reduced soil pH (Silvertown et al. 2006), and reduced pH could have reduced milkweed abundance. However, the relationship is correlative, and pH is an integrative measure that is correlated with other aspects of soil fertility. A second possibility is that higher pH is associated with higher calcium and mineralized nitrogen availability (Donahue et al. 1971), consistent with the negative relationship between milkweed abundance and soil bulk density. This could be tested with fertilizer studies that add N and Ca without altering the soil pH. A final possibility is that rocks from gravel roads, distributed by snowplows and other trucks could be causing local soil disturbance, and common milkweed could be responding positively to this disturbance. Further work is needed to separate the correlated effects of linear habitat, disturbance, nutrient availability, and soil pH on milkweed abundance with an experimental approach. Future studies with liming and fertilizer additions could assess what factors are causing milkweed abundances to increase or decrease over time.

In conclusion, we found that the abundance of common milkweed, the most common species sampled, did not vary across habitat types the same way that all milkweed species did. Butterfly, swamp and Sullivant's milkweed were found primarily in highly diverse remnant prairie areas. Thus, remnants are important as reservoirs for these species and should be protected. Common milkweed on the other hand, was most abundant in planted roadsides. Roadside habitat is very abundant in the Midwest. This indicates that the most economically feasible option may be to establish milkweeds in rural roadsides in the Midwest.

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Table 1. Estimates of stem densities per hectare for all milkweeds, and only common milkweed in remnant prairie, and seeded and unseeded roadside, conservation, and all combined restored prairie plantings. Medians are presented with 25% and 75% quantiles in parentheses, and means are presented with standard errors. Estimates for total milkweed densities by habitat include sites that were seeded with any milkweed species, not seeded with milkweed, and sites where it was unknown if milkweed was seeded.

	Statisitc	Remnant	Conservation	Roadside	Restorations Combined
Seeded	N		20	37	57
All Milkweeds	Median		194.6 (0 – 743.1)	1273.9 (212.3 – 4140.1)	530.8 (0 – 3184.7)
	Mean		845.3 (369.1)	3126.5 (733.5)	2326.1 (511.7)
Seeded	N		1	2	3
Common	Median		0 (0)	424.6 (0 – 849.3)	0 (0 – 849.3)
	Mean		0 (0)	424.6 (424.6)	283.1 (283.1)
Unseeded	N		7	2	9
All Milkweeds	Median		127.4 (0 – 424.6)	1804.7 (424.6 – 3184.7)	424.6 (0 – 3184.7)
	Mean		1390.7 (855.6)	1804.7 (1380.0)	1482 (695.5)
Unseeded	N		26	37	63
Common	Median		127.4 (0 – 530.8)	1061.6 (212.3 – 3184.7)	318.5 (0 – 1910.8)
	Mean		850.3 (337.9)	2330.4 (572.2)	1719.6 (373.1)
Total	N	5	47	46	93
All Milkweeds	Median	8704.8 (2070.1 – 14649.7)	212.3 (0 – 1433.1)	1273.9 (212.3 – 4246.3)	424.6 (0 – 2707.0)
	Mean	9522.3 (3660.4)	920.7 (225.7)	3259.5 (664.2)	2077.5 (366.7)
Total	N	5	47	46	93
Common	Median	849.3 (159.2 – 1592.4)	127.4 (0 – 636.9)	1061.6 (212.3 – 3184.7)	318.5 (0 – 1592.4)

	Mean	934.2 (400.2)	736.6 (212.0)	2486.0 (553.5)	1601.9 (306.2)

Table 2. Estimates of milkweed stems in Iowa, including new data from this study (*). Data are presented as means and standard errors (SE) to be comparable to earlier published estimates.

	stems/ha	SE	ha in Iowa	total # stems	SE
Planted Roadsides (total)	3259.5*	664.2	21,892	71,356,337	14,541,050
Asclepias syriaca	2486.0*	553.5			
Other *Asclepias*	773.5*	381.1			
Conservation Areas (total)	920.7*	225.7	39,014	35,920,847	8,804,687
Asclepias syriaca	736.6*	212.0			
Other *Asclepias*	184.1*	93.7			
Remnants (total)	9,522.3*	3,660	12,400	118,076,433	45,389,014
Asclepias syriaca	934.2*	400			
Other *Asclepias*	8588.1*	4,044			
Published studies					
Corn/ Soybeans	0.12		9,360,000	1,130,000	
CRP	413.4		663,000	274,084,200	
Unplanted Roadsides	36		365,189	13,146,804	
Sum				513,714,621	

Figure 1. Site locations. Background map outlines major Iowa Landforms.

Figure 2. Stem densities (x axis) and number of sites (y axis) containing common milkweed (A), and all milkweeds (B) across 93 restored prairies and five remnants.

Figure 3. Relationships between soil pH and bulk density and all milkweed species (A, C)) and common milkweed density (B, D). Milkweed densities are adjusted for other variables in the model. Insets show fitted model with 95% confidence interval.

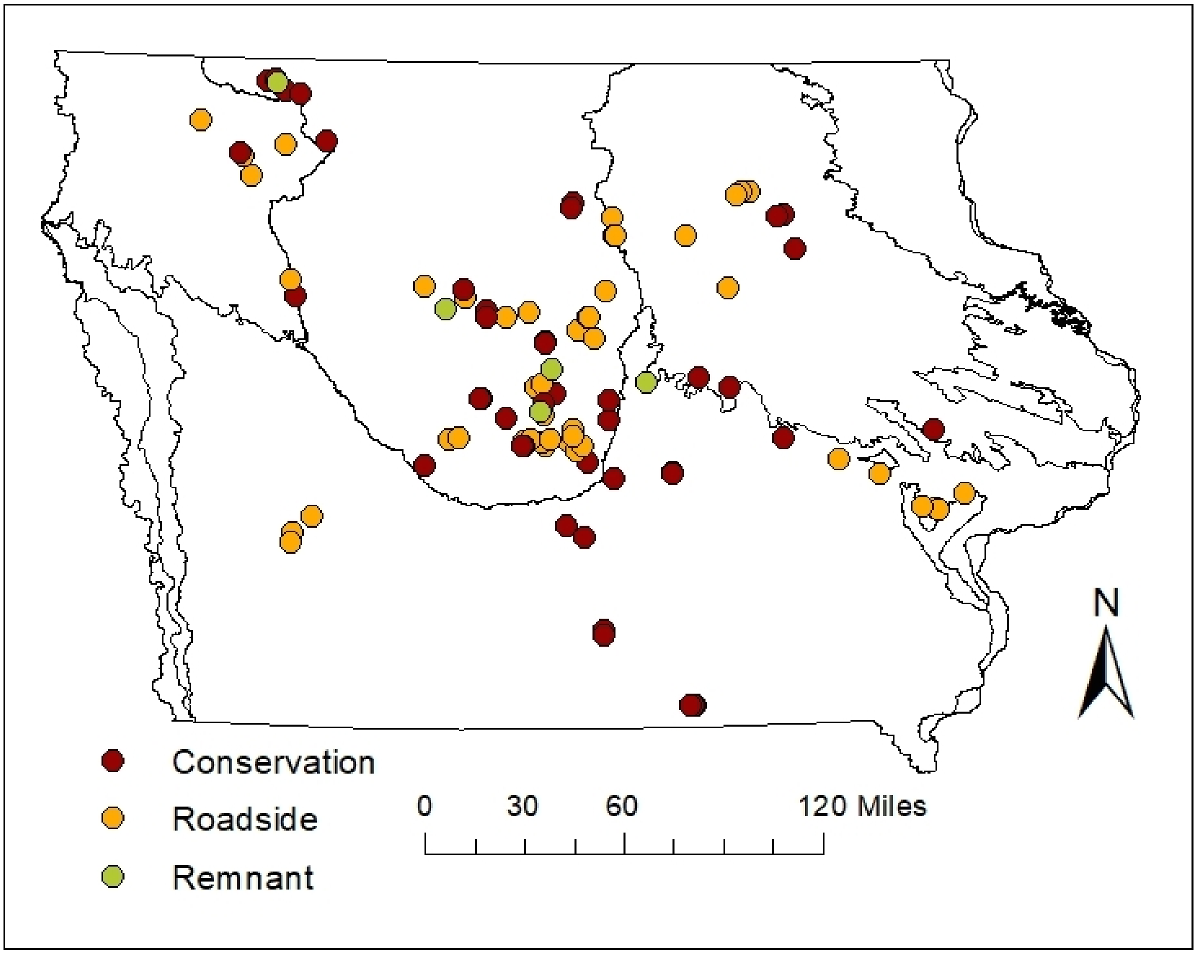
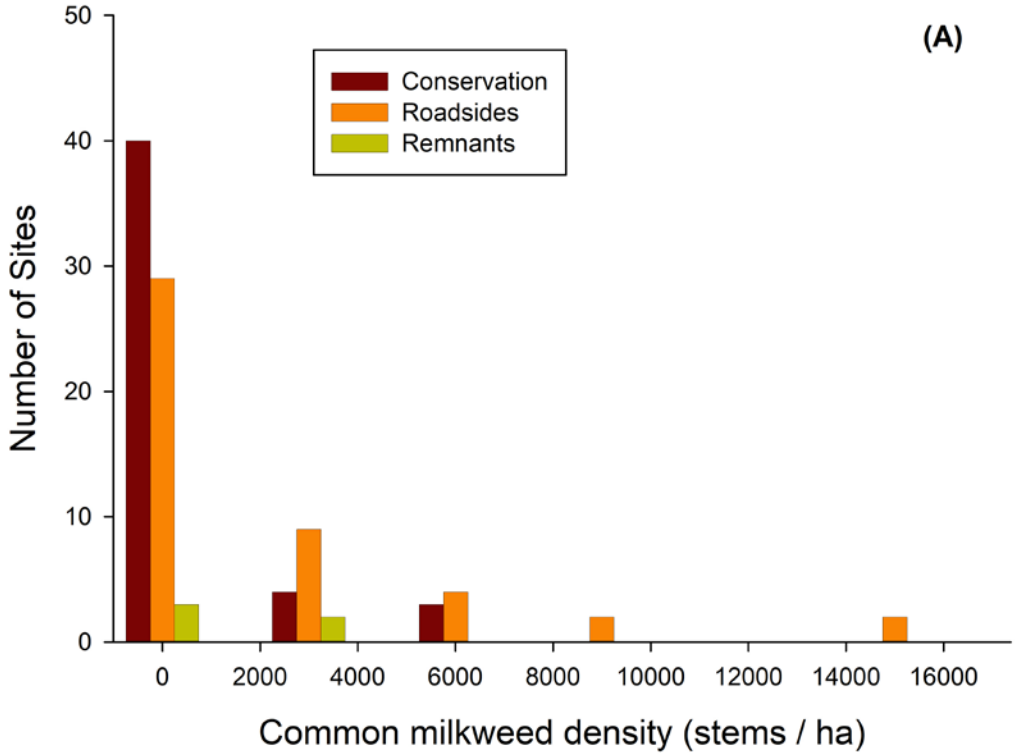


Figure 1.


(A)
Conservation
Roadsides
Remnants
Number of Sites
50
40
30
20
10
0
0
2000
4000
6000
8000
10000
12000
14000
16000
Common milkweed density (stems / ha)

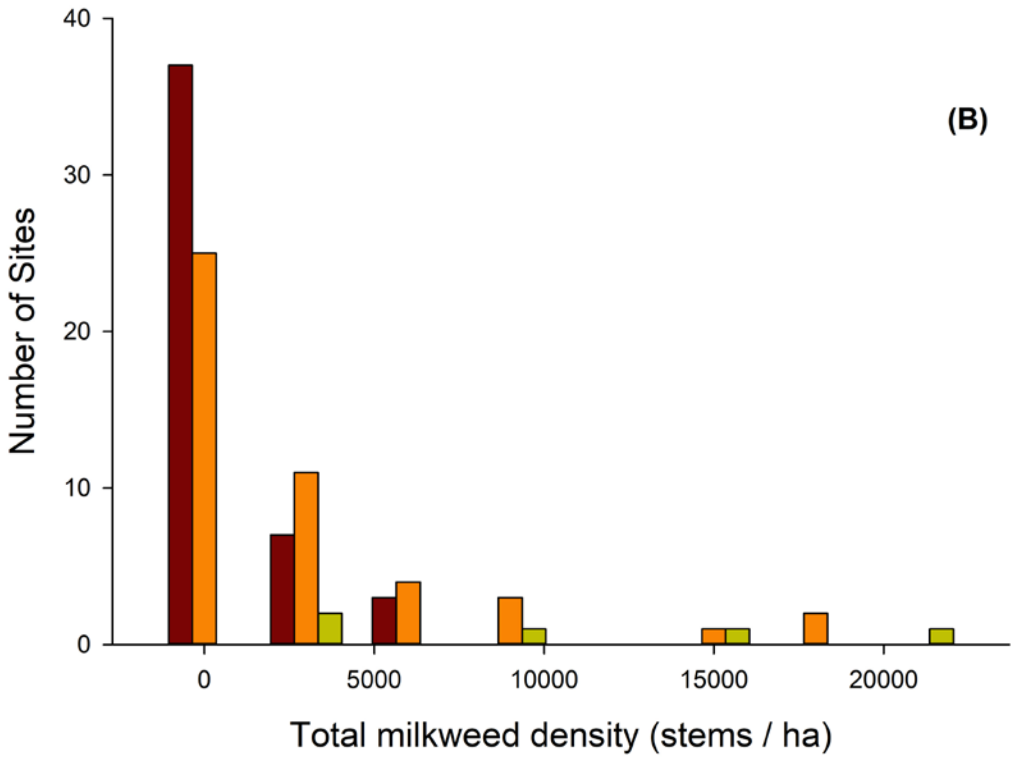

(B)
Number of Sites
40
30
20
10
0
0
5000
10000
15000
20000
Total milkweed density (stems / ha)

Figure 2.

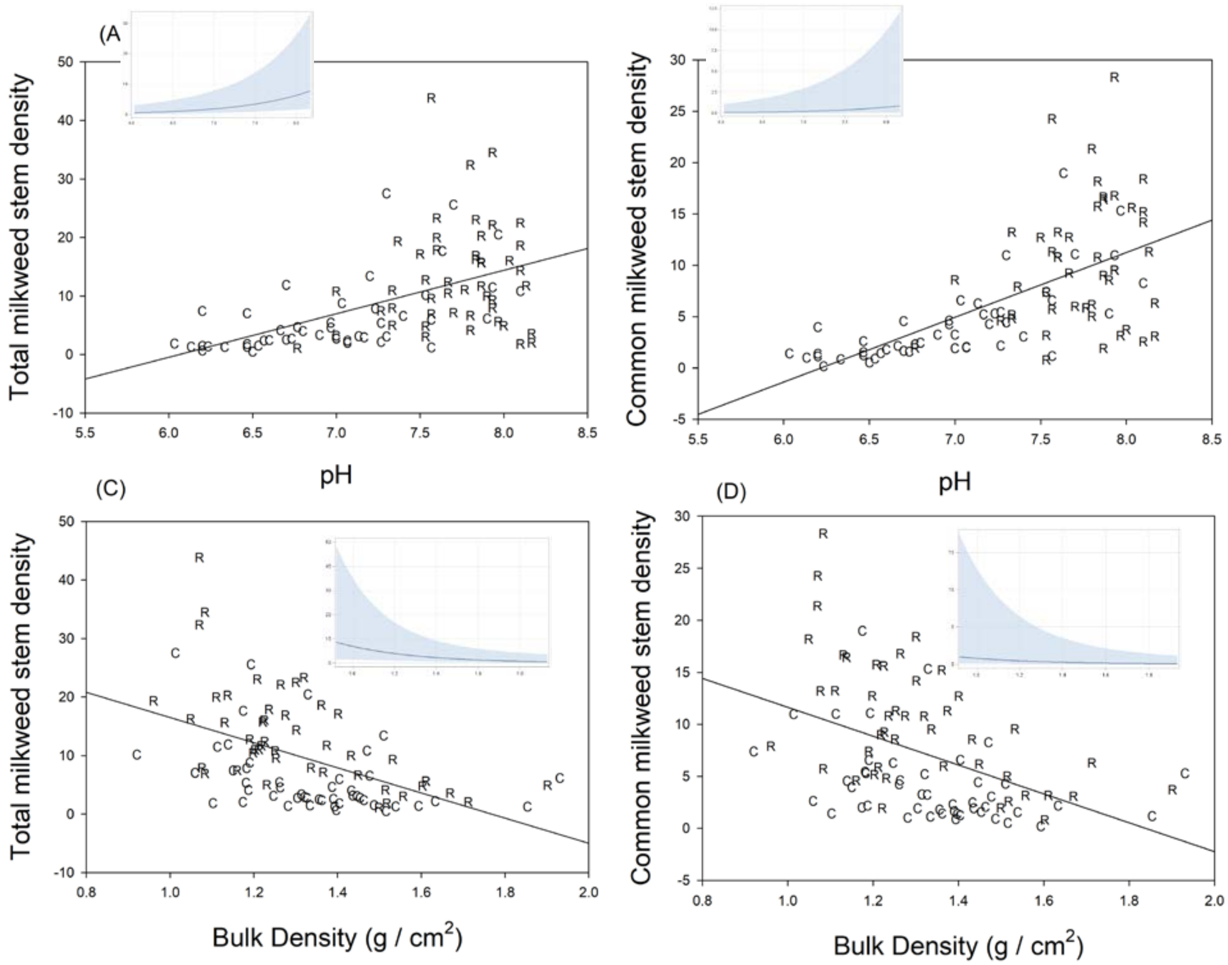


Figure 3.