Milkweed and floral resource availability for monarch butterflies (*Danaus plexippus*) in the United States

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The global decline of pollinators, particularly insects, underscores the importance of enhanced monitoring of their populations and habitats. However, monitoring some pollinator habitat is challenging due to widespread species distributions and shifts in habitat requirements through seasons and life stages. The monarch butterfly (*Danaus plexippus*), a migratory insect pollinator that breeds widely throughout North America, presents a unique case study for testing a sampling framework to overcome these challenges. Monarchs exhibit discrete resource needs across life stages (e.g., larval requirement for milkweed, adult requirement for floral nectar), utilizing many land use types across their extensive geographic range during breeding and migration seasons. The Integrated Monarch Monitoring Program (IMMP) uses a standardized protocol with a generalized random tessellation stratified (GRTS) sampling design to gather spatially balanced and ecologically representative information on monarch habitats within the United States. The IMMP is applicable to various land use types and habitats used by breeding monarchs and may be extended to sites outside of the GRTS design to collect data on non-random sites of interest, such as legacy or conservation sites. Additionally, the IMMP's modular design and publicly available training allows for broad participation, including involvement from community scientists. Here, we summarize habitat metrics (milkweed and floral resources) across 1,233 sites covering much of the monarch's breeding range. We examine variation in milkweed density and floral resource availability on probabilistic (random) and non-probabilistic (convenience) samples and among land use types (site types). Additionally, we assess resource availability within core geographies for monarch breeding and migration, specifically within the U.S. Fish and Wildlife Service's Monarch Conservation Units (western, northern, and southern United States). Milkweed density, floral frequency, and floral richness were higher on non-random sites and in the North region. Among site types, milkweed density was highest on Rights-of-Way and Unclassified Grassland, while floral frequency was lowest on Rights-of-Way. The IMMP represents the first field-based habitat monitoring program of this scale for monarchs, yielding a robust dataset on monarchs and their habitats across their breeding range and offering a framework for surveying the habitat of insect species with diverse habitat requirements or widespread distributions.

KEYWORDS

monarch butterfly, milkweed, *Asclepias*, floral resources, habitat assessment, monitoring, community science, pollinator

1 Introduction

The precipitous decline and continued risk of extinction facing the North American migratory monarch butterfly (*Danaus plexippus*) population could be better understood by improved monitoring of their breeding populations and habitats. Given that the monarch's decline has been linked to loss of breeding habitat (Pleasants and Oberhauser, 2013; Flockhart et al., 2015; Pelton et al., 2019) and, more recently, shifting climatic conditions (Zylstra et al., 2021, 2022), increasing the quantity and quality of breeding habitat has become a widely recommended strategy to compensate for historical habitat losses and create a more resilient landscape for their breeding and migration (Pleasants, 2017; Thogmartin et al., 2017). Additionally, sizable knowledge gaps persist with regard to the monarch's spatiotemporal distribution, status and trends, and sensitivity to environmental change in certain geographies and land uses. Expanding our knowledge of monarch habitat throughout its breeding range would not only enable the conservation community to more effectively prioritize conservation strategies, identify and mitigate threats, and adapt habitat management techniques, but also help meet regional and national initiatives to map and quantify changes in habitat.

Although many options to inventory and monitor pollinators at large scales have been explored or proposed (Williams et al., 2001; Lebuhn et al., 2013; Woodard et al., 2020), no pollinator habitat monitoring programs have been successfully implemented broadly across the North American monarch's breeding range, and none include both key components of productive monarch breeding habitat: floral resources and milkweed host plants. While many methods to inventory and monitor monarch habitat have been utilized at local scales (e.g., Hartzler and Buhler, 2000; Zaya et al., 2017; Dinsmore et al., 2019; Kaul and Wilsey, 2019; Svancara et al., 2019; Waterbury et al., 2019; Lukens et al., 2020; Spaeth et al., 2022), few have been implemented at large scales (Cariveau et al., 2019a, b) and have been met with limited success (e.g., Garfinkel et al., 2023). As such, existing assessments of milkweed host plant and nectar availability, along with monarch population viability, have largely been derived from small, localized datasets and expert opinion (Koh et al., 2016; Semmens et al., 2016; Cariveau et al., 2019a). Recognizing this data gap, a collaboration of scientists piloted the Integrated Monarch Monitoring Program (IMMP)[1] to assess key metrics of monarch and pollinator habitat, reproduction, adult resource use, larval survival, and parasitism, and to track trends in these metrics through time (Cariveau et al., 2019b).

The IMMP's vegetation monitoring protocol quantifies metrics specific to monarch habitat requirements (e.g., milkweed density) as well as data more broadly applicable to grassland pollinators (e.g., floral resource availability). In addition to accommodating conservation lands typically monitored for wildlife, the IMMP prioritizes a suite of randomly selected sites to gather a spatially and ecologically representative assessment of pollinator habitat across the United States. The protocol was tested by researchers and federal agencies in 2016 and by conservation professionals and community scientists in 2017, after which methods were modified slightly to improve efficiency of data collection procedures.

Here, we summarize the status of monarch and pollinator habitat through the lens of the IMMP, comparing milkweed and floral resources across geographical regions, land use types, and other site characteristics. These metrics can aid in refining our understanding of resource availability across the U.S. landscape and in turn, updating current habitat and population targets to guide conservation action.

2 Materials and methods

2.1 Study area

The Integrated Monarch Monitoring Program (IMMP) incorporates sampling on both random and non-random sites across the contiguous United States. Random sites are distributed such that they depict an unbiased representation, or background level, of milkweed and floral resources on the landscape. Random sites were generated via a generalized random tessellation stratified (GRTS) process, which ensures spatial balance and unbiased representation through stratified randomization. This method can represent multiple strata, reducing parameter estimate variability (Loeb et al., 2015). The IMMP GRTS process resulted in a spatially balanced set of locations within 10 × 10-km grid cells across the contiguous United States (Weiser and Thogmartin, 2018; Cariveau et al., 2019b). In areas east of the Rocky Mountains, random site locations are distributed among five land use types (hereafter 'site types'; Table 1). Participants verify site type during their first survey and rectify any geographic information system errors to ensure alignment with the categories defined in Table 1. Due to the patchiness of milkweed occurrence in the western United States, random sites are distributed among three estimated levels of milkweed habitat suitability (low, medium, high) (Dilts et al., 2019). Upon the first visit to a site, observers assign one of the site types defined in Table 1 for consistency with areas east of the Rocky Mountains. Non-random sites are selected by participants and must align with one of the site types described in Table 1.

Three site types are not represented in the GRTS draw but are included as a site type in the IMMP: Agricultural Conservation Land, Agricultural Edge, and Forest. Random Agricultural Conservation Land sites could not be pre-determined because spatial data for federal conservation programs (e.g., Conservation Reserve Program) are not publicly available. Instead, they may be selected by participants or identified when monitoring a random site that is found to be enrolled in a conservation program. Agricultural Edge sites are generated when paired with Agricultural Cropland surveys. Although monarchs are primarily associated with open habitats, we added the type Forest for cases in which observers selected a forested site containing monarch habitat (milkweed).

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1 https://monarchjointventure.org/mjvprograms/science/integrated-monarch-monitoring-program

Site Type	Code	Identifying Features
Protected grassland	PGS	Protected wild lands that are not forested; includes grassland, savanna, desert, and shrubland; herbaceous plants dominant; federal, state, county, and local public land; private land under conservation easement
Unclassified Grassland	UGS	Unprotected wild lands that are not forested; includes grassland, savanna, desert, and shrubland; herbaceous plants dominant; private land with no known conservation easement
Agriculture	AGC[2]	Crop fields: row crops, orchards, vineyards, etc.
	AGE[1,2]	Field edges with non-crop vegetation: fence row, in-field habitat strips, etc.
	ACL[1]	Conservation land that is enrolled in an agricultural conservation program (e.g., Conservation Reserve Program); excludes tree plantings
Rights-of-way	ROW	Roads with right-of-way habitat ≥ 4 m wide and safe parking/accessibility; power/transmission lines; some rail corridors
Developed	DEV	Areas associated with residential, commercial, industrial, or public development in rural, exurban, suburban, or urban areas; includes parklands and habitat within developed areas
Forest	FOR[1,2]	Areas characterized by tree cover (natural or semi-natural woody vegetation, generally more than 6 meters tall); tree canopy accounts for 25% to 100% of the cover

[1]Several site types were not present in the GRTS process: ACL, AGE, and FOR. Spatial data for federal ACL programs are not publicly available. Forest is not a primary land use containing monarch habitat (Bhowmik and Bandeen, 1976; Hartzler and Buhler, 2000). AGE sites are generated when paired with AGC sites.
[2]AGC, AGE, and FOR sites were excluded from analyses due to low representation in our sample.

2.2 Field survey methods

The IMMP instructs observers to begin monthly surveys when vegetation emerges in the spring until senescence in the fall for northern latitudes. In southern latitudes (below approximately 38 degrees N), spring and fall surveys are recommended to assess habitat condition and use by monarch butterflies during the time periods in which monarchs are present. Although the IMMP provides recommendations for survey frequency and timing, data recorded at any interval are accepted.

The IMMP is modular and consists of four protocols or "activities," designed to quantify metrics associated with (1) monarch habitat, (2) monarch eggs and larvae, (3) adult monarch

butterflies, and (4) monarch parasitism. Habitat surveys followed the IMMP's Activity 1: Milkweed & Blooming Plant Survey protocol, in which observers select a ≥0.4 hectare area, hereafter "plot," (typically a 1-ha square or rectangle) within the site of interest to conduct monitoring (Cariveau et al., 2019b; Monarch Joint Venture, 2021). When monitoring large sites (>5 hectares), surveyors may have placed multiple 1-ha plots within the site area to characterize the habitat more fully. In those cases, we averaged metrics from the plots to avoid pseudo replication. Plot location within non-random sites is either randomly determined or selected by the observer to represent a particular area; at random sites, plots are oriented from the latitude and longitude of the random point in the IMMP GRTS draw.

The IMMP's standard Activity 1 contains three options, of which the observer may conduct one to three: a milkweed survey, a blooming plant survey, and a meander survey (Figure 1). To conduct a milkweed survey, observers surveyed 100 1-m^2 subplots (0.5 m × 2.0 m) at 5-m increments along 500 m of parallel transects. In 2016 and 2017 as the IMMP was piloted, parallel transects were spaced across the entire site following methods outlined in Lukens et al. (2020). Within each subplot, observers recorded the number of milkweed plants and stems by species. Milkweed stems separated by soil were recorded as distinct plants, regardless of whether they were clonal or genetic individuals (following Kasten et al., 2016; Lukens et al., 2020).

To conduct a blooming plant survey, observers surveyed subplots along transects as described above for milkweed. They recorded the presence of non-grass flowering plants in bloom (hereafter, flowering plants) within the subplot frame to measure floral frequency. Observers either (a) identified each flowering plant to species (Level A), or (b) recorded the presence/absence of any flowering plants, without identifying the species (Level B).

For the meander survey, observers walked throughout the plot and recorded milkweed and flowering plant species. In addition to
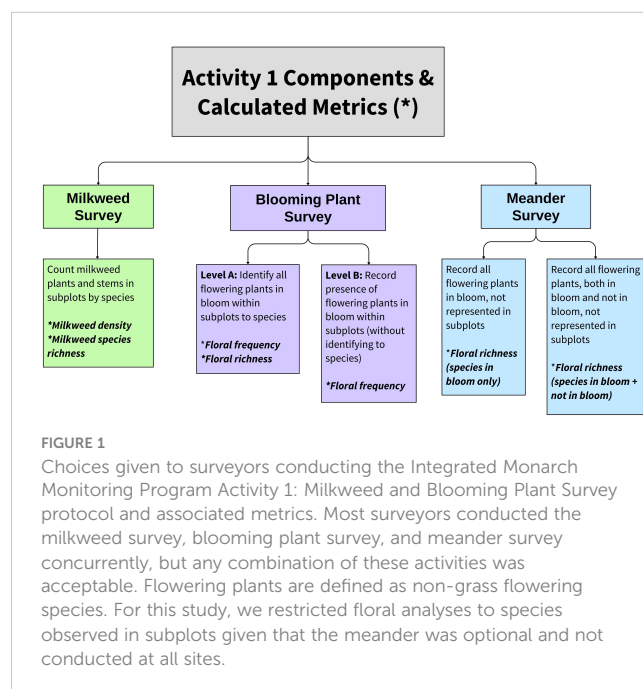
FIGURE 1
Choices given to surveyors conducting the Integrated Monarch Monitoring Program Activity 1: Milkweed and Blooming Plant Survey protocol and associated metrics. Most surveyors conducted the milkweed survey, blooming plant survey, and meander survey concurrently, but any combination of these activities was acceptable. Flowering plants are defined as non-grass flowering species. For this study, we restricted floral analyses to species observed in subplots given that the meander was optional and not conducted at all sites.

flowering plant species, observers could optionally record non-grass flowering species that were not currently in bloom and denote them as such. If a milkweed survey or blooming plant survey was conducted on the same date, only novel species were recorded in the meander survey.

Although sites ≥0.4 ha are encouraged in order to accommodate standard survey methods, any size site may be sampled using a modified 'census' Activity 1 survey. Instead of sampling via subplots, observers counted all milkweed plants present within the plot by species and/or recorded all flowering plant species present. Thus, floral frequency is not available for these surveys.

2.3 Participant training

Participants received training through either in-person workshops or through self-guided online modules. In-person training workshops were conducted by Monarch Joint Venture staff (MJV) over the course of 1–2 days. Training included both classroom instruction as well as field protocol and plant identification practice, typically involving identifying several examples of milkweed and flowering plant species. Online training modules contain a written guidebook and instructional videos, covering all aspects of the program including field protocols, plant identification, navigation, and data entry.

2.4 Data validation

Data were either entered directly into an online database during field surveys or transferred to the database from paper records. To minimize errors, the database was preloaded with plant lists sourced from the USDA Plant Database (United States Department of Agriculture (USDA) and Natural Resources Conservation Science (NRCS), 2022), restricting users to select and enter only species previously recorded within a given state. In cases where a species was found on a survey but unavailable in the database, the species was manually submitted to the database manager. The manager then verified with participants that the species was accurately identified to the best of their knowledge, not a similar species in the region, before adding it to the database list for that state. Additionally, the database allowed users to record flowering plant species by genus, used in cases where species identification was uncertain. Data managers cross-referenced electronic records with paper datasheets, when provided, and rectified any discrepancies.

2.5 Statistical analysis

2.5.1 Overview

We performed statistical tests in the R statistical programming language (version 4.2.2; R Core Team, 2021). We used mixed-effects logistic regression and zero-inflated negative binomial regression to examine whether site type (land use), region, and site selection type (random versus non-random) predicted milkweed density, floral richness, and floral frequency, as described in the respective sections

below. Three site types were excluded from analyses due to low representation in our sample: Forest (n = 1), Agricultural Crop Field (n = 15), and Agricultural Edge (n = 83). Sites were grouped into three broad regions of North, South, and West based on U.S. Fish & Wildlife Service (USFWS) Monarch Conservation Units (Figure 2). We included two additional covariates in the models to account for sampling differences among plots: transect layout (to account for differences in transect placement in the early (2016–2017) and later stages (2018–2022) of the program), and survey type (standard versus census surveys). Because plant phenology changes over the annual cycle, we included a covariate for day of year (day 1 = 1 January). To account for variable search area in the flowering plant surveys, we considered an additional covariate, the area sampled ($100m^2$ for standard surveys, variable for census and irregular surveys).

We used a two-step process to (a) select spatial and temporal random effects to include in null models for each response variable, and (b) compare models containing the modified null model and additional combinations of fixed effects. We considered plot identity as a random effect in the null model to account for expected but unmodeled spatial heterogeneity at the site level as well as repeated measures. We also controlled for temporal variation by considering year and month-nested-in-year as random effects.

For each response type, a global model comprising all fixed and random effects was evaluated for appropriate goodness of fit. For the floral frequency and richness models, a global model failed goodness of fit assessments, so reduced models balancing parsimony, goodness of fit, inferential interests, and data support were evaluated; parsimony in the milkweed models was sought as well. We evaluated alternative models based on the difference between the given model's second-order Akaike's Information Criterion (AICc) and the AICc of the best model (i.e., Δ AICc), and used an information-theoretic approach when selecting the best set of models for deriving inference. Where models were equally competitive (i.e., Δ AIC ≤2) in step (b), we selected the model with the lower AICc for inference.

2.5.2 Milkweed metrics
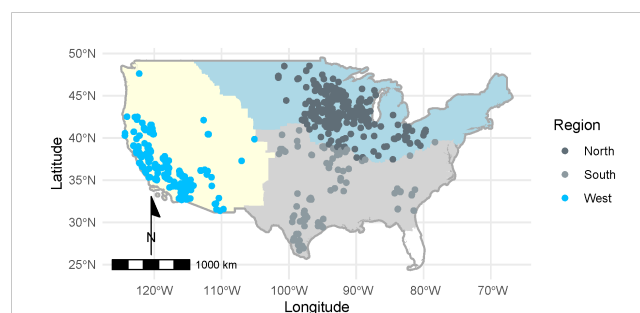
Milkweed density represents the number of plants observed per hectare. Because milkweed stems were not counted in the first year of the program, we used plant counts for our analysis. Although both species are known to support breeding monarchs (Greenstein et al., 2022), we excluded *Asclepias verticillata* (whorled milkweed) and *A. subverticillata* (horsetail milkweed) densities from statistical analyses because their biomass and growth patterns differ greatly from the other species observed and were not included in other landmark research on milkweed densities (Thogmartin et al., 2017) (although we report site occurrence and densities for these species in Supplementary Table S1).

During initial inspection of the data, we found that 42.7% of milkweed density values were 0. To address this preponderance of zeroes, we used a zero-inflated negative binomial model, with a binary logit and count component, jointly estimating separate coefficients for the prediction of zero-versus-non-zero probabilities and for count densities above zero. This modeling approach provided a way to distinguish structural zeros (species not present at a site) from sampling zeros (species present at a site but not sampled) (Halstead et al., 1991). A set of fixed and random effect covariates were evaluated in both the zero process and count process. We fit zero-inflated negative binomial models with the *glmmTMB* package (Brooks et al., 2017).

2.5.3 Blooming plant metrics

Floral frequency refers to the proportion of subplots containing at least one non-grass flower. Floral richness refers to the number of non-grass flowering species observed in bloom on the blooming plant survey subplots. We restricted analysis to species observed in subplots, given that the meander was optional. To summarize commonly occurring floral species across sites (Table 2), we collapsed all records by IMMP plot; that is, we generated a list of all floral species observed on each plot across all surveys.

Nine percent of sites were absent of blooming flowers but varied substantially by region. We modeled floral frequency as a mixed-effects logistic regression and floral richness as a zero-inflated

negative binomial mixed-effect regression (*glmmTMB* package) (Bates et al., 2015).

2.5.4 Model evaluation

All models of each response type were tested for overdispersion, zero inflation, and other model diagnostics with the *DHARMa* package (Hartig, 2022), the *check_model* command in the *performance* package (Lüdecke et al., 2021), and *diagnose* in the *glmmTMB* package (Brooks et al., 2017).

3 Results

3.1 Milkweed surveys

A total of 2,707 milkweed surveys were conducted on 1,227 unique sites during 2016–2022. Sampling frequency varied intra- and inter-annually, with some sites being sampled only once while others were sampled multiple times within and among years. On average, sites were surveyed twice per year (range = 1–21). Timing of surveys varied among sites, regions, and years, spanning from February to December within a season. Surveys occurred in 26 states, with 1,630 in the North (on n = 551 unique sites), 250 in the South (n = 112 sites), and 728 in the West (n = 564 sites) USFWS Monarch Conservation Units (Figure 2). Of 2,707 surveys, 975 (37%) occurred at randomly selected sites (n = 505). The remaining 1,732 surveys occurred at sites selected non-randomly (n = 722). A total of 330 surveys (years 2016 and 2017) used transect methodology following Lukens et al. (2020), 275 surveys followed the IMMP's modified census protocol, and 2,003 surveys used standard IMMP protocols for plot setup. After excluding sites in Forest (n = 1), Agricultural Crop Field (n = 15), and Agricultural Edge (n = 83), 2,608 surveys remained for model development (Table 2).

Milkweed was present on 57 percent of surveys (1,113 of 2,608). We observed 32 *Asclepias* species across sites and regions, along with two non-*Asclepias* species, *Cynanchum laeve* and *Matelea biflora* (Supplementary Table S1). For sites in which milkweed was present,

TABLE 2 Number of Integrated Monarch Monitoring Program surveys (n) included in models by site type (land use), site selection type (random, non-random), and region (North, South, and West Monarch Butterfly Conservation Units).

Site Type	Code	North n Milkweed, floral frequency, floral richness		South n Milkweed, floral frequency, floral richness		West n Milkweed, floral frequency, floral richness	
		Random	Non-random	Random	Non-random	Random	Non-random
Protected Grassland	PGS	189, 195, 192	599, 601, 531	8, 8, 4	70, 70, 66	353, 357, 313	178, 179, 139
Unclassified Grassland	UGS	76, 76, 76	137, 141, 122	6, 8, 8	36, 36, 32	1, 2, 2	108, 108, 17
Agricultural Conservation Land	ACL	2, 2, 2	243, 243, 215	-, -, -	6, 77, 77	-, -, -	-, -, -
Rights-of-way	ROW	22, 290, 284	20, 20, 20	-, 13, 9	2, 2, 0	-, -, -	-, 12, 10
Developed	DEV	34, 33, 21	42, 41, 21	3, 3, -	48, 53, 33	1, 1, -	72, 72, -

Sample size (n) is reported for surveys in each model type: milkweed, floral frequency, and floral richness.

two species were observed on average (median = 1, range = 1–7). A greater number of species were observed in the western region (17) compared to the North and South (North = 13, South = 13). In the North, *Asclepias syriaca, A. verticillata*, and *A. incarnata* were the most ubiquitous species observed across sites, with *A. syriaca* growing at highest mean densities on random sites and *A. verticillata* highest on non-random sites. *Asclepias syriaca*, *A. viridis*, and *A. asperula* were most commonly observed across sites in the South, and similar to the North, *A. syriaca* grew at highest mean densities on random sites. *Asclepias linearis* grew at highest mean densities on non-random southern sites. In the West, the top-three most ubiquitous species were *Asclepias fascicularis*, *A. eriocarpa*, and *A. speciosa*, with *A. speciosa* growing at high mean densities on random sites and *A. subverticillata* highest on non-random sites.

The best model describing variation in milkweed density excluded transect layout (p's for both the conditional and zero-inflation components >0.38) from the global model (Table 3). The best model explained 78.8% of the variation, with most variation explained by the random effects ($R^2_{marginal}$ = 0.136, $R^2_{conditional}$ = 0.788), especially plot identity. Milkweed density was greater in the North region compared to the West region. Mean density appeared lower in the South but was imprecisely estimated (Figure 3). Predicted milkweed densities were 40% higher in randomly selected Protected Grassland in the North (estimated marginal mean = 841.0 plants per hectare, 95% confidence interval (CI) = 618.4–1141.6) compared to the West (602.8 [370.9–978.5]) and 23% higher than the South (686.4 [394.4–1193.5]) (Table 4). Milkweed density was lower for randomly collected samples (approximately one-third lower) as well as those collected using census protocols (three-quarters lower). Over all regions and site types (land use), milkweed density peaked during mid-July (day of year = 200). Rights-of-Way and Unclassified Grassland had the highest mean density of milkweed, whereas Agricultural Conservation Land had the lowest (Table 4).

3.2 Blooming plant surveys

A total of 2,742 blooming plant surveys were conducted on 1,225 unique sites from 2016–2022. Of these, 1,661 surveys occurred in the North, 809 in the West, and 272 in the South USFWS Monarch Conservation Units; this includes repeat visits to sites within and among years. Observers used Lukens et al. (2020) transect methodology on 330 site visits (in 2016 and 2017), standard IMMP surveys on 2,050, and modified census survey on 362 site visits. Within standard survey types, Level A surveys (where flowering plants were identified to species) occurred on 2,316 visits, and Level B (presence of any flowering plants were recorded without identifying the species) on 64. Fewer than 100 subplots were surveyed on 97 site visits, typically due to poor weather or small site size. The mean number of visits each site received within a year ranged from 1.40 (2020) to 3.80 (2016), ranging from one to 12 visits within a year. Sites were distributed across the North (n = 548), South (n= 113), and West (n = 564), with 505 (41%) selected via the IMMP randomized GRTS sites, and 720 selected non-randomly by the observer.

A total of 2,200 species were recorded across all sites (1,658 native and 378 non-native). The most frequently observed native species were *Rudbeckia hirta* (n = 322), *Achilea millefolium* (n = 293), *Monarda fistulosa* (n = 220), *Erigeron strigosus* (n = 200) and *Erigeron annuus* (n = 198). The most frequently observed non-native species included *Trifolium pratense* (n = 305), *Cirsium arvense* (n = 245), *Trifolium repens* (n = 235), *Medicago lupulina* (n = 234) and *Melilotus officinalis* (n = 225). Frequently observed species varied by region, with only *Achillea millefolium* represented in the top 10 across all regions (Table 5).

On sites where subplots were surveyed, floral frequency ranged from 0 to 1 (mean = 0.39, median = 0.33, standard deviation = 0.31). At least one flower was detected in subplots on 91% surveys overall (n = 2,164), 97% in the North (n = 1,572), 92% in the South (n = 227), and 71% in the West (n = 365).

Neither global model for floral frequency or floral richness could be fit with plot identity as a random effect so subsequent model development omitted it. *Post-hoc* exploration of the best models, adding in the plot random effect, yielded similar parameter estimates and addressed the regional differences in zeros compared to the models without it. The model of floral richness (with plot identity as a random effect), however, appeared overfitted and is not considered here any further.

The best model of floral frequency, with plot identity added *post-hoc* as a random effect, explained 31% of the variation ($R^2_{marginal}$ = 0.183, $R^2_{conditional}$ = 0.312, n = 2254 surveys), consisted of five fixed effects and random effects for month nested in year as well as plot identity (Table 6; Figure 4). Floral frequency was more than 25% lower in the South and West compared to the North; for example, the marginal mean frequency in random Protected Grassland sites was 0.15 (95% CI = 0.09–0.24) in the South and 0.18 (0.13–0.27) in the West versus 0.24 (0.18–0.32) in the North (Table 7). The mean marginal predicted floral frequency was significantly lower on Rights-of-Way (0.43, 95% CI = 0.32–0.54) than Agricultural Conservation Land (0.58 [0.48–0.67]), Developed (0.58 [0.42–0.72]), and Unclassified Grassland (0.57 [0.48–0.66]) but not statistically different (p = 0.12) from Protected Grassland (0.50 [0.42– 0.57]). Random sites had nearly half the floral frequency of non-random sites (0.24 [0.18–0.32] versus 0.50 [0.42–0.57], respectively).

The best model of floral richness, explaining 28% of the variation ($R^2_{marginal}$ = 0.167, $R^2_{conditional}$ = 0.278, n = 2194 surveys), consisted of the effects of region, site type, whether the site was randomly sampled, and the day of year (Table 8; Figure 5). As with floral frequency, floral richness was approximately 25% lower in the South (e.g., Agricultural Conservation Land = 8.25 species [7.09–9.84 species]) and West (7.31 [6.09–8.78]) compared to the North (10.80 [9.36–12.46]) (Table 9). Similar to floral frequency, floral richness was one-quarter lower on Rights-of-Way sites (5.74 species) compared to each of the other land use types (>7.94 species).

As evident in the temporal random effects, flower presence varied annually and, when present, varied over months nested within years. The month-year patterns for blooming flower frequency and floral richness were highly correlated (r = 0.844 [95% CI: 0.736–0.910], t_{46} = 10.66, p = <0.001) and apparent auto-

TABLE 3 Parameter estimates and standard errors (SE) for the best zero-inflated negative binomial regression describing milkweed density (plants per hectare, excluding *Asclepias verticillata* and *A. subverticillata*) collected by the Integrated Monarch Monitoring Program, 2016–2022.

Conditional	Estimate	SE	z	P
Intercept	4.269	0.621	6.875	<0.001 ***
Site-Selection Type	-0.296	0.113	-2.627	0.009 **
Survey Type	1.340	0.220	6.082	<0.001 ***
Region: South	-0.203	0.239	-0.850	0.396
Region: West	-0.333	0.211	-1.578	0.115
Day of Year, knot = 1	-2.516	1.360	-1.850	0.064
Day of Year, knot = 2	5.855	0.857	6.833	<0.001 ***
Day of Year, knot = 3	-9.595	1.746	-5.494	<0.001 ***
Site Type: DEV	0.300	0.291	1.029	0.303
Site Type: PGS	0.379	0.184	2.057	0.040 *
Site Type: ROW	0.906	0.264	3.436	0.001 ***
Site Type: UGS	0.803	0.222	3.622	<0.001 ***
Plot Identity	1.598	1.264	—	—
Month: Year	0.004	0.066	—	—
Zero Process				
Intercept	-17.443	2.641	-6.605	<0.001 ***
Site-Selection Type	1.708	0.463	3.688	<0.001 ***
Survey Type	10.829	1.681	6.444	<0.001 ***
Region: South	11.603	1.651	7.029	<0.001 ***
Region: West	169	1.448	8.889	< 2e-16 ***
Day of Year	0.006	0.003	1.910	0.056
Site Type: DEV	3.754	1.677	2.238	0.025 *
Site Type: PGS	0.005	0.752	0.006	0.995
Site Type: ROW	-2.007	1.105	-1.817	0.069
Site Type: UGS	0.611	0.861	0.710	0.478
Plot Identity	59.711	7.727	—	—
Month: Year	0.439	0.663	—	—

Region estimates for the South and West are relative to the North while site type estimates are relative to Agricultural Conservation Land (ACL). For site selection type, effects of random sites are relative to non-random sites. For survey type, effects of standard surveys are relative to census surveys. Significant predictor variables (p < 0.05) are denoted with asterisks: p < 0.05 (*), p < 0.01 (**), and p < 0.001 (***).

correlation in the random effect of month nested in year (r's ≥ 0.295 at lag 1) indicated the possibility of an unmodeled climate signal.

3.3 Association of milkweeds with floral resources

Collectively, milkweed density data showed weak positive associations with floral frequency (r = 0.066 [95% CI: 0.026–0.107], t_{2319} = 3.202, p = 0.001) and floral richness data (r =

0.064 [95% CI: 0.022–0.105], t_{2260} = 3.029, p = 0.002). However, the parameter estimates for site type from the best models for floral frequency and floral richness were negatively correlated with milkweed density (r = -0.44 and -0.97, respectively). In other words, site types with high milkweed densities tended to have lower floral resources. For example, Rights-of-Way offered higher milkweed density but lower floral resources whereas Developed sites demonstrated the opposite pattern.

4 Discussion

This study provides the first nationwide, field-based depiction of milkweed and floral resources across the monarch's North American breeding range. The program gathered data in novel combinations of geographies and site types (land uses), identifying substantial variation in milkweed and floral resources among regions, site types, and site selection types (random versus non-random). We demonstrate the IMMP's potential to overcome the limitations in scope, geography, and frequency of sampling associated with other field-based methods for assessing pollinator habitat (Hines and Hendrix, 2005; Williams et al., 2012; Smart et al., 2021), as well as the bias associated with non-random sampling (Kinkead et al., 2019; Weiser et al., 2020). For example, we evaluated milkweed or floral resources on 564 sites in the western United States, a geography previously lacking a comprehensive evaluation of pollinator habitat on such a large scale. Although not all site type and geography combinations are thoroughly sampled, program growth can enhance our ability to characterize habitat across these spaces and at finer scales. Moreover, we emphasize that key to this assessment was the broad participation from multiple stakeholders, including community scientists, which was facilitated by major governmental and nonprofit active engagement in the IMMP.

4.1 Site selection type

Unique to large-scale community science programs, the IMMP is building an ecologically representative picture of baseline pollinator habitat via its inclusion of randomly selected sites. Our findings indicate that non-random sites, those selected by observers, do not offer an accurate portrayal of monarch habitat resources across broad landscapes. Milkweed density, floral species richness, and floral frequency exhibited distinct patterns on random versus non-random sites. Milkweed was more likely to be absent from random sites and occurred at lower densities than on non-random sites. A random site was also much more likely to be absent of flowering species; however, where they were present, richness was equivalent to that of a non-random site. Floral frequency, on the other hand, was lower on random sites, but these sites were not any less likely than non-random sites to have flowers present. These results are consistent with other studies demonstrating higher abundance of focal species on non-random sites (Kinkead et al., 2019; Weiser et al., 2020), emphasizing the importance of considering these factors when utilizing datasets reliant on user-selected sites (Pleasants et al., 2017, Pleasants et al.,2023). Despite this
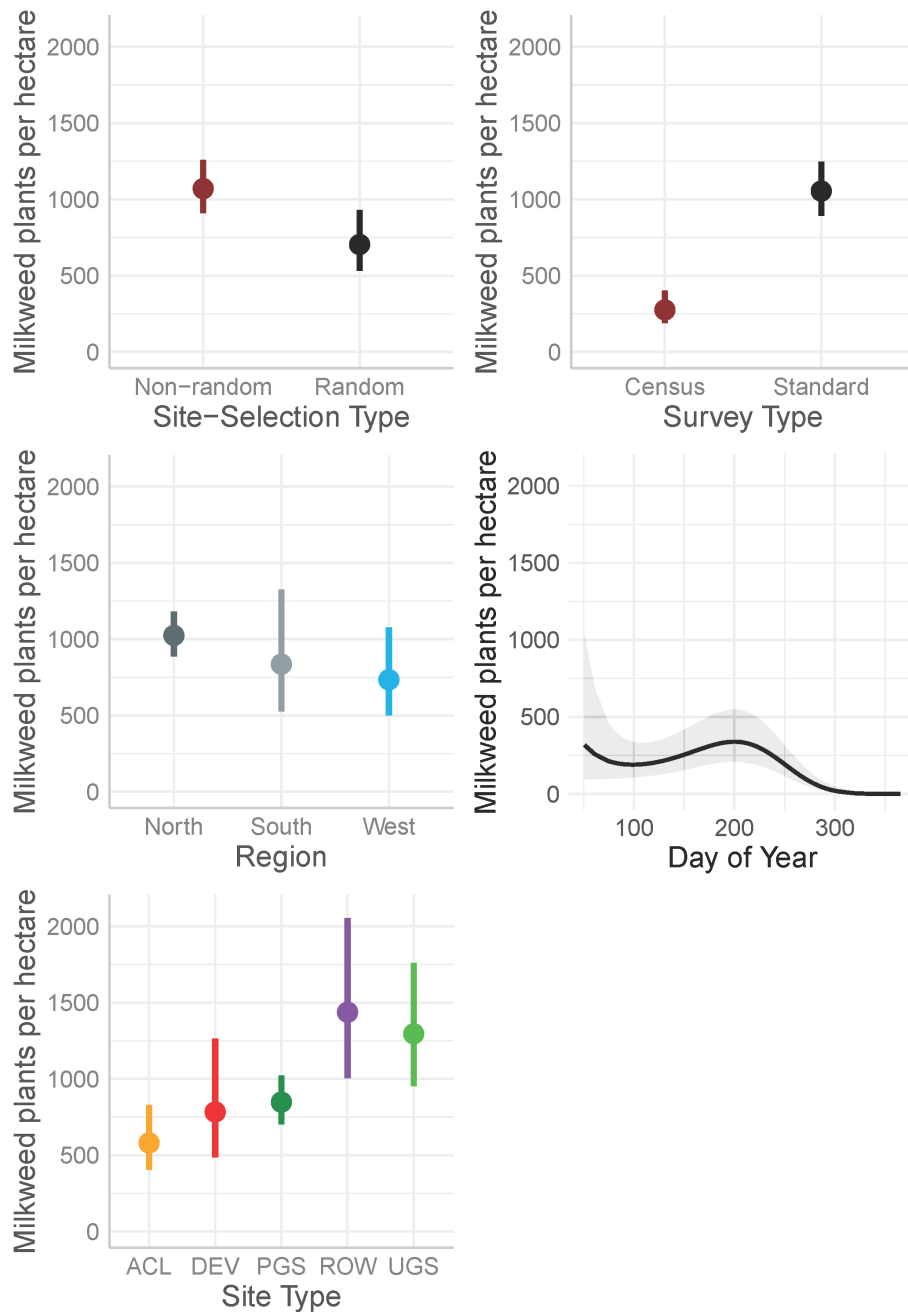
FIGURE 3
Marginal effects on mean milkweed density (plants per hectare, excluding *Asclepias verticillata* and *A. subverticillata*) estimated from a zero-inflated negative binomial model from data collected by the Integrated Monarch Monitoring Program, 2016–2022. Day of year effect is depicted for the North region where data were most abundant. Error bars and gray ribbon represent 95% confidence intervals. ACL, Agricultural Conservation Land; DEV, Developed; PGS, Protected Grassland; ROW, Rights-of-way; UGS, Unclassified Grassland.

limitation, non-random sites offer valuable insights into the potential for various site types to contribute to pollinator habitat goals.

One potential confounding factor not explored in this study is the management of study sites; 59% of the non-random sites in this study were classified as being managed for conservation. The higher milkweed density, floral frequency, and species richness on non-random sites are likely a reflection of targeted conservation management. As a result, we recommend leveraging data from spatially balanced random sampling designs to estimate resources at

scale (Cariveau et al., 2019b). Further, we advise against using non-spatially balanced data to extrapolate resource availability across large scales (Pleasants et al., 2017; Pleasants et al.,2023).

4.2 Site type

Our study presents a nuanced perspective on the potential for various land use types to serve as habitats for monarch butterflies.

TABLE 4   Model-based marginal mean estimates (with standard errors (SE) and 95% confidence intervals (CI)) of milkweed plants per hectare (excluding *Asclepias verticillata* and *A. subverticillata*) from a zero-inflated negative binomial regression of sampled Integrated Monarch Monitoring Program surveys collected 2016–2022.

Region	Site Type	Random				Non-random			
		Mean	SE	95% CI	n	Mean	SE	95% CI	n
North	ACL	575.88	130.84	[368.93, 896.99]	2	874.63	142.83	[635.08, 1203.40]	243
South	ACL	469.97	152.54	[248.76, 887.11]	0	713.76	193.43	[419.66, 1213.29]	64
West	ACL	412.74	129.88	[222.74, 763.55]	0	626.86	166.45	[372.51, 1052.67]	0
North	DEV	777.34	204.92	[463.69, 1302.24]	21	1180.57	293.02	[725.82, 1920.01]	29
South	DEV	634.37	215.28	[326.18, 1233.05]	0	963.46	305.17	[517.86, 1791.51]	29
West	DEV	557.12	199.14	[276.51, 1121.86]	0	846.14	288.57	[433.67, 1650.66]	0
North	PGS	841.05	131.98	[618.38, 1141.63]	189	1277.34	121.70	[1059.76, 1539.46]	597
South	PGS	686.36	194.00	[394.43, 1193.52]	8	1042.41	249.72	[651.81, 1665.49]	67
West	PGS	602.79	149.40	[370.86, 978.54]	333	915.50	188.29	[611.76, 1368.96]	144
North	ROW	1425.40	226.20	[1044.39, 1944.72]	287	2164.81	455.41	[1433.36, 3269.20]	22
South	ROW	1163.25	333.99	[662.64, 2041.09]	13	1766.68	543.29	[966.95, 3227.19]	2
West	ROW	1021.61	267.84	[611.12, 1707.50]	0	1551.57	450.32	[878.46, 2740.39]	11
North	UGS	1284.80	255.63	[869.91, 1895.3]	76	1951.29	302.65	[1439.78, 2644.02]	134
South	UGS	1048.52	326.35	[569.68, 1927.42]	6	1592.42	434.34	[933.02, 2715.68]	36
West	UGS	920.84	260.62	[528.78, 1601.24]	1	1398.52	345.40	[861.88, 2268.42]	19

(Plants per acre estimates are provided in Supplementary Table S3). Note that these are model-based values, not summaries of the data, and therefore, contain predicted values where no samples were collected. Estimates are for standard surveys.

We detected several differences in measures of monarch breeding and foraging habitat (milkweed density, floral species richness, floral frequency) among site types. On Developed sites, we observed a higher likelihood of milkweed occurrence than on Agricultural Conservation Land, but when present, the densities were not statistically different. Our model estimates for milkweed densities on random Developed sites was notably higher than those reported by Johnston et al. (2019), who estimated baseline milkweed density in four U.S. metropolitan areas: Minneapolis-Saint Paul, Minnesota (North), Chicago, Illinois (North), Kansas City, Missouri (South), and Austin, Texas (South). Johnson et al.'s (2019) mean baseline density, averaged across their site types, was 26 stems per hectare in the North and 18 stems per hectare in the South, equivalent to approximately 9 and 6 plants per hectare (respectively) when applying a three stems per plant conversion factor as per the methods of (Thogmartin et al., 2017). Both densities are substantially lower than our model estimates of 190 plants per hectare for random sites in the North and 186 in the South. On the other hand, our model estimate for Developed non-random sites in the North (267 plants/hectare) closely resembled their two highest land use type means for enhanced sites in Chicago. Johnston et al. (2019) report 483 and 880 stems per hectare for developed open space (conservation and non-conservation), equivalent to approximately 161–293 plants per hectare.

We found similar floral frequency and richness in Developed areas and natural spaces (Unclassified Grassland, Protected Grassland, Agricultural Conservation Land), unlike other studies

(Lynch et al., 2021). Although plant species richness often peaks at moderate or high levels at urban densities (Pyšek, 1993; Knapp et al., 2008; McKinney, 2008), our site types lack this thematic resolution. The broad categorization of IMMP Developed sites, coupled with differences in sampling design, may explain disparities between our model's estimation of milkweed and floral resources and those of other studies. For example, the IMMP's Developed site classification is determined by the extent of impervious surface in the surrounding landscape, amalgamating parks, open spaces, and gardens. In contrast, Johnston et al. (2019) included high-density areas, and other studies on floral resources further refine site types into more specific categories (e.g., McKinney, 2008; Lynch et al., 2021). Despite these differences, our findings indicate that certain developed spaces can contribute to achieving monarch conservation targets by offering milkweed and floral resources comparable to other grassland landscapes.

Our data indicate that Rights-of-Way are dense with milkweed but comparatively impoverished of floral resources, exhibiting lower flower frequency and richness compared to other site types. This aligns with previous research highlighting the prevalence of milkweed in roadside environments (Hartzler and Buhler, 2000; Hartzler, 2010; Kasten et al., 2016; Dee & Baum, 2019; Cariveau et al., 2019a). Model predictions of densities on northern random and non-random Rights-of-Way ranged from 569–795 plants per hectare (respectively), similar to 508 plants per hectare reported for *Asclepias syriaca* on Minnesota roadsides (Kasten et al., 2016). Although Kasten et al. (2016) presented mean densities for this

TABLE 5 Most frequently encountered blooming plant species on plots by nativity and region (North, South, and West Monarch Butterfly Conservation Units).

NATIVE					
North (n = 548)		South (n = 113)		West (n = 564)	
Species	n	Species	n	Species	n
Rudbeckia hirta	291	Oxalis stricta	30	Larrea tridentata	187
Achillea millefolium	222	Rudbeckia hirta	30	Ambrosia dumosa	142
Monarda fistulosa	215	Gaillardia pulchella	22	Eriogonum fasciculatum	88
Ratibida pinnata	190	Geranium carolinianum	22	Cylindropuntia echinocarpa	86
Erigeron strigosus	188	Chamaecrista fasciculata	21	Opuntia basilaris	85
Heliopsis helianthoides	184	Oenothera speciosa	20	Artemisia tridentata	84
Erigeron annuus	183	Verbena halei	19	Eriogonum inflatum	76
Asclepias syriaca	167	Ratibida columnifera	18	Purshia tridentata	57
Verbena stricta	139	Glandularia bipinnatifida	17	Achillea millefolium	55
Dalea purpurea	116	Achillea millefolium	16	Ferocactus cylindraceus	55
Erigeron philadelphicus	116	Allium canadense	16		
NON-NATIVE					
North		South		West	
Species	n	Species	n	Species	n
Trifolium pratense	296	Medicago lupulina	25	Erodium cicutarium	126
Cirsium arvense	243	Anagallis arvensis	14	Centaurea solstitialis	46
Trifolium repens	215	Ambrosia artemisiifolia	12	Lactuca serriola	37
Medicago lupulina	207	Trifolium repens	12	Hirschfeldia incana	35
Melilotus officinalis	201	Taraxacum officinale	10	Erodium botrys	28
Daucus carota	180	Daucus carota	9	Malva parviflora	26
Taraxacum officinale	153	Sherardia arvensis	9	Hypochaeris glabra	24
Silene latifolia	138	Trifolium campestre	9	Sonchus asper	23
Trifolium hybridum	125	Calyptocarpus vialis	8	Artemisia ludoviciana	21
Medicago sativa	124	Kummerowia striata	8	Carduus pycnocephalus	21
				Plantago lanceolata	21
				Vicia villosa	21

Data include all species observed on all survey types, regardless of bloom status. Nativity status is obtained from USDA Plants Database (United States Department of Agriculture (USDA) and Natural Resources Conservation Science (NRCS), 2022).

species alone (whereas we combined all species except for *A. verticillata* and *A. subverticillata*), *A. syriaca* was the most common species encountered in the North and grew at highest densities on random sites. Kaul and Wilsey (2019) reported a greater mean density on Iowa roadsides (1,274 plants/hectare), but this difference may be attributed to their inclusion of *Asclepias verticillata* in density calculations, which, as our data indicate (Supplementary Table S1), tends to grow in very high densities. In the South, Rights-of-Way density estimates (1,163–1,767 plants/hectare) were approximately 30 percent lower than those reported by Baum and Mueller (2015), who estimate 1,600–2,400 plants per hectare on Oklahoma roadsides.

The observed low floral frequency on Rights-of-Way indicates untapped potential to offer high-quality breeding resources for monarchs through targeted efforts to enhance floral resources. For example, conservation management such as integrated vegetation management (IVM) is designed to promote desirable (typically native) low-growing plant communities through ecologically sound practices (Nowak and Ballard, 2005; Yahner and Hutnik, 2004). IVM techniques, such as selective herbicide application and fall mowing, have been shown to increase floral resource abundance (Russell et al., 2018; Kuder, 2019), with some exceptions (Mahan et al., 2020), highlighting the opportunity to implement focused improvements in areas where floral resources are low and milkweed densities are already high.

TABLE 6 Parameter estimates and standard errors (SE) from the best model explaining floral frequency from Integrated Monarch Monitoring Program surveys conducted 2016–2022.

	Estimate	SE	z	P
Intercept	0.430	1.594	0.270	0.787
Site Type: DEV	0.006	0.359	0.017	0.986
Site Type: PGS	-0.331	0.214	-1.544	0.122
Site Type: ROW	-0.615	0.293	-2.098	0.036 *
Site Type: UGS	-0.022	0.253	-0.089	0.929
Region: South	-0.610	0.221	-2.755	0.006 **
Region: West	-0.358	0.192	-1.868	0.062
Survey Duration (min)	0.509	0.085	6.003	<0.001 ***
Site Selection Type	-1.114	0.148	-7.507	<0.001 ***
Day of Year, knot = 1	-6.086	3.490	-1.744	0.081
Day of Year, knot = 2	1.360	1.548	0.879	0.379
Day of Year, knot = 3	-5.447	3.088	-1.764	0.078
Plot Identity	0.371	0.609	—	—
Month: Year	0.274	0.523	—	—

Site type estimates are relative to Agricultural Conservation Land (ACL); region estimates for the South and West are relative to the North. For site selection type, effects of random sites are relative to non-random sites. Significant predictor variables (p < 0.05) are denoted with asterisks: p < 0.05 (*), p < 0.01 (**), and p < 0.001 (***).

Agricultural Conservation Lands depicted the opposite pattern of Rights-of-Way, with relatively low densities of milkweed but relatively higher floral frequency and richness. Unexpectedly, milkweed densities on Agricultural Conservation Land were lower than both Protected and Unclassified Grassland, contradicting predictions by Thogmartin et al. (2017), which assumed that Agricultural Conservation Land had the highest potential for milkweed density. This finding highlights an opportunity to improve practices in northern agricultural conservation programs to better align with densities found on other grassland types. Novel practices targeting pollinators, such as the Conservation Reserve Program's CP-42 Pollinator Habitat program, could facilitate this improvement. The IMMP dataset also contains information on conservation program and site management, which could be used to more specifically evaluate program management and outcomes, considering the variability in resources provided by different conservation practices (Smart et al., 2021).

Observed milkweed densities for Agricultural Conservation Land (287–390 plants/hectare) and Protected Grassland (399–543 plants/hectare) in the North were lower than Lukens et al. (2020) reported densities on restored conservation grasslands in Minnesota, Wisconsin, and Iowa. Notably, Lukens et al.'s dataset is a subset of the overall IMMP dataset, representing 276 of 2,707 surveys. Model estimates for Unclassified Grassland (303–1,285) closely resembled Lukens et al.'s reported mean density of 1,390 plants per hectare. Although all grassland types had higher densities than Kaul and Wilsey (2019) estimated mean for Iowa conservation plantings (approximately 71 plants/hectare using a 3 stem/plant conversion factor), they were lower than their mean for remnant

prairies (approximately 2,902 plants/hectare). In the South, milkweed densities for Protected Grassland and Unclassified Grassland were both lower than Baum and Mueller (2015) estimate for managed prairie in Oklahoma. Their range of 2,400–2,700 plants per hectare is approximately 3.5 times higher than observed in Protected Grassland (686 plants/hectare) and 2 to 2.5 times higher than observed in Unclassified Grassland (1,049 plants/hectare).

Our findings align with Smart et al. (2021), demonstrating similar floral resource availability among upper Midwest grassland types. Unclassified Grassland, Protected Grassland, and Agricultural Conservation Land site types exhibited relatively comparable floral frequency and richness levels. Although fewer floral resources were observed on Rights-of-Way compared to Agricultural Conservation Land overall, this difference did not reach statistical significance when considering only random (i.e., background) site selection types in the North (odds ratio = 1.85, p = 0.11). Among surveyed grassland types, Unclassified Grassland—primarily privately owned grassland—had the highest milkweed densities, underscoring its importance as monarch breeding habitat. We lacked sufficient samples of Agricultural Edge habitats, which have been shown to provide high levels of floral resources (Lynch et al., 2021), and Agricultural Crop Fields, which may also provide pulses of floral availability (Williams et al., 2012; Mallinger et al., 2016; Hemberger and Gratton, 2023). Additional surveys and inclusion of these site types in future analyses could provide a more comprehensive understanding of the complex resource availability among grassland types at large scales.

4.3 Region

We found that both milkweed and floral resources varied significantly by region, emphasizing the importance of applying regionally appropriate goals and standards for restoring or managing pollinator habitat. Milkweed was more likely to occur on sites in the North than the South or West, but when present, the density was similar across regions. Despite the lack of statistical significance, the general patterns in density we observed among regions are similar to those documented by Spaeth et al. (2022). Spaeth Jr et al. assessed milkweed on western U.S. rangelands (largely equivalent to Unclassified Grassland in the West and western portions of the North and South), finding that milkweed densities are highest in mid-latitude areas of the North, lowest in the South, and greatest in the easterly areas of their study area and lowest farther West (differences in methodology make absolute comparisons of densities difficult). Similarly, we found that flowers were more likely to be present in the North, with both floral richness and frequency notably higher in this region compared to the West or South.

One limitation of our study and possible influence on regional estimates is the lack of sampling within Agricultural Crop Fields (and therefore exclusion from our analysis). The northern United States, in particular, is characterized by extensive agricultural activity and since the widespread adoption of herbicide-tolerant corn and soybeans, milkweed has largely disappeared from these fields (Hartzler, 2010;
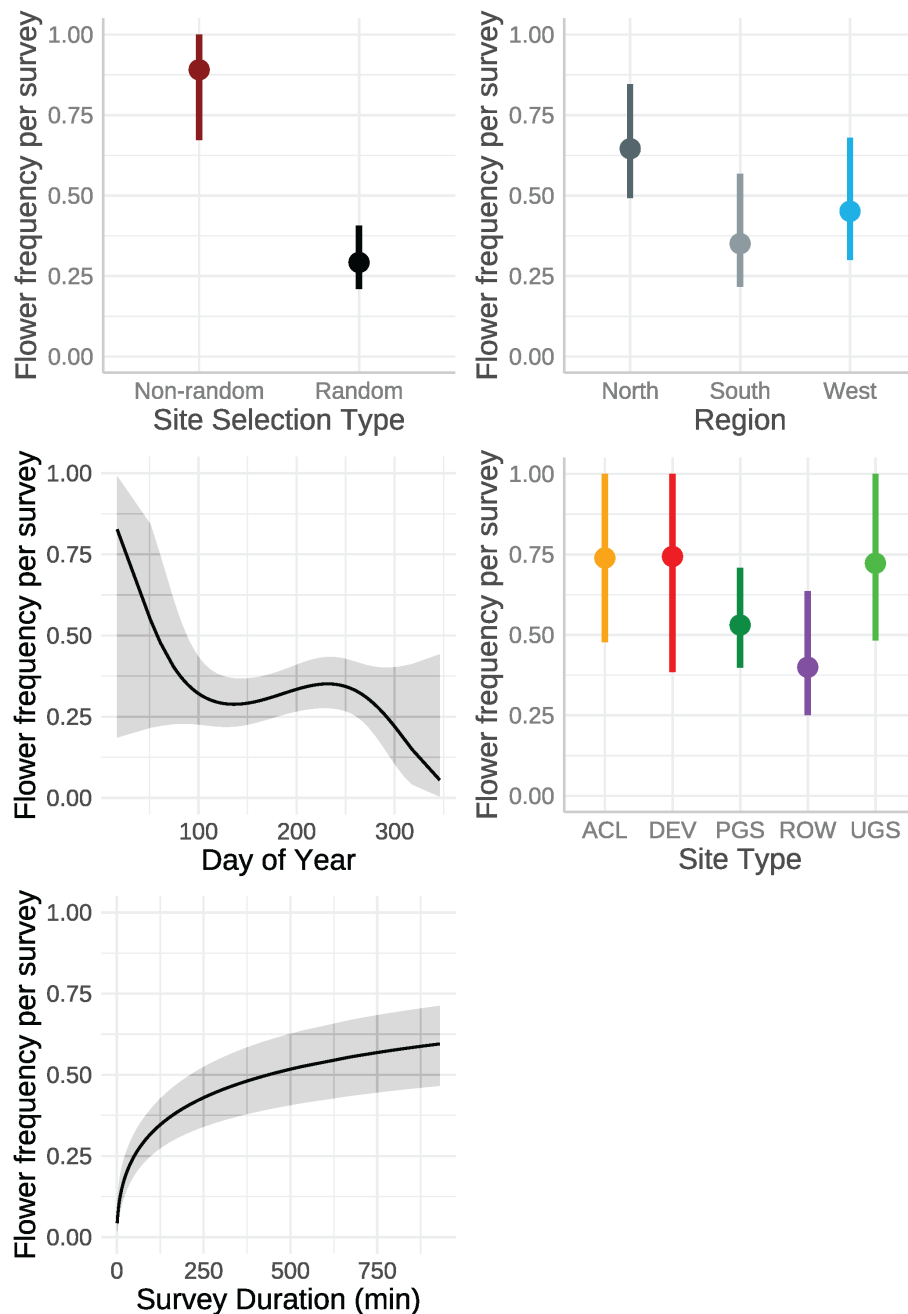
FIGURE 4
Marginal effects on mean floral frequency estimated from a mixed-effects logistic regression from data collected by the Integrated Monarch Monitoring Program, 2016–2022. Error bars and gray ribbons represent 95% confidence intervals. ACL, Agricultural Conservation Land; DEV, Developed; PGS, Protected Grassland; ROW, Rights-of-way; UGS, Unclassified Grassland.

Pleasants and Oberhauser, 2013). Lacking samples from these areas could lead to an underrepresentation of sites in which milkweed does not occur in the North region. Nevertheless, our data indicate that increasing the quantity of milkweed in the South and West may be best accomplished by increasing its distribution across the landscape, rather than focusing on increasing densities where it is already present. Furthermore, estimates of milkweed density generated from primarily northern datasets (Hartzler and Buhler, 2000; Hartzler, 2010; Pleasants and Oberhauser, 2013; Zaya et al., 2017) may best represent only the North, and are unlikely to be suitable for

nationwide application. This finding supports the approach taken by Koh et al. (2016) to consider ecoregional differences when developing nationwide models of pollinator resource availability.

4.4 Survey timing and methodology

Milkweed densities and floral resources responded differently to survey timing and methodology. Although varying by region, milkweed density overall was highest during mid-July, consistent

TABLE 7 Model-based marginal mean estimates with standard errors (SE) and 95% confidence intervals (CI) of floral frequency from a mixed-effects logistic regression of sampled Integrated Monarch Monitoring Program surveys collected 2016–2022.

Region	Site Type	Random				Non-random			
		Probability	SE	95% CI	n	Probability	SE	95% CI	n
North	ACL	0.310	0.056	[0.212, 0.429]	2	0.578	0.053	[0.472, 0.677]	243
South	ACL	0.196	0.050	[0.116, 0.313]	0	0.427	0.065	[0.306, 0.556]	77
West	ACL	0.239	0.055	[0.149, 0.361]	0	0.489	0.070	[0.355, 0.624]	0
North	DEV	0.311	0.075	[0.186, 0.473]	33	0.580	0.083	[0.414, 0.729]	41
South	DEV	0.197	0.062	[0.103 0.346]	3	0.428	0.081	[0.266, 0.607]	53
West	DEV	0.240	0.071	[0.129, 0.403]	1	0.491	0.098	[0.309, 0.675]	72
North	PGS	0.244	0.035	[0.182, 0.318]	195	0.496	0.039	[0.421, 0.571]	601
South	PGS	0.149	0.037	[0.090, 0.238]	8	0.348	0.058	[0.245, 0.468]	70
West	PGS	0.184	0.033	[0.129, 0.257]	357	0.407	0.052	[0.311, 0.511]	179
North	ROW	0.195	0.036	[0.135, 0.275]	290	0.425	0.061	[0.312, 0.547]	20
South	ROW	0.117	0.033	[0.066, 0.198]	13	0.287	0.066	[0.176, 0.431]	2
West	ROW	0.145	0.037	[0.087, 0.232]	0	0.341	0.074	[0.214, 0.497]	12
North	UGS	0.305	0.049	[0.219, 0.408]	76	0.572	0.050	[0.472, 0.667]	141
South	UGS	0.207	0.046	[0.115, 0.306]	8	0.421	0.068	[0.296, 0.557]	36
West	UGS	0.250	0.048	[0.151, 0.347]	2	0.483	0.070	[0.351, 0.618]	108

Note that these are model-based values, not summaries of the data, and therefore, contain predicted values where no samples were collected.

with peak timing recorded by other studies (Lukens et al., 2020). Although we detected fluctuations in floral resource metrics throughout the year, our sample did not yield statistically significant insights into the timing of floral availability. The IMMP provides, but does not enforce, recommendations for the timing and frequency of surveys; therefore, some surveys may have occurred outside of optimal time periods, affecting measured values. Additional samples would strengthen our ability to detect phenological patterns in floral resource availability within and among years. Regarding methodology, milkweed was more likely to be present and occur at higher densities on sites with standard survey methods compared to modified census surveys. Floral richness increased with greater sample area, and floral frequency increased with survey duration. We suspect, however, that these differences are a product of (a) participants selecting census surveys intentionally where resources are low, as a rapid way to assess the few resources present, and (b) larger, more diverse sites inherently taking longer to survey.

Our models explained three-quarters of the variation in milkweed density and one-quarter of the variation in floral resource availability. Variables not included here such as soil type, annual weather variation, elevation, distance to water, land use and disturbance history, and management are known to influence milkweed and floral dynamics and may account for the unexplained variability in our models (Dee and Baum, 2019; Kaul and Wilsey, 2019; Svancara

et al., 2019; Tracy et al., 2019; Waterbury et al., 2019; Spaeth et al., 2022). Weather, in particular, may have affected this dataset and the regional variation we observed in milkweed and floral metrics. During 2000–2019, the southern United States experienced a high number of drought events while western states experienced substantial periods of severe drought conditions (Leeper et al., 2022). Furthermore, while plot identity, representing site-level variation, emerged as a significant predictor of milkweed presence and density and floral frequency, it did not integrate effectively into floral richness models and was consequently excluded. With expanded sampling efforts, this variable, along with climate metrics, may provide crucial insight into the heterogeneity of milkweed and floral resource availability among sites and regions (Weiser et al., 2019b).

4.5 Association of milkweeds with floral resources

Our study revealed a negative correlation between milkweed and floral availability across study areas. Sites with high-quality breeding habitat (milkweed) tended to exhibit lower levels of foraging resources (floral richness and frequency). Previous research on monarch use of habitat found elevated adult monarch abundance

TABLE 8 Parameter estimates and standard errors (SE) from the best model describing variation in floral richness, derived from a zero-inflated negative binomial regression of Integrated Monarch Monitoring Program surveys collected 2016–2022.

Conditional	Estimate	SE	Z	P
Intercept	1.864	0.583	3.196	0.001 **
Area sampled (m^2)	0.002	0.001	1.980	0.048 *
Region: South	-0.149	0.063	-2.378	0.017 *
Region: West	-0.416	0.062	-6.758	<0.0001 ***
Site Type: DEV	0.093	0.097	0.965	0.335
Site Type: PGS	0.039	0.062	0.633	0.526
Site Type: ROW	-0.346	0.073	-4.735	<0.0001 ***
Site Type: UGS	-0.029	0.071	-0.401	0.688
Day of Year, knot = 1	-0.049	1.183	-0.042	0.967
Day of Year, knot = 2	0.944	0.482	1.957	0.050
Day of Year, knot = 3	-0.929	0.847	-1.096	0.273
Month: Year	0.063	0.252	—	—
Zero Process				
Intercept	-5.340	0.471	-11.336	<0.0001 ***
Site Selection Type	1.272	0.304	4.181	<0.0001 ***
Region: South	1.646	0.680	2.421	0.0155 *
Region: West	3.165	0.465	6.804	<0.0001 ***

For site selection type, effects of random sites are relative to non-random sites. Significant predictor variables (p < 0.05) are denoted with asterisks: p < 0.05 (*), p < 0.01 (**), and p < 0.001 (***).
Region effects (South and West) are relative to North; effects of site type are relative to Agricultural Conservation Land (ACL).

and oviposition at sites characterized by both milkweed and high plant species diversity (Kral-O'Brien et al., 2020), which indicates that although not all flowering species in the current study may offer foraging value, they may affect behavior. These results underscore the importance of managing landscapes to support both milkweed and floral resources to provide quality resources for all life stages.

4.6 Future directions

Despite the vast geographic range and sample size in this project, targeted sampling could enhance inferences about pollinator habitat in specific spaces and time periods. Certain combinations of site types and geographic regions were absent from our sample (e.g., Agricultural Conservation Land in the South and West), limiting inferences about habitat availability in those areas. Because recent studies demonstrate the importance of the agricultural sector in contributing to monarch habitat and population targets (Pleasants and Oberhauser, 2013; Thogmartin et al., 2017; Grant et al., 2022; Dilts et al., 2023), future IMMP sampling within this site type would be beneficial. Furthermore, large data gaps remain in the southeastern United States, Great Plains region, and Pacific Northwest (Figure 2). Additional samples from these geographies would enhance our

understanding of regional resource availability and at finer scales than we were able to achieve with this analysis.

Conservation practitioners would also benefit from an improved understanding of how monarchs and pollinators interact with habitats of varying quality. We recognize that the sites surveyed and flowering species documented may not offer equal value to monarchs (Nail et al., 2015; Grant et al., 2020; Antonsen et al., 2021; Bruce et al., 2022; Scott et al., 2023). The IMMP's surveys of adult and immature monarchs offer opportunities to explore such relationships. These additional metrics can be leveraged to investigate monarch response to habitat suitability, variation in monarch survival and reproductive success among site types, habitat characteristics, and regions, and adult foraging preferences at regional scales.

Finally, these data are applicable beyond monarchs, and can elucidate patterns in the spatiotemporal availability of floral resources for other pollinators. National-scale assessments of floral resource availability are currently estimated through a combination of expert opinion and models based on 30 m resolution satellite imagery (Koh et al., 2016). The IMMP's field-based, species-level resolution offers opportunities for improved mapping of breeding habitat for specialist species, identifying temporal gaps in resource availability, and investigating patterns of non-native and invasive forb coverage.

4.7 Conclusion

This study demonstrates the potential of the IMMP's monitoring framework to robustly characterize pollinator habitat across multiple regions and site types. Because prior work has demonstrated strong positive associations between pollinators, particularly bees, and floral resource availability, these data may lend insight into pollinator health more broadly (Lane et al., 2020, 2022; Rotondi et al., 2023; Ammann et al., 2024). Furthermore, given that 1,233 unique plots were sampled within seven years, 41% of which were randomly selected, the IMMP is on track to achieve sample sizes necessary to detect robust trends in milkweed densities through time (Weiser et al., 2019a; Weiser et al.,2020). As sample sizes increase, so does our ability to evaluate trends at finer scales, particularly within specific land use types, regions, and time periods.

This research provides land managers, conservation practitioners, and policy makers with an understanding of the role that various land use classes play in supporting pollinators and their habitat. This information warrants consideration when creating or revising goals within monarch conservation strategies (e.g., Mid-American Monarch Conservation Strategy, Western Monarch Butterfly Conservation Plan). The IMMP provides robust metrics to enhance population and habitat modeling processes that have largely relied on expert opinion and limited datasets. Reassessing targets derived from these models can help refine our understanding of habitat needs and, in turn, allow managers to direct conservation efforts more effectively. Furthermore, a keen understanding of both current and potential habitat conditions can help in prioritization of on-the-ground conservation actions.
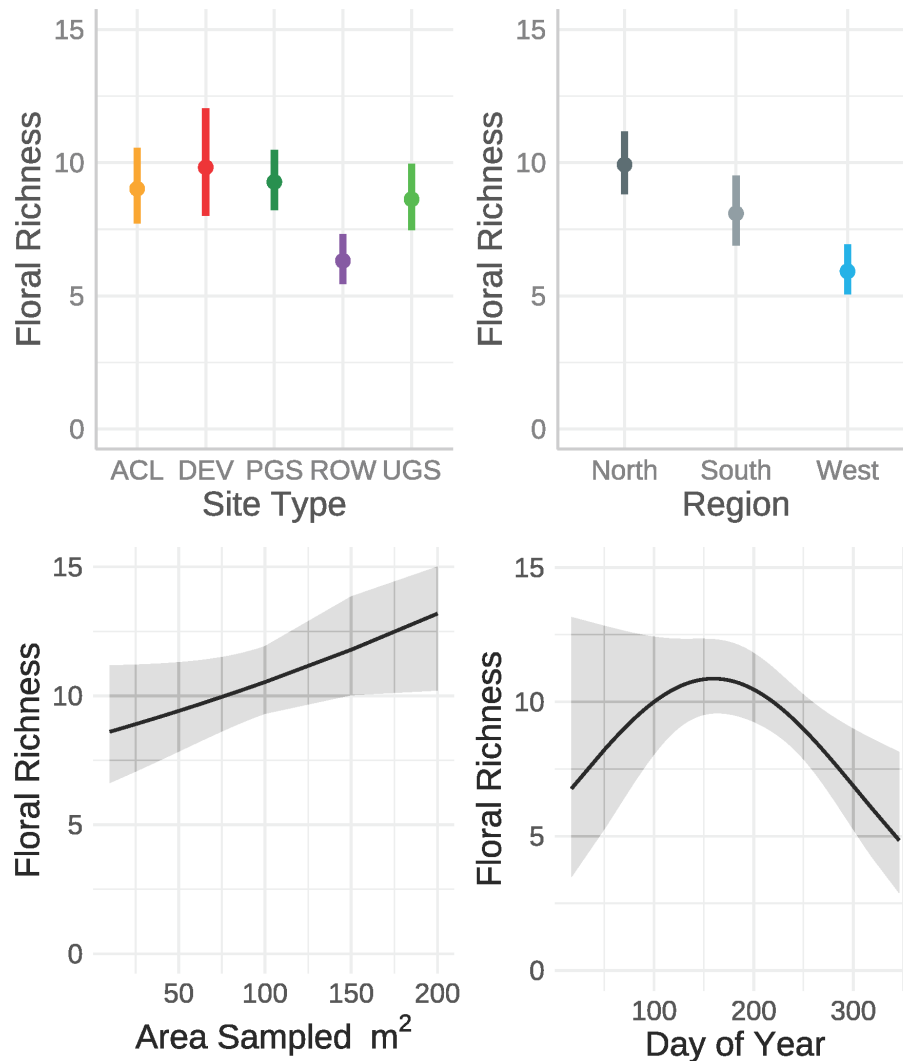
FIGURE 5
Marginal effects on floral richness estimated from a zero-inflated negative binomial regression from data collected by the Integrated Monarch Monitoring Program, 2016−2022. Error bars and gray ribbons represent 95% confidence intervals. ACL, Agricultural Conservation Land; DEV, Developed; PGS, Protected Grassland; ROW, Rights-of-way; UGS, Unclassified Grassland.

TABLE 9 Model-based marginal mean estimates, standard errors (SE), and 95% confidence intervals (CI) of floral richness from a zero-inflated negative binomial mixed-effects regression of sampled Integrated Monarch Monitoring Program surveys (n) collected 2016−2022.

		Random				Non-random			
Region	Site Type	Mean Richness	SE	95% CI	n	Mean Richness	SE	95% CI	n
North	ACL	6.97	0.58	[5.92, 8.20]	2	10.8	0.79	[9.36, 12.46]	243
South	ACL	5.39	0.51	[4.47, 6.50]	0	8.35	0.70	[7.09, 9.84]	77
West	ACL	4.72	0.46	[3.90, 5.72]	0	7.31	0.68	[6.09, 8.78]	0
North	DEV	8.21	0.84	[6.72, 10.03]	33	12.73	1.26	[10.49, 15.44]	41
South	DEV	6.35	0.71	[5.11, 7.90]	3	9.84	1.04	[8.00, 12.10]	53
West	DEV	5.56	0.66	[4.41, 7.02]	1	8.62	1.02	[6.83, 10.87]	72
North	PGS	7.80	0.51	[6.85, 8.87]	195	12.08	0.73	[10.73, 13.60]	601
South	PGS	6.03	0.54	[5.07, 7.18]	8	9.34	0.76	[7.96, 10.96]	70

(Continued)

TABLE 9 Continued

Region	Site Type	Random				Non-random			
		Mean Richness	SE	95% CI	n	Mean Richness	SE	95% CI	n
West	PGS	5.28	0.42	[4.51, 6.18]	357	8.18	0.66	[6.99, 9.58]	179
North	ROW	6.80	0.47	[5.93, 7.79]	290	10.53	0.80	[9.07, 12.23]	20
South	ROW	5.26	0.49	[4.38, 6.31]	13	8.14	0.77	[6.76, 9.81]	2
West	ROW	4.60	0.42	[3.84, 5.51]	0	7.13	0.72	[5.86, 8.68]	12
North	UGS	7.25	0.54	[6.26, 8.40]	76	11.24	0.79	[9.80, 12.89]	141
South	UGS	5.61	0.53	[4.65, 6.76]	8	8.69	0.77	[7.31, 10.33]	36
West	UGS	4.91	0.46	[4.10, 5.89]	2	7.61	0.7	[6.35, 9.12]	108

The best model did not contain Site Selection Type as a covariate, so these estimates are those from a competing model with this covariate. Note that these are model-based values, not summaries of the data, and therefore, contain predicted values where no samples were collected.

The IMMP offers a robust dataset and standardized methodology that can be adopted by researchers seeking to answer a multitude of questions about monarch ecology and pollinator habitat suitability (Monarch Joint Venture, 2021)[1]. Future monitoring efforts could adopt elements of the IMMP's sampling framework where relevant to enrich data on milkweed and floral resource availability across the country. To make substantial advancements in evaluating and tracking change in pollinator habitat, monitoring would be beneficial in geographies and land uses where data gaps currently exist.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

LL: Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration. JT: Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration. WT: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – review & editing, Writing – original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer JP declared a past co-authorship with the author WT to the handling editor.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1330583/full#supplementary-material

1 https://monarchjointventure.org/mjvprograms/science/integrated-monarch-monitoring-program

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