

# Distribution, phenology, and land cover preference risk assessments of four South-Central US milkweeds (*Asclepias* spp.) important for monarch butterflies

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## Research Article

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## Abstract

South-Central US milkweeds (*Asclepias* spp.) are critical adult nectar and larval food resources for producing the first spring and last summer/fall generations of declining eastern migratory monarch butterflies (*Danaus plexippus*). MaxEnt niche models were developed for North American ranges of four important South-Central US milkweeds: *Asclepias asperula* ssp. *capricornu*, *A. viridis*, *A. oenotheroides*, and *A. latifolia*. Twelve models per species utilized subsets of six to eight of 95 edapho-topo-climatic variables chosen by a random subset feature selection algorithm. Milkweed weekly phenology was compared between early and late season periods of monarch activity. Novel land cover preference risk assessments were developed for milkweeds through land cover utilization-availability analyses, incorporating a novel sample bias reduction method for citizen science data before calculation of relativized electivity index ( $E^*$ ) land cover preference. *Asclepias a. ssp. capricornu* and *A. viridis* occurred more frequently during early season monarch activity, while *A. oenotheroides* and *A. latifolia* occurred more frequently during late season monarch activity. Milkweed utilization of roadsides varied from 6–31%. Developed-Open Space and Grassland Herbaceous land classes generally had highest benefit among milkweeds. Cultivated Crops and Shrub/Scrub had high risk. Combined milkweed high  $E_i^*$  kernel density estimation surfaces resolved interior and coastal corridors of milkweed land cover preference providing functional connectivity for the monarch spring and fall migrations. A potentially critical gap in milkweed land cover benefit connectivity was identified in South Texas. Milkweed land cover preference risk assessments can be used to prioritize milkweed habitat conservation for enhancing monarch migration connectivity across the South-Central US.

## Introduction

The monarch butterfly (*Danaus plexippus*) recently became a candidate for US listing as federally endangered or threatened (USDI FWS 2020). Eastern migratory monarchs are unique among insects in flying up 3,000 km in their fall migration from breeding sites as far north as southern Canada to overwintering sites in Central Mexico (Urquhart and Urquhart 1978), with the same butterflies returning in the spring. Spring remigrants lay eggs in the South-Central US from Texas to Oklahoma on milkweeds (*Asclepias* spp.), their primary larval host plants (Malcolm et al. 1993). Therefore, milkweed habitat in the South-Central US (Texas, Oklahoma, Louisiana, and Arkansas) is critical for development of the first generation, which forms the basis for subsequent generations that migrate and reproduce further north (Flockhart et al. 2013; Oberhauser et al. 2017). Milkweeds are also preferred nectar plants of adult monarchs (USDA NRCS 2015a,b; 2018) and can be important for fueling the spring and fall migrations (Brower et al. 2006; Hobson et al. 2020). Because of the importance of South-Central US milkweed habitat for maintaining monarch functional connectivity along the migratory corridors, spatially explicit risk assessments for milkweed habitat are needed to inform regional monarch conservation planning efforts (Moreno-Sanchez et al. 2019). Species spatial risk assessments are a category of spatial environmental or ecological risk assessment (e.g., Suter 2007; van Westen and Greiving 2017) applied in the context of a spatially explicit species habitat model, that can facilitate conservation planning (Duggan et al. 2015; Hashim et al. 2017). The significant long-term decline in the eastern monarch overwintering population (Semmens et al. 2016) has been primarily attributed to the loss of milkweed habitat in the Midwest US for second and third generation larvae (Oberhauser et al. 2017; Pleasants 2017; Thogmartin et al. 2017; Stenoien et al. 2018; Taylor et al. 2020), and adult mortality within the Central Mexico overwintering grounds (Brower et al. 2004, 2012, 2017; Ries et al. 2015). A combination of factors, including milkweed breeding habitat loss, climate change, and deforestation of overwintering habitat, may represent the greatest risks to eastern migratory monarch butterflies (Malcolm 2018; Wilcox 2019). Demographic models of Oberhauser et al. (2017) indicate that increasing milkweed and nectar availability for monarchs in both the northern and southern parts of the breeding range may be the most efficient strategy for promoting monarch population growth. Few studies have focused on monarch conservation with respect to population risks in the South-Central US (but see Tracy et al. 2019; Kantola et al. 2019a), and risks to milkweeds in this southern region have yet to be studied.

The US Fish and Wildlife Service (USFWS; Tuggle 2014) has identified *A. a. ssp. capricornu* (antelopehorns), *A. viridis* (green antelopehorn), and *A. oenotheroides* (zizotes milkweed), as the most important milkweed species for monarchs in Texas, and the USDA Natural Resource Conservation Service (USDA NRCS 2015c) has targeted these three species for conservation efforts in their South-Central subregion (Texas, Oklahoma, and Kansas). Spring first generation larval reports on these three species in the South-Central US include *A. oenotheroides* in South Texas (Calvert 1996), *A. viridis* in Texas and western Louisiana, and *A. a. ssp. capricornu* in Texas (Lynch and Martin 1993). Fall last generation larval reports along roadsides and adjacent fields in Texas are from (in order of abundance) *A. viridis*, *A. a. ssp. capricornu*, *A. oenotheroides*, and *A. latifolia* (broadleaf milkweed) (Calvert 1999). *Asclepias latifolia* is also reported as a common host plant for the last generations of late summer/fall monarch larvae in west Texas (Brym et al. 2020; also unpublished data, D. Berman and K. Baum). We focus on the three milkweed species identified as the most important for monarchs in the South-Central US by the USFWS, as well as *A. latifolia*. All four of these native milkweed species are herbaceous perennials blooming mostly from spring to summer (Woodson 1954), but they can bloom in the fall in the South-Central US with favorable late-season precipitation (Calvert 1999) or in response to disturbance management practices that generate regrowth (Baum and Sharber 2012; Baum and Mueller 2015). This study compares the annual weekly phenology of the four milkweeds in the South-Central US with respect to periods of early and late season monarch activity.

Niche models for milkweed species provide important information about the actual and potential geographic distributions of critical adult and larval monarch food resources. Lemoine (2015) developed current and future climate MaxEnt niche models for eight individual and combined common North American milkweed species, including *A. viridis*. Dilts et al. (2019) developed MaxEnt niche models for 13 milkweed species (including *A. asperula* ssp. *asperula*, spider milkweed) in the western US. Svancara et al. (2019) developed current and future climate MaxEnt niche models for *A. speciosa* (showy milkweed) and *A. incarnata* (swamp milkweed) in Idaho. Kass et al. (2020) found that combined stacked climatic niche models of 20 *Asclepias* spp. and 21 roosting tree species served as valuable biotic variables for MaxEnt niche models of the southern portion of the monarch fall migration from South Texas to Mexico. Except for range-wide MaxEnt models developed for *A. viridis* (Lemoine 2015), range-wide models for South-Central US milkweed species are lacking, and we develop them for this study.

The suitability of land use/land cover (LULC) classes represents an important source of risk to *A. syriaca* (common milkweed) habitat in the Midwest. *Asclepias syriaca* has significantly declined over the last century in conjunction with agricultural intensification (Boyle et al. 2019), including recent increased

use of glyphosate herbicides among corn and soybean crops (Pleasants 2017; Stenoien et al. 2018). Waterbury et al. (2019) found that *A. speciosa*, *A. incarnata*, and other Northwestern US milkweeds rarely utilized land covers of cultivated crops, developed, pasture/hay, and mixed and evergreen forest, and major habitat threats included invasive plants, herbicide use, and mowing. In comparison to data on *A. syriaca* in the Midwest (Hartzler 2010; Pleasants 2017; Kaul and Wilsey 2019) and *A. speciosa* in the Northwest, information is lacking on the utilization and risk of different LULC types for South-Central US milkweeds. We take a hierarchical approach (see Wilting et al. 2010 and Online Resource 1 Introduction) to assess species land cover preference risk for milkweeds, first defining the core habitat of milkweeds using an ensemble of feature-selected MaxEnt niche models. We then use a subset of high spatial resolution milkweed occurrences from citizen science iNaturalist data within the core habitat to develop novel land cover preference risk assessments for milkweed habitat from land cover utilization/availability analyses. Ogawa and Mototani (1991) performed the only other study of which we are aware that applied utilization/availability analysis to assess plant land cover selection (for further background on utilization/availability analyses, see Online Resource 1 Introduction). We also develop a novel citizen science data sample bias reduction method to reduce the weight of milkweed observations in oversampled areas of higher human population density and closer road proximity. Land cover classifications for milkweeds were assessed using both a land cover GIS database and manual classification with publicly available internet aerial and ground imagery, and milkweed percent utilizations of roadside right of way (ROW) versus non-ROW habitats were also determined.

The objectives of this study were to (1) develop MaxEnt niche models that identify core edapho-topo-climatic habitats for each of the four study species, *A. a. ssp. capricornu*, *A. viridis*, *A. oenotheroides*, and *A. latifolia*, (2) compare the relative weekly phenology of the four milkweed species with respect to early and late season monarch activity within modeled South-Central US milkweed core habitats, and (3) use land cover utilization/availability analysis and a land cover electivity index to develop novel individual and seasonal combined land cover preference risk assessments across the South-Central US. Results are discussed in the context of monarch conservation.

## Materials And Methods

### Occurrence data

Historical (1834–2018) milkweed occurrence data throughout the entire North American ranges for the four study species were obtained from iNaturalist (2018a), SEINet (2017), Global Biodiversity Information Facility (GBIF 2017), vPlants (2017), 2017 correspondence with various herbaria (Kansas State University [KSU], Missouri State University [MSU], Nebraska State University [NSU]), the Oklahoma Vascular Plant Database (OVDP; various herbaria, see Hoagland et al. 2017), and Texas survey data from our laboratory and various collaborators (Janice Bush, University of Texas at San Antonio [UTSA], 2017; David Berman and Kristen Baum, Oklahoma State University [OSU], 2017). Additional data representative of the known county distributions of milkweed species (Kartesz 2015) was obtained through georeferencing SEINet, vPlants, and OVDP records in various counties from which we otherwise lacked specific locations. From 388 to 979 occurrence points per species were available for modeling after spatial thinning to 10 km. Partitioned data of subspecies for wide ranging species can yield better quality niche models than data of the combined subspecies (Gonzalez et al. 2011). Consequently, we partitioned data for *A. a. ssp. capricornu* to the East from *A. a. ssp. asperula* to the West (for details on the subspecies boundaries, see Online Resource 1 Methods). For milkweed phenology analyses, 2011–2021 iNaturalist milkweeds records over MaxEnt core habitats (see below) in the South-Central US were thinned to remove exact date/year/location duplicates, and further thinned to within 30 km for every year/week combination to reduce spatiotemporal bias in phenology. In utilization/availability analyses for the land cover preference risk assessment, 2014–2018 (within two years of 2016 land cover data) iNaturalist milkweed occurrence data at ca. 30-m resolution within core habitat for the South-Central US study area were spatially thinned to 1-km (for all occurrence data Excel files, see Online Resource 1 Table 1).

Table 1

*Asclepias* spp. MaxEnt model train and test Area Under the Curve (AUC) accuracy statistics and overfitting (AUCdiff = AUCtrain – AUCtest) (X± SD) from n = 12 models per species that were selected by the random subset feature selection algorithm<sup>a</sup>

Species	Pseudoabsence AUC (AUC <sub>psa</sub> )			Background/Presence AUC (AUC <sub>bgp</sub> ) <sup>b</sup>			AUC <sub>bgp</sub> % of AUC <sub>psa</sub>
	Train	Test	Diff	Train	Test	Diff	Test
<i>A. asperula</i> ssp. <i>capricornu</i>	0.972 ± 0.002	0.965 ± 0.004	0.006 ± 0.002	0.913 ± 0.002	0.904 ± 0.005	0.009 ± 0.004	93.6 ± 0.2%
<i>A. viridis</i>	0.963 ± 0.002	0.952 ± 0.003	0.011 ± 0.002	0.889 ± 0.002	0.871 ± 0.003	0.019 ± 0.003	91.5 ± 0.1%
<i>A. oenotheroides</i>	0.856 ± 0.007	0.845 ± 0.015	0.011 ± 0.011	0.822 ± 0.006	0.805 ± 0.013	0.016 ± 0.011	95.3 ± 0.3%
<i>A. latifolia</i>	0.926 ± 0.006	0.924 ± 0.005	0.002 ± 0.006	0.890 ± 0.004	0.881 ± 0.005	0.008 ± 0.005	95.4 ± 0.1%

<sup>a</sup>See Online Resources 1 Tables 4–8 for 12 MaxEnt model variables and variable parameters per species, and Tables 9–12 for statistics of the individual models.

<sup>b</sup>Default AUC type for MaxEnt models

### Study area boundaries

The background evaluation extents for niche modeling each of the four focal South-Central US milkweed species were represented by 500-km buffers around convex hull polygons from the milkweed occurrence points, which together extended over much of central eastern, southeastern, and southwestern North America. The land cover preference risk assessments for each milkweed species were confined to a South-Central US study area comprising Arkansas and the

majority of Oklahoma, Texas, and Louisiana (Fig. 1). This study area excluded Mexico to the South due to the lack of a land cover data set for Mexico that matched the thematic resolution of the 2016 National Land Cover Dataset (NLCD) (Homer et al. 2015, Multi-Resolution Land Characteristics Consortium [MRLC] 2017) for the US, especially in terms of distinguishing important Pasture/Hay and Grassland/Herbaceous land cover classes (Fig. 1). The western edge of the South-Central US region consisted of the western distribution limit for *A. a. ssp. capricornu* in West Texas and Oklahoma (Woodson 1954) (see Occurrence data, above). The eastern South-Central US boundary consisted of the eastern boundary of Arkansas and northern Louisiana, and the Mississippi River in southern Louisiana (Fig. 1).

## Niche modeling

An initial set of 95 environmental variables at 1-km resolution was used in developing MaxEnt niche models, including 57 climatic indices (Hijmans et al. 2005; Zomer et al. 2007, 2008; Trabucco and Zomer 2010; WorldClim 2017), 14 topographic indices (Lehner et al. 2008; Evans et al. 2014), and 24 edaphic indices (Hengl et al. 2017) (Online Resource 1 Table 2). Anthropogenic and land cover variables were intentionally excluded from the niche models to facilitate a more independent assessment of species affiliation with land cover through the land cover preference risk assessment (see below) (for justification of initial variable selection, see Online Resource 1 Methods). MaxEnt (Phillips et al. 2006) version 3.3.3 models were developed from milkweed locations using the R-software (R Core Team 2017) dismo package (Hijmans et al. 2011). The 1-km milkweed resolution occurrence locations were thinned by a 10 km spatial filter for reducing sample bias and spatial autocorrelation among the data (Boria et al. 2014). We generally followed methods described in Tracy et al. (2018) for generation of background and pseudoabsence points and calculation of AUC, TSS, and overfitting (for details, see Online Resource 1 Methods).

For each milkweed species, we utilized the random subset feature selection algorithm (RSFSA) to evaluate performance of thousands of MaxEnt models developed from random combinations of subsets of 3 to 25 of the 95 variables, limiting correlation of variables to less than  $|0.7|$  (Tracy et al. 2018) (for further details, see Online Resource 1 Methods and Tracy et al. 2018, 2019). A total of 48 feature selected MaxEnt models were projected, 12 for each of the four species, and the 12 binary calibrated models per species were assembled into a feature subset ensemble (FSE), with the area of 100% model frequency consensus used to represent milkweed core habitats (e.g., Porfirio et al. 2014) (for further details on niche model calibration, consensus, and variable ranking, see Online Resource 1 Methods and Tables 13–16).

## Phenology relative to monarch activity

Spatiotemporally thinned iNaturalist milkweed occurrence data with plant images were used to develop weekly stacked phenophase histograms and phenoperiod Gantt charts for niche modeled core habitat of each milkweed in the South-Central US. Phenophase histograms were visually assessed to estimate the best weeks for distinguishing between early and late season growth, which for all species was regarded as the periods from 1–33 weeks (January to mid-August) and 33–52 weeks (mid-August to December). The early and late season plant frequency data were fitted to curves using CurveExpert software (Hyams 2010). Milkweed species weekly phenology was analyzed with respect to two important 11-week periods of monarch activity in the South-Central US (unpublished data) based upon monarch larval observations from Journey North (2017), Monarch Larva Monitoring Project (2017), and iNaturalist (2018a,b), and monarch adult migration observations from Journey North (2017): (1) March to mid-May, representing the first appearance of remigrant adults at the beginning of March in South Texas, and extending to the ending of maturation for most first generation monarch larvae around mid-May in northern Oklahoma; and (2) mid-August to October, representing the first appearance of late generation larvae from reproductive mid-summer migrants around mid-August in northern Oklahoma and extending to the passing of the majority of fall migrants through South Texas by the end of October (for further details on phenophase classifications and statistical analysis, see Online Resource 1 Methods; for excel histogram charts and R script for analyses, see Online Resource 1 Tables 1 and 3, respectively).

## Land cover preference risk assessment

The hazard that various 2016 NLCD land covers represented for milkweed colonization were categorized using the estimated preference of each milkweed species for each land cover class within the South-Central US MaxEnt identified core habitat (see above). The spatial combination of hazard (milkweed preference) and exposure (milkweed core habitat) was used to develop milkweed land cover preference risk assessment maps. Thus, our risk assessment represents land use preferences of milkweed species and not risk as measured by direct land cover-related hazards or threats (e.g., herbicide use; Waterbury et al. 2019). Milkweed land cover preferences were estimated based upon a utilization/availability analysis and an electivity index for occurrence of milkweeds among 2016 NLCD land cover classes. Land cover utilization/availability analysis relies heavily on accurate land cover classifications for milkweed occurrences. Images for individual iNaturalist milkweed occurrences were examined to determine the NLCD land cover class within a 15 m radius of the location and within the context of the adjacent surroundings according to the 2016 NLCD legend (MLRC 2021) using historical imagery for 2014–2018 from Google Earth Pro (2021) and Google Maps (2021) Street View. Manually determined land cover classifications for milkweed occurrences were compared with classifications derived from the NLCD 2016 spatial database. In addition, the general habitat of the milkweed location was manually classified using the imagery into road ROW versus non-road habitats, and habitat utilization was analyzed among species using Chi-squared tests for independence (for further details on manual land cover classifications using imagery and further general habitat subdivisions, see Online Resource 1 Methods).

The observed proportions of milkweeds in various land cover classes are also sensitive to errors from sample bias in citizen science data related to human population density and distance to roadways (e.g., Geldmann et al. 2016, Zhang and Zhu 2018). Milkweed occurrence counts were weighted to reduce these biases using a novel target group-based *Histogram Bin Ratio Weighting (HBRWt)* method. This method assumes that (1) the spatial distribution of a large target group of taxa related to the taxa of interest represents a good estimate of citizen science sample bias from various sources (e.g., Ranc et al. 2017), and (2) the percent frequency distribution of the target group occurrences with respect to the spatial sources of bias (e.g., road proximity), should ideally approximate the percent frequency distribution of randomly generated points with respect to the sources of bias. These approximating assumptions provide an objective basis of correcting for sample bias that leads to more conservative estimates of milkweeds occurring within human population-dense areas or in proximity to roads. The HBRWt method involved first constructing histograms of either human population density or distance to roads for two sets of data in

the study area: (1) 10,000 random points; and (2) up to 10,000 target group points, where the target group is 30m resolution 2014–2018 iNaturalist records for major families of monarch preferred nectar plants (e.g., Asteraceae and Apocynaceae). In a particular human population bin range, if the random point percent frequency was 10% and the target group percent frequency was lower at 5%, the HBRWt adjustment factor for population density,  $PopDenHBRWt$ , was  $10\%/5\% = 200\%$  upwards for any milkweed point occurring within the population density bin (a raw count of one became two). The road distance HBRWt correction factor,  $RoadDistHBRWt$ , was similarly calculated within nested larger human population bins. The final employed combination human population and road distance correction factor,  $PopRoadHBRWt$ , for a given milkweed observation was calculated as  $PopDenHBRWt \times RoadDistHBRWt$ , and values were normalized such that  $PopRoadHBRWtN$  summed to the raw count per species (for further details, see Online Resource 1 Methods).

Corrected land cover data for each  $PopRoadHBRWtN$  weighted occurrence point was used to calculate the actual percentage of milkweed species per land cover,  $r_i$ . We tabulated the 2016 NLCD land cover class raster cells falling within the MaxEnt core habitat to calculate the expected or available percent of land cover,  $p_i$ . An omnibus chi-square goodness-of-fit test was used to determine whether  $r$  significantly differed from  $p$  ( $P < 0.05$ ), combining classes containing less than five expected counts of milkweed occurrences. If the omnibus test was significant, we calculated 95% Bonferroni confidence intervals (BCIs) of  $r_i$  for each land cover class and identified land cover classes where  $p_i$  fell outside of the 95% BCI of  $r_i$  (e.g., Neu et al. 1974; Byers et al. 1984; Manly et al. 2002; Kelly and Elle 2020).

To visualize differences in milkweed land cover electivity, we used the R electivity package (Quintans 2019) to calculate Vanderploeg and Scavia's (1979) relativized electivity index ( $E_i^*$ ; also referred to as Vanderploeg and Scavia's electivity index) for each land cover class:  $E_i^* = [W_i - (1/n)]/[W_i + (1/n)]$ , where  $i =$  the  $i^{\text{th}}$  land cover class,  $W_i = (r_i/p_i)/(\sum r_i/p_i) - 1$ ,  $r_i$  is the proportion of the  $i^{\text{th}}$  land cover class utilized,  $p_i$  is the proportion of the  $i^{\text{th}}$  land cover class available, and  $n$  is the number of land cover classes. The relativized electivity index incorporates several other electivity indices, including the forage ratio,  $r/p$  (Savage 1931; Ivlev 1961), and Chesson's (1978) alpha,  $W$ , which is also known as Vanderploeg and Scavia's (1979) selectivity coefficient and Manly's standardized selection index (Manly et al. 1972, 2002; Chesson 1978; Höner et al. 2010). Lechowicz (1982) recommended use of  $E^*$  over several other electivity indices due to better approximation of a range from  $-1$  to  $1$ , where  $-1$  indicates negative selectivity (avoidance), zero indicates random selectivity (neutral), and  $+1$  indicates positive selectivity (preference). For calculating combined species  $E_i^*$ , individual milkweed species  $E_i^*$  values were phenologically partitioned by multiplication with the species percentage occurrence for either the early or late 11-week period of monarch activity determined from the above milkweed phenology analysis. Phenologically partitioned values of  $E_i^*$  for the four species were then added for each benefit/risk category (for details on statistical analyses of  $E^*$  in previous studies, the combination of  $E_i^*$  across species, construction of  $E_i^*$  category maps, and high  $E_i^*$  category kernel density estimates (KDEs), see Online Resource 1 Methods; for additional procedures, and scripts for R and ArcPython, see Online Resource 1 Table 3).

## Results

### Niche modeling

The RSFSA results for niche model variable subset selection were used to determine that subsets of six to eight of the 95 variables were the optimal smallest sizes for producing higher performing MaxEnt models of the four milkweed species (Online Resource 1 Figs. 4–7, A-C). After generating MaxEnt models from thousands of random variable subsets of the selected subset sizes, the compared model selection criteria of  $AUC_{psa}$  (pseudoabsence AUC used for most other niche modeling other than MaxEnt) and  $AIC_{bg}$  (background AIC; Tracy et al. 2018) were both consistently effective in producing three replicates of 250 out of 3,000 models with significantly higher  $AUC_{psa}$  and lower  $AIC_{bg}$  than replicates of 250 random models out of 3,000 for all four milkweed species (Online Resource 1 Figs. 4–7, D-E; for further details, see Online Resource 1 Methods). Average values for test  $AUC_{psa}$  in the RSFSA-selected 12 models were highest for *A. a. ssp. capricornu* and *A. viridis*, at 0.965 and 0.952, respectively (Table 1). Lower average test  $AUC_{psa}$  values of 0.924 and 0.845 were produced for selected models of *A. latifolia* and *A. oenotheroides*, respectively (Table 1). Values of test  $AUC_{bgp}$  (MaxEnt default AUC) ranged from 0.805 to 0.904 for the different milkweed species and were on average about 5–8% lower than test  $AUC_{psa}$ . Model  $AUC_{psa}$  overfitting ( $AUC_{psa\_diff}$ ) was similar across the four species, ranging from 0.002 to 0.011, giving an average value of 0.008, which is a little lower than the average value for  $AUC_{bgp}$  overfitting ( $AUC_{bgp\_diff}$ ) of 0.013 (Table 1).

Top ranked variables in terms of permutation importance, frequency of appearance in models, and correlation groupings from the three sets of 250 RSFSA-selected MaxEnt models varied widely across the four milkweed species (Online Resource 1 Tables 4, 13–16). Of 60 top ranked variables (15 per species) in RSFSA-selected models of the four milkweed species, 66% were climatic (28% WorldClim, 43% SuppClim, 30% AET/PET indices), 30% were edaphic, and 3% were topographic (Online Resource 1 Table 4) (for MaxEnt response curves of important variables and further results related to variable importance, see Online Resource 1 Results, Figs. 8–11).

### Core habitat distributions

The MaxEnt core habitat for *A. a. ssp. capricornu* primarily occupied the southeastern portion of the South-Central Semiarid Prairies from western Oklahoma to Central Texas (Fig. 2a). *Asclepias viridis* core habitat occurred along the eastern edge of the South-Central Semiarid Prairies from Kansas to Texas and included the southern Central Irregular Prairies, the eastern portion of the Ozark Ouachita Appalachian Forests (excluding the mountainous ecoregions), the western portion of the Southeastern USA Prairies, and the eastern Texas portion of the Texas Louisiana Coastal Plains (Fig. 2b). The MaxEnt core habitat of *A. oenotheroides* was concentrated along the southeastern edge of the South-Central Semiarid Prairies and northern portions of the Tamaulipas Texas Semiarid Plain. *Asclepias oenotheroides* core habitat included southern portions of the Texas Louisiana Coastal Plain, and portions of various Level II ecoregions in Mexico, including the Dry Gulf of Mexico Coastal Plains and Hills and Interior Depressions (Fig. 2c, Online Resource 1 Fig. 16). The core eastern habitat of *A.*

*latifolia* included the West-Central portion of the South-Central Semiarid Prairies from southwestern Kansas and southeastern Colorado to eastern New Mexico and northwest Texas, and portions of the northern Chihuahuan Desert (Fig. 2d).

## Phenology relative to monarch activity

All four South-Central US milkweeds exhibited bimodal early and late season peaks in vegetative frequency. *Asclepias a. ssp. capricornu* and *A. viridis* had larger early-season peaks that corresponded and occurred more frequently during early season monarch activity from March to mid-May (Fig. 3). *Asclepias oenotheroides* had a relatively larger late season peak, and early and late season peaks were similar in magnitude for *A. latifolia*, and both these species occurred more frequently during late season monarch activity from mid-August to October (Fig. 4). The two seasonal peaks were associated with the first and second early vegetative phenophases. Peak flowering generally corresponded well with peaks in vegetative frequency, except for late season flowering in *A. latifolia*, which peaked earlier than the overall vegetative peak (Figs. 3–4).

## Land cover preference risk assessments

The 2016 NLCD land cover classification had an overall accuracy of 43% at milkweed locations in the study area, and we used our manual land cover classifications for calculating milkweed land cover utilization ( $r_i$ ) (Online Resource 1 Table 17). The histogram bin ratio weighting sample bias adjustment effectively reduced the raw citizen science percentage utilization of roadside habitats for the four milkweed species by 24–55%, from 24–59% in the raw counts to 6–31% for the adjusted *PopRoadHBRWtN* counts (Fig. 5., Online Resource 1 Figs. 21–25). Roadside habitat utilization was significantly highest for *A. latifolia*, and *A. asperula ssp. capricornu* utilized roadsides to a significantly greater extent than *A. viridis* (Fig. 5; Chi-squared tests for independence;  $P < 0.05$ ).

The land cover classes with highest utilization by at least three of the four milkweed species were Grassland Herbaceous, followed by Developed, Open Space (Fig. 6a). These land covers generally dominated the most common general habitats utilized by the four milkweeds: Field/Meadow and Rural Road ROW. Developed Medium and High intensity land covers also dominated within Rural Road ROW habitats (Online Resource 1 Figs. 21, 30). The land cover classes with the generally highest expected availability ( $p_i$ ) in the milkweed core habitats included Grassland Herbaceous, Shrub/Scrub, and Cultivated Crops (Fig. 6b). The two land cover classes of benefit (high  $E_i^*$ ) for most milkweeds (except *A. latifolia*) were Developed-Open Space and Developed-Low Intensity (includes Developed, Medium and High intensity for *A. oenotheroides*; Fig. 6c). Cultivated Crops and Shrub/Scrub were prominent high-risk (low  $E_i^*$ ) land cover for all four milkweeds (Fig. 6c). *Asclepias a. ssp. capricornu* benefit land covers were concentrated around Developed-Open Space of major urban areas in Central Texas. The largest areas of more available high-risk land covers for *A. a. ssp. capricornu* centered around Cultivated Crops and Pasture/Hay in the southeastern portion of the core habitat in the East Central Texas Plains, and Shrub/Scrub and Cultivated Crops in portions of western Texas and Oklahoma (Figs. 6b-c, 7a). Main areas that benefit *A. viridis* included the highly available land covers of Grassland Herbaceous in North Central and East Texas and Central and Northeast Oklahoma. Areas of high risk for *A. viridis* included two highly available land covers, Cultivated Crops in portions of West Central Oklahoma and coastal Texas, and Evergreen Forest in East Texas (Figs. 6b-c, 7b). Areas of main benefit to *A. oenotheroides* consisted of sparsely distributed Developed Low and Medium intensity and Developed-Open Space land covers around major metropolitan areas of Dallas/Fort Worth, Austin, and San Antonio. High-risk land covers for *A. oenotheroides* were concentrated in Shrub/Scrub and Grassland Herbaceous land covers in South Texas and portions of North and West Texas (Figs. 6c, 7c). No land covers could be statistically categorized as of benefit to *A. latifolia*, except for Other, which included various land covers with five total unadjusted milkweed occurrences. The highest  $E_i^*$  value land covers in the Other category for *A. latifolia* included Developed-Low Intensity and Pasture Hay, and these were mapped as the most beneficial land covers in calculating the *A. latifolia* benefit KDE isopleths (Fig. 7d) and for calculating the milkweed species combination high  $E_i^*$ . Shrub/Scrub, Grassland Herbaceous, and Cultivated Crops land covers were all highly available and of high risk for *A. latifolia* (Fig. 6b-c), and they dominated most of its core habitat (Fig. 7d). Higher resolution views of the  $E_i^*$  land cover preference risk assessments revealed more detailed contrasts in land cover preference risk, such as for *A. oenotheroides* around urban areas of San Antonio and South Texas (e.g., Online Resource 1 Figs. 35–36).

Both the early and late season partitioned combination milkweed land cover preference risk assessment high  $E_i^*$  KDE surfaces and isopleths identified similar regional densities of milkweed high benefit land cover (Figs. 8–9). The combined high  $E_i^*$  85% KDE isopleths (Figs. 8–9) resolved comparable major spring and fall interior and coastal corridors of land cover benefit for milkweed. The combined high  $E_i^*$  85% KDE isopleth extended further into the Coastal Funnel in the fall compared to the spring (Fig. 9). The densest regions of milkweed land cover preference risk within the Central Funnel included core habitat for *A. a. ssp. capricornu*, *A. viridis*, and *A. latifolia* in western Oklahoma, *A. latifolia* habitat in West Texas, and *A. oenotheroides* habitat in South Texas (Figs. 7, 9). In the Coastal Funnel, the highest milkweed land cover preference risk was seen in South Texas *A. oenotheroides* habitat and central coastal Texas *A. viridis* and *A. oenotheroides* habitats (Figs. 7, 9). There was a potentially critical gap in milkweed habitat in South Texas within the Tamaulipas-Texas Semiarid Plain and southern Western Gulf Coastal Plain ecoregions, where much *A. oenotheroides* core habitat was at high land cover preference risk (Figs. 1, 7c, 8–9).

## Discussion

### Niche modeling

The RSFSA revealed that subsets of six to eight of 95 variables were optimal for maximizing performance of MaxEnt models of the four milkweed species. Tracy et al. (2019) and Kantola et al. (2019b) also found that six and eight variables was an optimal subset size for MaxEnt models using RSFSA with large sets of 80 and 119 variables, respectively. Consistent with previous niche modeling studies using RSFSA, we found significantly improved values of  $AUC_{psa}$  and  $AIC_{cbg}$  for selected models over random models, but overfitting was only sometimes improved (Tracy et al. 2018, 2019; Kantola et al. 2019b). We found that  $AUC_{psa}$  criterion reduced overfitting in more RSFSA replications than the  $AIC_{cbg}$  criterion, as found by Kantola et al. (2019b), but the  $AIC_{cbg}$  criterion can

yield lower overfitting with RSFSA in some cases (e.g., Tracy et al. 2018), or the two criteria may be equal in efficacy with regards to overfitting (Tracy et al. 2019).

The overall average test MaxEnt background/presence  $AUC_{bgp}$  for the four milkweed species niche models was 0.87 (range 0.81 to 0.90), which was very similar to the average of test  $AUC_{bgp}$  values of 0.86 (range 0.76–0.91) reported for the western ranges of 13 milkweeds by Dilts et al. (2019), but lower than the test  $AUC_{bgp}$  values of 0.98 and 0.93 reported for the Idaho ranges of two milkweeds by Svancara et al. (2019). Our values of test  $AUC_{bgp}$  were 5–8% lower than pseudoabsence  $AUC_{psa}$ , and this was probably a result of lower false negative error rates that would arise in  $AUC_{psa}$  since the pseudoabsence data were buffered 20-km from presence points. In contrast,  $AUC_{bgp}$  considers as absences the background and presence points that can overlap the vicinity of true presence points to yield higher false negative error rates. MaxEnt default  $AUC_{bgp}$  is more suitable for making comparisons between MaxEnt model studies, and  $AUC_{psa}$  is best for comparisons of MaxEnt with other types of niche models, such as GLM.

Our feature selection results revealed the usefulness of incorporating additional climate variables in niche modeling beyond the typically employed 19 WorldClim indices (Bradie and Leung 2016), including the SuppClim and AET/PET indices, supporting our previous findings (Tracy et al. 2018, 2019; Kantola et al. 2019b). This is the first study to find that soil taxa are important variables for niche modeling of milkweeds, with soil taxa variables highly ranked in niche models of all four South-Central US species. Previous studies by Dilts et al. (2019) and Svancara et al. (2019) established that single edaphic variables were important in niche models of two studied western milkweed species, percent sand for *A. a. ssp. asperula*, and soil depth for *A. speciosa*, respectively. For example, we found that percent cover of *usterts* (Vertisols order) was the highest-ranking variable for niche modeling of *A. oenotheroides*, and the prevalence of *usterts* at a 1-km scale could be seen across the core habitat of *A. oenotheroides* in Texas (Online Resource 1, Table 4, Figs. 10a, 37).

## Core habitat distributions and subspecies boundaries

Our models confirmed the importance of the South-Central US as core habitat for *A. viridis*, which included eastern Texas and Oklahoma and parts of western Arkansas and Louisiana but excluded most of Illinois and all of Indiana (Fig. 2b). These results contrast with the 0.5 probability contour for the MaxEnt distribution of *A. viridis* from Lemoine (2015) that extended past Illinois east to Indiana, but excluded most of Oklahoma, Texas, and Louisiana. The differences probably arise from our inclusion of a more representative number of *A. viridis* occurrence data to the West and South.

The 100% MaxEnt consensus model core habitat of *A. a. ssp. capricornu* generally resided well within the subspecies boundary, but it approached the boundary near the confluence of the Pecos River and Rio Grande in Texas (Fig. 2a). Our data supports the suggestion by Singhurst et al. (2015) that species status may be warranted for *A. a. ssp. capricornu* and *A. a. ssp. asperula* based upon clear differences in their morphology and distribution (see Woodson 1954). Further studies are needed to determine the distribution, frequency, and degree of hybridization in these subspecific taxa, and our models indicated that it is important to include data from the southern Pecos River and Coahuila state.

## Phenology relative to monarch activity

Brower et al. (2018) found that early season monarch spring migratory activity in north central Florida coincided well with the vegetative phenology of the local milkweed monarch larval host, *A. humistrata* (pinewoods milkweed). Waterbury et al. (2019) found that phenology of Idaho and Washington *A. speciosa* was also well synchronized with early spring monarch arrival and oviposition. Similarly, we found that both early and late season monarch activity was generally well coordinated with early and late season peaks in milkweed vegetative phenology of the four studied milkweeds in the South-Central US. *Asclepias latifolia* represented an exception, with an early season vegetative peak occurring after monarch spring activity. However, the fall peak for *A. latifolia* corresponded well to late season monarch activity. Observed peaks in milkweed weekly vegetative phenology generally corresponded to seasonal peaks in flowering phenology, except for the fall peak for *A. latifolia*, which had little flowering.

The bimodal early and late season peaks in weekly vegetative frequency and the gaps between early and late season early vegetative phenophases for all four milkweeds (Figs. 3–4) may reflect late emergence of some individuals or resprouting following favorable late summer/early fall rainfall in certain years, which can be promoted by mid-summer disturbance. Calvert (1999) reported above average rainfall in the fall of 1996 produced abundant resprouting and peak October flowering in all four studied species across Central Texas. We have also observed late September/early October flowering of *A. a. ssp. capricornu* and *A. oenotheroides* in Central Texas following above average September 2018 rainfall without disturbance (Online Resource 1 Figs. 38–39). Nabhan et al. (2015) suggested that subspecies of *A. asperula* also may resprout following early summer damage. Late season resprouting of *A. viridis* has also been reported following summer rain (Dee and Palmer 2019) and summer disturbance, such as burning (Baum and Sharber 2012) or mowing (Baum and Mueller 2015; Dee and Baum 2019). *Asclepias oenotheroides* has the highest number of buds per root biomass of all four species, and *A. latifolia* is the only clonal species we studied (Pellissier et al. 2016). These more developed vegetative reproduction traits probably favor the observed relatively greater late season frequencies of *A. oenotheroides* and *A. latifolia*.

## Land cover preference risk assessments

The highest land cover preference risk was found with Cultivated Crops for all four milkweed species. Waterbury et al. (2019) similarly found cultivated croplands had low utilization for northwestern milkweeds. We found a few *A. oenotheroides* in Cultivated Crops, and *A. latifolia* occurred in cultivated crops in cotton fields of the Texas panhandle in the 1960's to 1970's before the increased use of glyphosate resistant cotton (S. Feagley, Soil and Crop Sciences Department, TAMU, retired, personal communication). The greater vegetative root budding of *A. oenotheroides* and the clonal nature of *A. latifolia* probably make these species relatively more tolerant of cultivation. The rhizomatous *A. syriaca*, an important monarch host plant of the Midwest (Malcolm et al. 1993), was once abundant in cultivated fields (Yenish et al. 1997), where it was commonly utilized by monarch larvae, but where it now has been much reduced by increased herbicide use (Hartzler 2010; Pleasants and Oberhauser 2013; Zaya et al. 2017). Widespread herbicide use could also be lowering occurrence of *A. oenotheroides* and *A. latifolia* in Cultivated Crops in the South-Central US.

The Shrub/Scrub land cover class also represented high land cover preference risk for all four milkweeds, which could be related to lower soil moisture and anthropogenically lowered disturbance regimes in this land cover that fosters woody encroachment of open meadow milkweed habitats. Waterbury et al. (2019) found relatively low utilization of northwestern milkweeds for shrub/scrub, which they attributed to higher aridity. The Pasture/Hay land cover class represented high risk only for *A. a. ssp. capricornu*. The lower utilization of Pasture/Hay by *A. a. ssp. capricornu* may be related to a generally lower abundance of this species over the eastern portion of its range where Pasture/Hay is more abundant rather than to any lower suitability of Pasture/Hay for this milkweed compared to other species (Figs. 1, 2a, 6).

Grassland Herbaceous land cover was of high benefit for *A. viridis* and *A. oenotheroides*, no risk for *A. a. ssp. capricornu*, and high risk for *A. latifolia* (Fig. 6). Waterbury et al. (2019) found highest utilization of northwestern milkweeds for grassland/herbaceous cover. *Asclepias latifolia* favors grasslands, plains and prairies, trails, rocky canyon slopes, railways, and roadsides (Woodson 1954; Hart et al. 2000; Nabhan et al. 2015). Lower disturbance leading to less open areas in contemporary anthropogenically managed Grassland Herbaceous land covers may disfavor *A. latifolia*.

The Developed-Open Space and Developed-Low Intensity land covers, which commonly included roadsides and urban areas, were preferred by two to three of the four milkweed species, except for *A. latifolia*. Webb (2017) found that both *A. viridis* and *A. a. ssp. capricornu* occurred at higher frequency on roadsides compared to adjacent lands in Oklahoma. *Asclepias viridis*, along with *A. syriaca* and a variety of other milkweeds, are also common along roadsides in other states (e.g., Kaul et al. 1991; Kasten et al. 2016; Cariveau et al. 2020). In contrast, northwestern milkweeds had low utilization of developed land covers (Waterbury et al. 2019).

We endeavored to increase the accuracy of our land cover preference risk assessment by improving the quality of the input data sources through (1) using feature selected edapho-topo-climatic species distribution models to define core habitats, (2) using a manual land cover classification, (3) reducing sample bias in species occurrence surveys among the different land cover classes, and (4) minimizing temporal discrepancies between species occurrence data and the land cover classification. The overall accuracy of 43% for the 2016 NLCD classifications at our milkweed occurrence sites was very low, justifying our decision to develop a manual land cover classification from Google Earth Pro and Google Map imagery. The low NLCD accuracy is probably due to the prevalence of milkweeds in edge habitats that are more prone to classification error, such as roadsides classified by NLCD as adjacent Grassland Herbaceous or Shrub/Scrub habitats rather than as Developed ROW land covers. The use of our novel histogram bin weighting sample bias reduction method lowered the frequency percentage of the four milkweed species in roadside ROW habitats by 24–55%, helping compensate for the natural bias of iNaturalist observations along roadsides (Online Resource 1 Figs. 22–25). However, there is still the potential for substantial error in the land cover risk assessment. For example, it is possible that our sample bias reduction method could be over-compensating for the potential bias of citizen science records near roads if a milkweed species has a greater affinity for disturbed habitats related to roadsides than the larger target group of nectar plants (see also Ranc et al. 2017).

## Implications for monarch butterfly conservation

The individual species and phenologically partitioned combined milkweed land cover preference risk assessments resolved major corridors of milkweed land cover benefit that may be especially important for providing monarch adult nectar and larval host plants for both the spring migration and the first generation as well as the last summer generation and fall migration. The identified early and late season corridors of milkweed land cover benefit are similar and are mostly encompassed within the previously identified Central and Coastal monarch fall migratory funnels of Tracy et al. (2019). The spring monarch migration is dispersed, and spring migratory routes are more difficult to identify than fall migration routes (Solensky 2004), which have been clearly defined (Calvert and Wagner 1999; Howard and Davis 2009; Tracy et al. 2019). Taylor (2019) described two major monarch spring migratory pathways through Mexico into Texas based upon spring first sightings of Journey North, a primary interior pathway and minor coastal pathway. These spring migratory pathways correspond well with our fall migratory Central and Coastal funnels (Tracy et al. 2019), respectively (Fig. 9).

Large western portions of the Central Funnel consist of neutral to high-risk land cover for milkweed in both the early and late season, including areas in western Oklahoma and Central Texas where *A. viridis* and *A. a. ssp. capricornu* are more frequent during the early season and where *A. latifolia* is more frequent in West Texas during the late season (Fig. 9). Increasing habitat for *A. viridis* and *A. a. ssp. capricornu* in western Oklahoma and west-central Texas would especially benefit the spring migration, while increasing *A. latifolia* habitat in West Texas should benefit late generation monarchs and fall migrants. A potential critical connectivity gap in milkweed land cover benefit was identified in *A. oenotheroides* core habitat in South Texas (Figs. 8–9, Online Resource 1 Figs. 34–35). Providing additional *A. oenotheroides* milkweed habitat in South Texas may improve both spring and fall connectivity for the monarch migration.

We found from 6–31% of our milkweed occurrences were associated with roadsides in our study area, depending on the species. Management of roadside habitats is receiving increased focus for benefitting pollinator species in general (Hopwood et al. 2015; Phillips et al. 2020), and milkweeds and monarchs (Fischer et al. 2015; Kasten et al. 2016; Kaul and Wilsey 2019; Knight et al. 2019; Cariveau et al. 2019, 2020; Monarch CCAA/CCA Development Team 2020). Roadside habitats can be a threat to monarchs from roadkill (Kantola et al. 2019a; Mora Alvarez et al. 2019). Phillips et al. (2019) found roadside pollinator populations were higher a few meters away from the roadway, and Keilsohn et al. (2018) suggested that placing nectar plants a few meters from the roadway edge may reduce roadkill. Enhancement of milkweeds in urban gardens to benefit monarchs is also receiving attention (Fitzgerald 2015; Baker and Potter 2019). However, predation in urban gardens can sometimes be higher than in rural habitats, potentially making them an ecological trap (Baker and Potter 2020).

Southern milkweeds are shade intolerant species that are apparently adapted to patchwork disturbance from historical bison grazing and wildfires in the Great Plains (USDA NRCS 2015c). Disturbance in anthropogenic areas from mowing and burning favors growth of Midwest milkweeds, such as *A. syriaca* (Kaul and Wilsey 2019), as well as *A. viridis* (Baum and Sharber 2012; Baum and Mueller 2015) and probably other South-Central US milkweeds. For example, regular late season mowing of grasslands in Oklahoma can increase the cover of *A. viridis* (Dee et al. 2016; Dee and Baum 2019). Periodic mowing is probably a critical disturbance factor needed to maintain open habitat for continued milkweed colonization and persistence in roadside and grassland habitats (Kaul and

Wilsey 2019). Leone et al. (2019) reported that monarchs were more abundant at sites managed by prescribed fire compared to grazing. Timing of mowing or burning in fields, roadsides, and urban open spaces can be especially important to maximize seasonal milkweed availability to monarchs for adult nectar resources and larval food plants (Baum and Sharber 2012; Baum and Mueller 2015; Fischer et al. 2015; Knight et al. 2019; Haan and Landis 2019a, 2019b, 2020). Mowing of milkweed habitats at the wrong time during the spring and late summer/fall breeding seasons can reduce habitat availability for pollinators (Hopwood et al. 2015; Phillips et al. 2019; Waterbury et al. 2019), including immature and adult monarchs (Cariveau et al. 2020; Monarch Joint Venture 2020), and potentially reduce milkweed recruitment, establishment, and/or spread.

Ecoregions with areas of high Cultivated Crop and Shrub/Scrub cover that overlap core milkweed habitats should be a major focus for mitigating monarch habitat loss through restoring or creating monarch habitat. Examples of approaches to mitigate land cover preference risk to milkweeds and monarch butterflies for the South-Central US study area are programs of the USDA NRCS (2015c; 2016a,b) and USFWS, as well as the National Fish and Wildlife Foundation and Texas Soil and Water Conservation Board (2016). These initiatives incentivize management practices to maintain and enhance grasslands and that maximize species richness, including nectar species. Management practices with the potential to increase milkweed and nectar plant populations in grasslands include brush management, prescribed burning, prescribed grazing, and mowing (USDA NRCS 2015a).

## Conclusion

This study further demonstrated the effectiveness of the random subset feature selection algorithm to improve performance of MaxEnt niche models with smaller variable sets and generate ensemble models that efficiently highlight core habitats for conservation and risk assessment. Milkweed land cover preference risk assessments facilitated separate estimation of the impacts of land cover classes on otherwise edapho-topo-climatically suitable milkweed habitats. Milkweed conservation in South-Central US Grassland Herbaceous and Developed land covers, including roadsides and urban areas, has potential to benefit monarch conservation by conserving or increasing critical milkweed nectar and breeding resources. The combined milkweed high  $E_i^*$  85% KDE isopleths resolved important corridors in the Central and Coastal monarch migratory funnels where high benefit land cover for milkweeds provide adult nectar and larval food resources critical to functional connectivity for the spring and fall migrations through the South-Central US region. A potential critical gap in monarch migration functional connectivity was identified in South Texas. Milkweed habitat corridors and gaps highlight valuable areas for potential mitigation measures to conserve or restore habitat.

## Declarations

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### Conflicts of interest/Competing interests

The authors declare that they have no conflict of interest in this publication.

### Availability of data and material

Online Resource 1 includes raw data and data summaries.

### Code availability

Online Resource 1 includes R and python codes used in analyses.

### Author contributions

Planning for the study involved all authors, including JLT, TK, KAB, and RNC. JLT developed the analysis framework and methodology, assembled some of the species occurrence data, and performed some of the niche model analysis, all of the weekly phenology analysis, and most of the land cover preference risk assessment analysis. TK also assembled species occurrence data and carried out some of the niche model and land cover preference risk assessment analyses. JLT led the writing with TK, KAB, and RNC assisting. All authors gave approval for the final revision and are accountable for all aspects of the work.

### Ethics approval

Not applicable.

### Consent to participate

Not applicable.

## Consent for publication

Not applicable.

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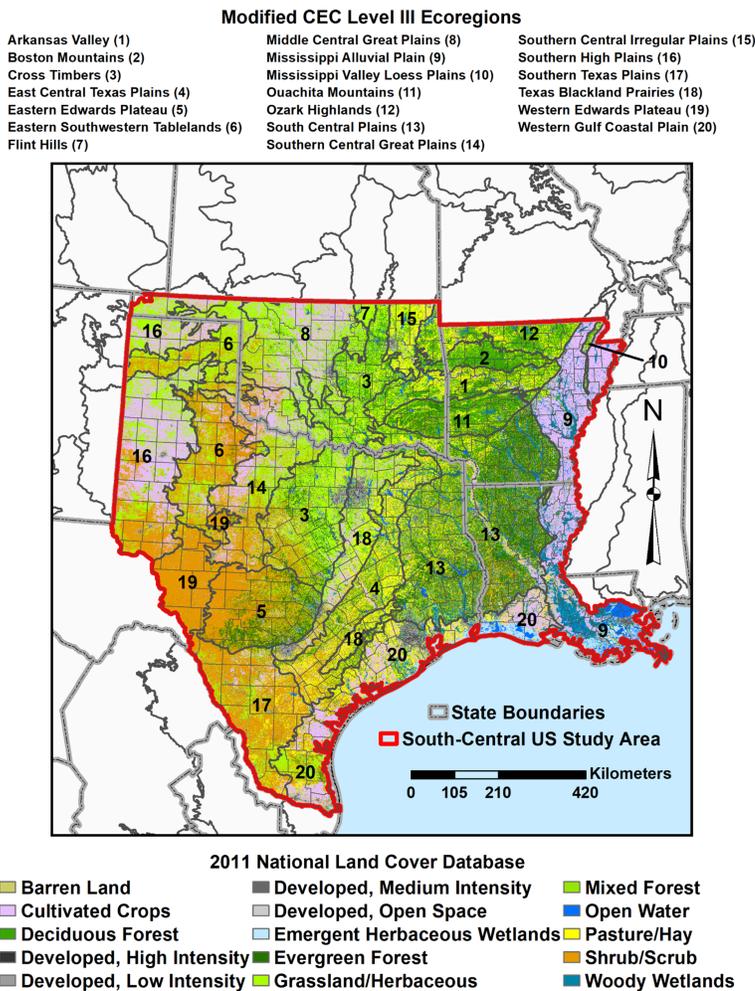
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## Figures



**Figure 1**  
South-Central US study area for land cover preference risk assessment analyses with land cover classes of the 2016 National Land Cover Database (Homer et al. 2015; MLRC 2017) and modified CEC (2005) Level III ecoregions

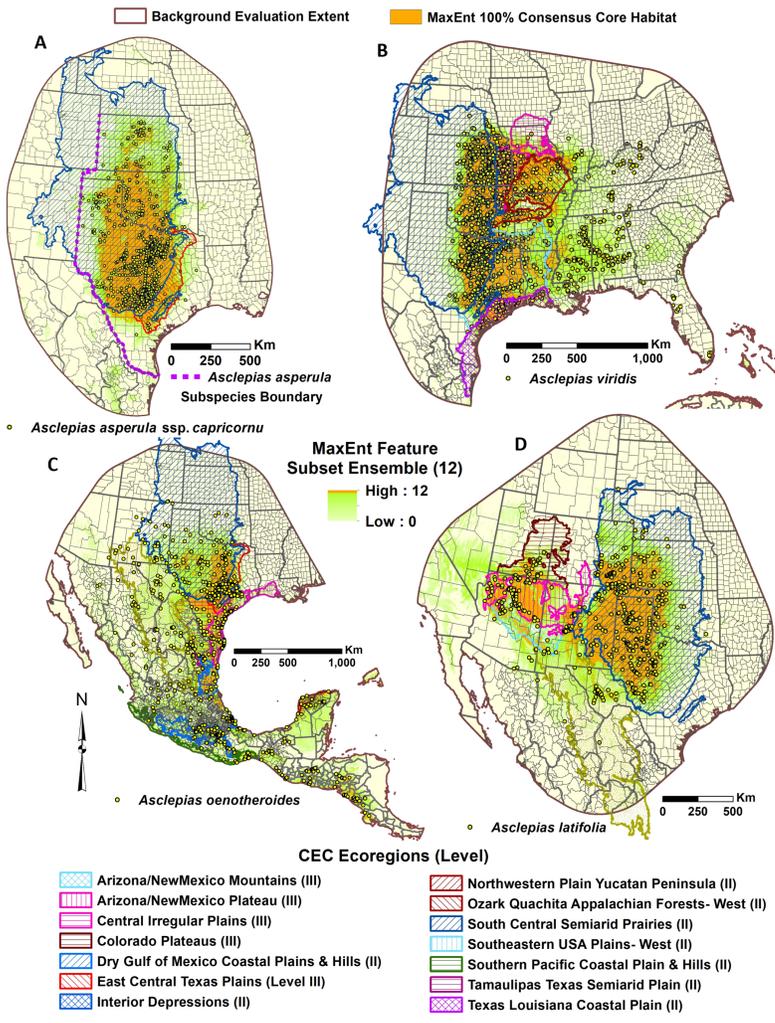


Figure 2

*Asclepias* spp. MaxEnt frequency consensus for selected feature subset ensembles of 12 distribution models (1834-2018), including MaxEnt 100% consensus core habitats and CEC (2005) ecoregions, for (a) *A. asperula ssp. capricornu*, with subspecies western distribution boundary (see Online Resource 1 Figs. 1-3), (b) *A. viridis*, (c) *A. oenotheroides*, and (d) *A. latifolia* (for larger images, see Online Resource 1 Figs. 12-16)

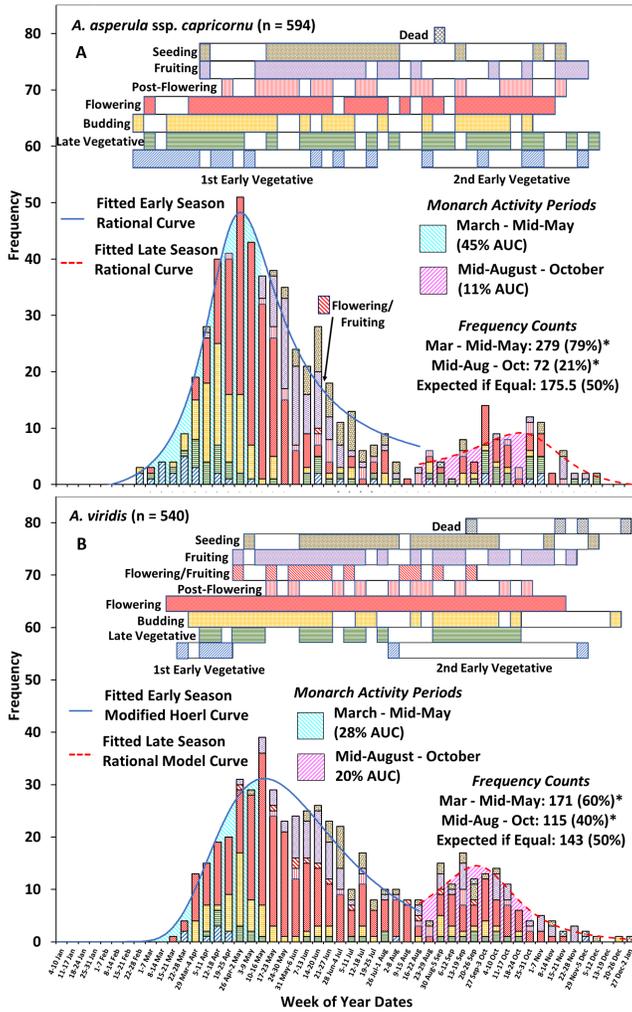


Figure 3

Asclepias spp. annual (2011-2020) weekly stacked phenophase histograms and phenoperiod Gantt charts (= legend) for MaxEnt core habitats within South-Central US study area (n = spatio-temporally thinned locations), with percent of total area under fitted nonlinear curves for the monarch activity periods of March through mid-May and mid-August through October: (a) *A. asperula ssp. capricornu* and (b) *A. viridis*, (for larger images, fitted curve formulae, and R2 values, see Online Resource 1 Figs. 17-18). The two-tailed 95% Bonferroni confidence intervals for early and late season frequency percentages with asterisks fall outside of the expected random frequency of 50%, assuming they were equal (omnibus Chi-squared Goodness of Fit Tests,  $P < 0.05$ )

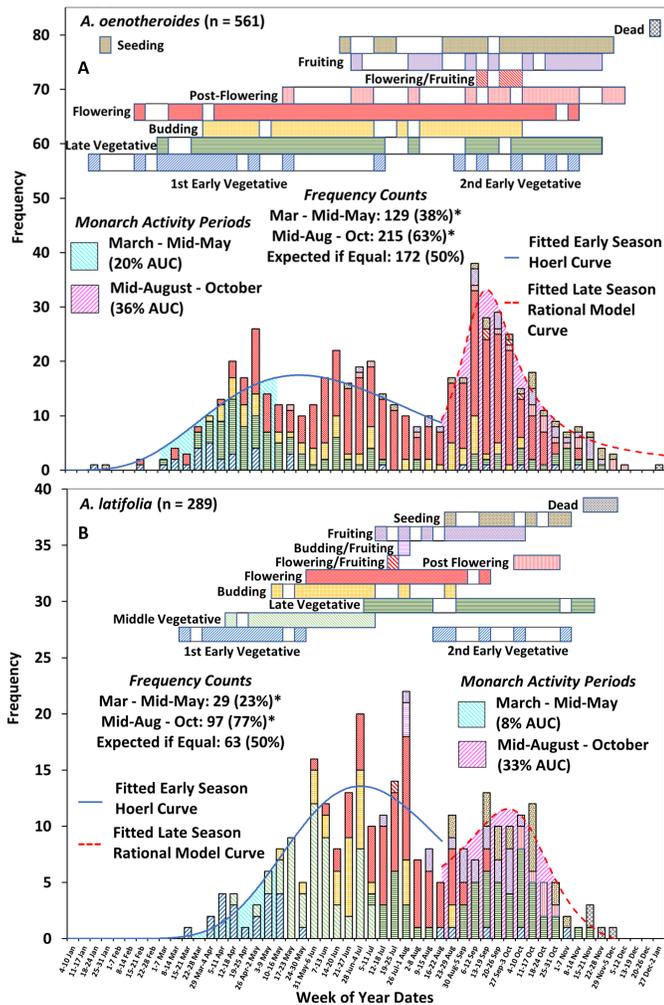


Figure 4

Asclepias spp. annual (2011-2020) weekly stacked phenophase histograms and phenoperiod Gantt charts (= legend) for MaxEnt core habitats within South-Central US study area (n = spatio-temporally thinned locations), with percent of total area under fitted nonlinear curves for the monarch activity periods of March through mid-May and mid-August through October: (a) *A. oenotheroides* and (b) *A. latifolia*, (for larger images, fitted curve formulae, and R2 values, see Online Resource 1 Figs. 19-20). The two-tailed 95% Bonferroni confidence intervals for early and late season frequency percentages with asterisks fall outside of the expected random frequency of 50%, assuming they were equal (omnibus Chi-squared Goodness of Fit Tests,  $P < 0.05$ )

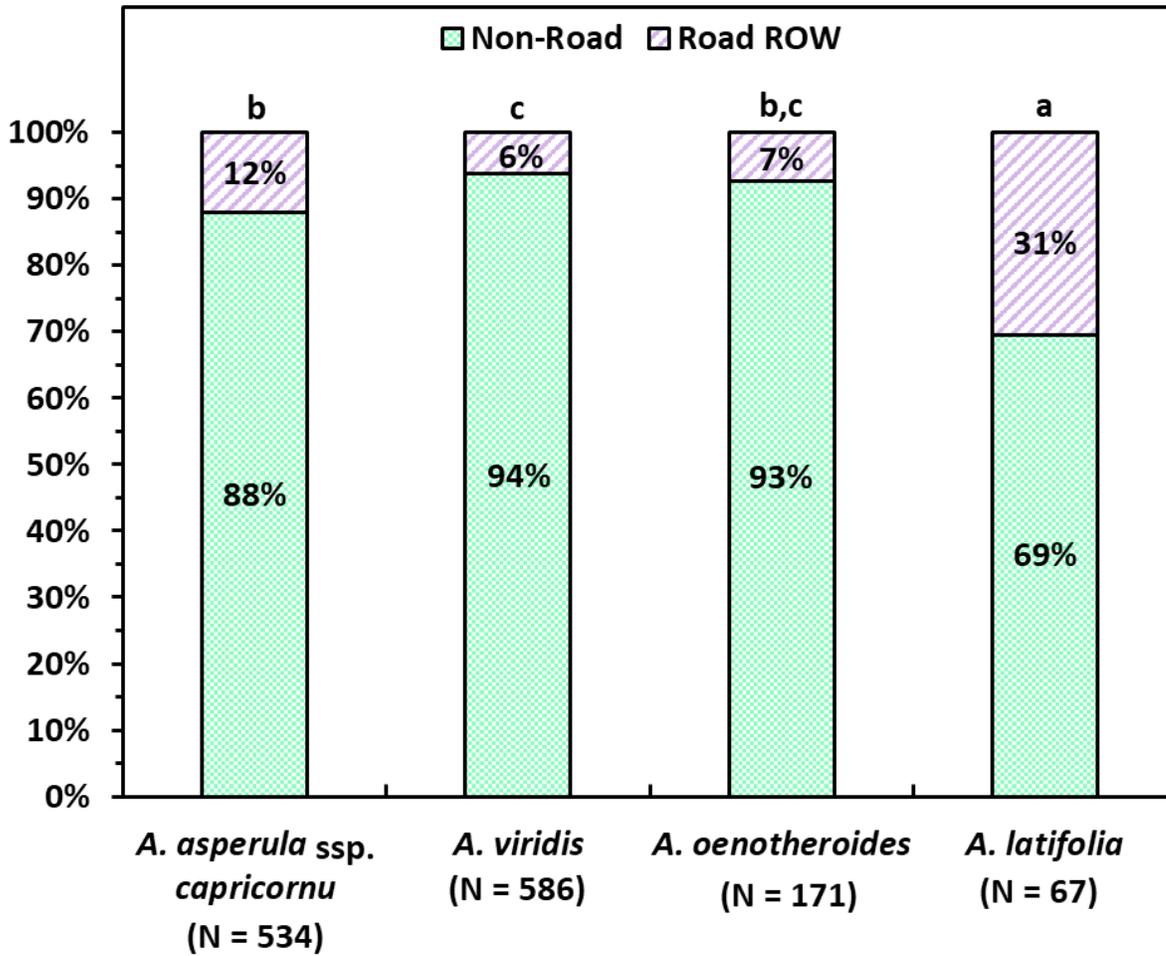


Figure 5  
 Asclepias spp. percentage utilization (2014-2018) of road right of way (ROW) versus non-road habitat types within MaxEnt core habitats for observation data weighted by human population and road distance (PopRoadHBRWtN) (bars with different letters have independent distributions according to an omnibus Chi-squared test followed by pairwise Chi-squared tests with Holm's correction of p-values for multiple comparisons;  $P < 0.05$ ) (for corresponding pie charts with further habitat subdivisions for raw unweighted, human population weighted, and road distance weighted data, and relationships with land cover classes, see Online Resource 1 Figs. 21-30)

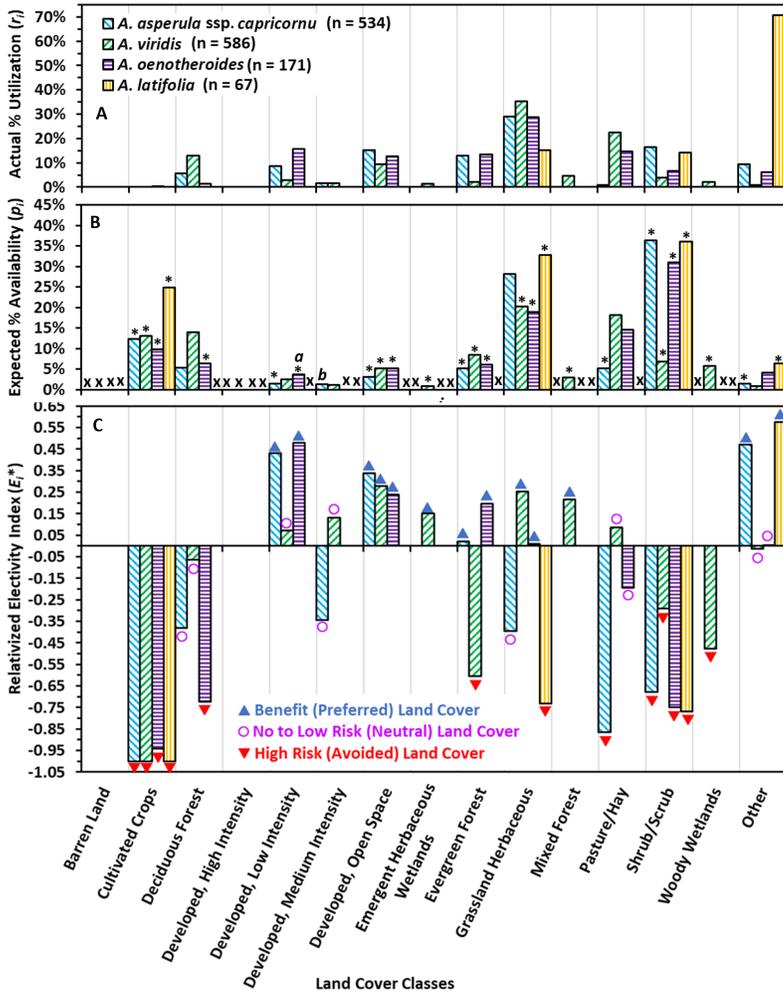


Figure 6

Land cover class utilization/availability analysis (2014-2018) for *Asclepias* spp. in South-Central US within MaxEnt core habitats for (a) actual percent utilization of land cover classes ( $r_i$ ) by *Asclepias* spp. ( $n$  = locations weighted by human population and road distance, PopRoadHBRWtN); (b) expected percent availability ( $p_i$ ) for land cover classes, where values of  $p_i$  with asterisks fall outside of the two-tailed 95% Bonferroni confidence intervals for  $r_i$  ( $r$  significantly differed from  $p$  for all *Asclepias* spp.; Chi-squared Goodness of Fit Test,  $P < 0.05$ ); and (c) land cover relativized electivity index ( $E_i^*$ ) for *Asclepias* spp., where land covers with significant differences noted in (b) are marked with colored arrows. Values of  $p_i$  (b) with "x" had less than five expected milkweed occurrences and were combined into the "Other" category, or Developed, High and Medium intensities were combined with Developed, Low Intensity when marked with "a", or Developed, High Intensity was combined with Developed, Medium Intensity when marked with "b"

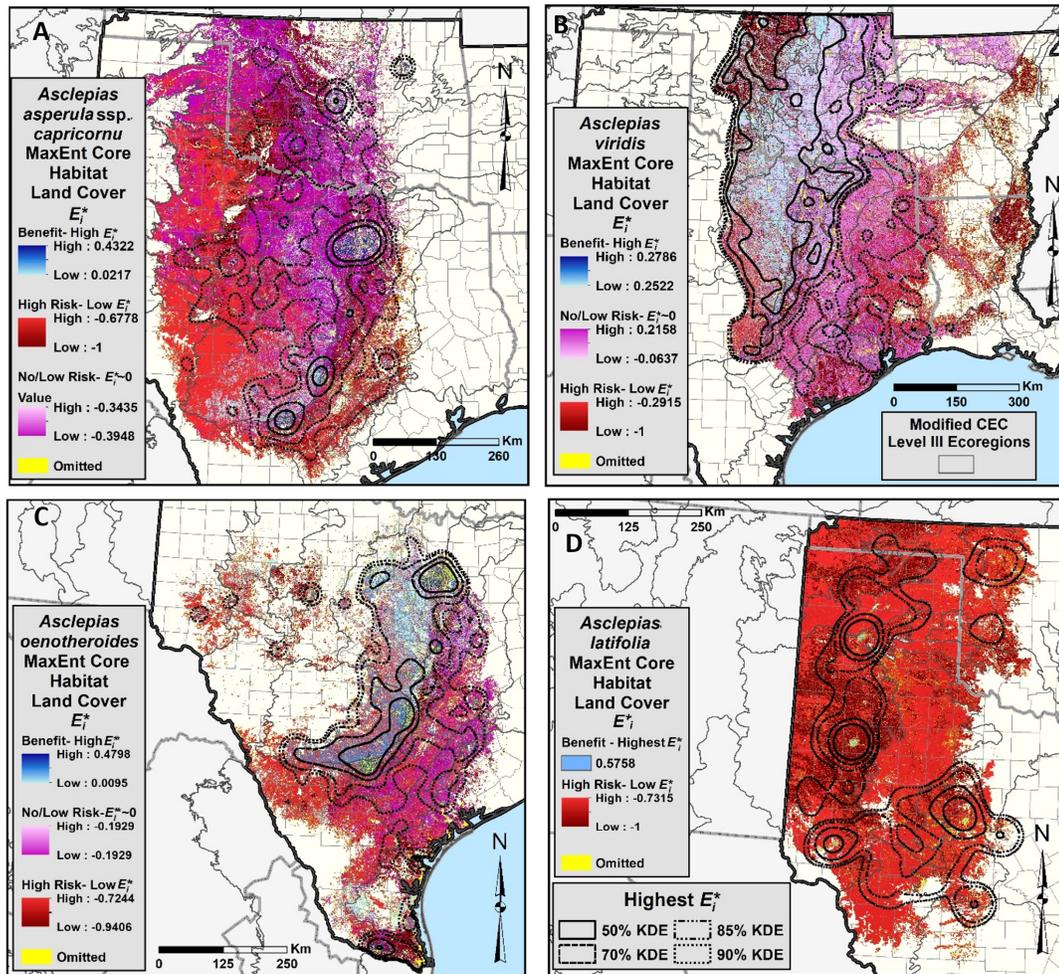


Figure 7

*Asclepias* spp. land cover preference risk assessments (2014-2018) according to land cover relativized electivity,  $E_i^*$ , over MaxEnt core habitats (Fig. 4) within the South-Central US study area, including KDE isopleths for high milkweed land cover benefit  $E_i^*$  and modified CEC (2005) Level III ecoregions (see Fig. 1 for ecoregion legend): (a) *A. asperula ssp. capricornu*, (b) *A. viridis*, (c) *A. oenotheroides*, and (d) *A. latifolia* (for larger images, see Online Resource 1 Figs. 31-36)

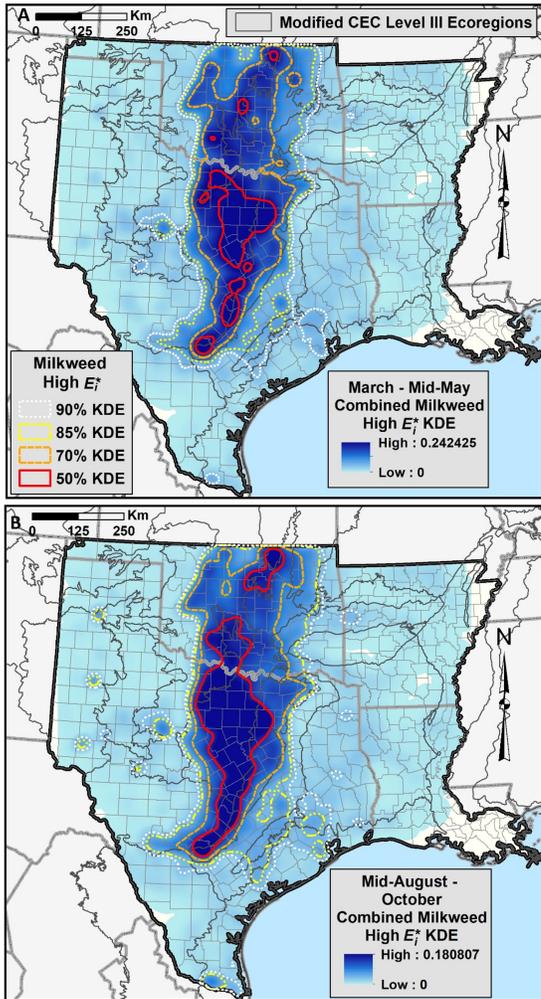


Figure 8

Kernel density estimation (KDE) surface for combined *Asclepias* spp. high benefit land cover relativized electivity index,  $E_i^*$  (2014-2018), over MaxEnt core habitat in the South-Central US for the monarch activity periods of (a) March through mid-May (mean high  $E_i^*$  KDE of 0.0261) and (b) mid-August through October (mean high  $E_i^*$  KDE of 0.0236), with KDE isopleths and modified CEC (2005) Level III ecoregions (see Fig. 1 for ecoregion legend; see Figs. 3-4 for phenology)

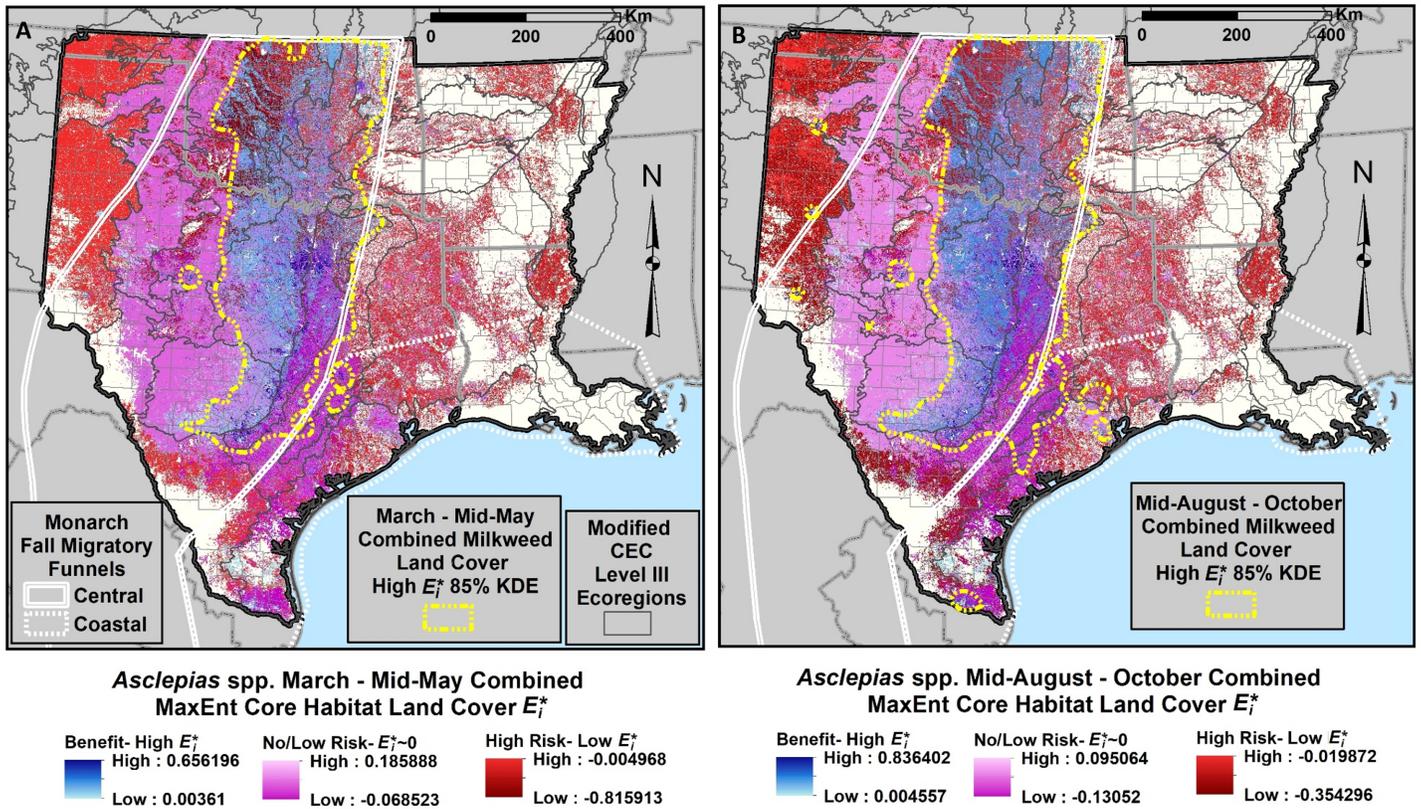


Figure 9

Combined *Asclepias* spp. land cover preference risk assessments (2014-2018) according to land cover relativized electivity index,  $E_i^*$ , categories over MaxEnt core habitats and combined high  $E_i^*$  85% kernel density estimate (KDE) isopleths (Fig. 8) for the monarch activity periods of (a) March through mid-May and (b) mid-August through October, with modified CEC (2005) Level III ecoregions over the South-Central US study area and fall monarch migratory funnels from Tracy et al. (2019) (see Fig. 1 for ecoregion legend; see Figs. 3-4 for phenology)

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [TracyetalMilkweedsMSOnlineResource118Jul2021.docx](#)