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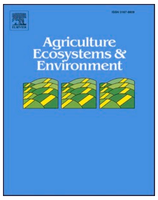

Cultivated milkweed hosts high diversity of surface-active and soil-dwelling arthropods in a New England case study

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ABSTRACT

New land uses can drive complex changes to local biodiversity. In the Northeastern U.S., cultivated milkweed has arisen as a new crop with potentially promising outcomes for monarch butterflies, but has unknown effects on surface-active and soil-dwelling arthropods. We assessed differences in arthropod communities among nearby sites containing milkweed and three common regional land uses: conventional corn, conventional hay, and forest, representing a spectrum of high to low land use intensity. In each land use, we sampled surface-active and soil-dwelling arthropods, and we classified organisms at the taxonomic order level for all collected arthropods and at the taxonomic genus level for surface-active beetles. To address differences in functional traits between sites, we measured organisms' body sizes and calculated average body mass, total biomass, and abundance of arthropods in small, medium, and large size classes. In almost all analyses, taxonomic diversity values were significantly higher in the milkweed site than in corn and similar between the milkweed and hay sites. Milkweed had significantly higher diversity of surface-active arthropods than forest (for both orders and beetle genera), but did not have higher diversity of soil-dwelling arthropods, indicating possible different mechanisms driving aboveground versus belowground trends. Community composition differed significantly among land uses (demonstrated in NMDS ordination plots), with milkweed most similar to hay. Body size analyses demonstrated high total biomass and generally higher abundance of larger individuals in milkweed than in other land uses, with the exception of corn, which was dominated by large carabid beetles. We discuss the implications of our findings to land use properties and ecological function. Our case study indicates promising benefits of milkweed cultivation for soil biodiversity and soil health, with more research needed to validate and build from our results.

1. Introduction

Land use drives local patterns in biodiversity and biological composition (Newbold et al., 2015; Turner et al., 2007), and new uses can cause uncertain changes. While most ecological studies focus on systems that are widespread or have long been prominent, studying novel systems allows researchers and land managers to glean an early understanding of potential effects. For example, despite initial trepidation around the ecological effects of *Cannabis sativa* (hemp) production, studies have shown this crop can serve as important habitat to pollinators (O'Brien and Arathi, 2019) and that secondary compounds in this plant can repel root-knot nematodes, a major agricultural pest (Kayani et al., 2012). On the other hand, the relatively new and growing use of tarps on agricultural fields has shown preliminary negative effects on soil biodiversity and respiration, possibly due to heating soils to inhospitable levels (Birthisel et al., 2019). Whether positive or negative, impacts of land use on biological communities are important to track to elucidate conservation and functional implications (Cardinale et al., 2012; Foley, 2005).

Common milkweed (*Asclepias syriaca*) is a native plant found in many North American ecosystems, which some farmers have started to intentionally grow. Milkweed agriculture is driven by a new market for

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milkweed floss, an insulative material found within milkweed's seedpods with potential use in textiles (Hassanzadeh and Hasani, 2017). Milkweed is a promising economic pursuit for farmers, with the price per acre of milkweed estimated between $800 and $1000, as compared to around $660 for corn (USDA, 2021). Milkweed agriculture has a number of potential ecological benefits, including restoring area of milkweed cover, which has experienced widespread declines in the past several decades due to land use change and targeted exclusion (Pleasants and Oberhauser, 2013). Additionally, milkweed production could offer an alternative to synthetic fibers, provide forage for pollinator species, and serve as a larval host plant for monarch butterflies (Landis, 2017). Development of milkweed fields will undoubtedly impact other biological communities, although the direction and dynamics of effects are unclear.

Surface-active and soil-dwelling arthropods, including beetles, spiders, springtails, and mites, are an important ecological group often affected by land use patterns and practices (Cole et al., 2002; Ford et al., 2013; Jerez-Valle et al., 2014; Lindo and Winchester, 2006; Wardle et al., 1999). This group spans a number of size classes and functional roles. Beetles, for example, can be larger than 100 mm or as small as a fraction of a millimeter, while mites and springtails are usually smaller than 2–4 mm. While some arthropod groups are primarily predators (spiders), others can be primarily detritivores or fungivores (Oribatida mites), herbivores (flea beetles), or omnivores (many Carabid beetles and springtails) (Dindal, 1990). Many studies have found a relationship of decreasing arthropod diversity with increasing agricultural intensity, such as with increasing tillage or usage of synthetic inputs (House and Parmelee, 1985; Rodríguez et al., 2006; Tsiafouli et al., 2015). This is concerning because surface-active and soil-dwelling arthropods serve a number of key roles, including contributing to decomposition, controlling pests, and maintaining soil structure, ultimately relating to ecosystem services including nutrient cycling, carbon storage, agricultural production, and disease and pest control (Angst et al., 2017; Badorreck et al., 2012; Barrios, 2007; Kinnebrew et al., 2021). Therefore, preserving high diversity of these organisms in agricultural landscapes can lead to a wide array of benefits. Milkweed, which is a perennial plant with minimal tillage needs and does not have a history of domestication, might harbor more diverse and abundant surface-active and soil-dwelling arthropod communities than other common agricultural land uses.

Broadly understanding the effect of land use on arthropod communities requires a wide variety of sampling and analytical tools. Apart from analysis of taxonomic diversity, which is a common and valuable method, representation and knowledge of communities can be enriched with analyses of functional traits (e.g. morphological, physiological, and life history characteristics that indicate how an organism responds to and interacts with its community and environment) (Lyashevska and Farnsworth, 2012; Violle et al., 2007; Wood et al., 2015). Body size is one functional trait used commonly in ecological studies. The distribution of body sizes in arthropod communities reflects land use change because landscape conditions and management, such as the availability of food substrates, tilling, and the use of pesticides, can make a habitat more or less hospitable for arthropods of certain sizes (Chown and Gaston, 2010). For instance, some studies find that disturbance can more negatively affect large-bodied arthropods, perhaps due to lower fecundity and higher dependence on environmental factors, such as vegetation complexity (Chown and Gaston, 2010; Tsiafouli et al., 2015). Body size is a valuable addition to taxonomic analyses because it helps spell out the functional implications of a community, for example allowing calculations of total biomass, which can key into the metabolic potential of a community (Saint-Germain et al., 2007).

Biodiversity assessments can also be enriched by increasing the sampling methods and taxa studied (Ricketts et al., 2016; Rosser, 2017; Sabu et al., 2011; Storch and Šizling, 2008). For instance, many sampling methods convey a narrow view of an ecosystem, for example by capturing relatively more aboveground or belowground organisms, which each respond differently to environmental change (Sabu et al., 2011; Wardle et al., 2004). Additionally, many ecological studies base their analyses on one taxonomic resolution or scope (e.g. focusing on beetles, or only using family-level data). While some studies have found that using higher taxonomic levels (i.e. family or order level) produces similar results to species-level analyses (Terlizzi et al., 2009; Timms et al., 2013), other studies have found that confining studies to one taxonomic resolution may paint an incomplete or biased picture (Rosser, 2017; Storch and Šizling, 2008). Therefore, incorporating multiple sampling methods and taxonomic resolutions helps achieve a more holistic and multidimensional picture of biodiversity patterns.

In this case study, we compare surface-active and soil-dwelling arthropod communities under a milkweed site with three regionally common land uses: silage corn, hay (perennial forage grasses and legumes), and forest. These land uses represent a gradient of land use intensity, allowing us to assess where arthropod communities under milkweed fall along this gradient. This is the first study that we know of to assess the impacts of cultivated milkweed on surface-active and soil-dwelling arthropod communities. Therefore, in order to glean a broad understanding of possible ecological effects and potential benefits of this novel and expanding crop, we use a wide variety of sampling and analytical tools. Using two different arthropod sampling methods and analyzing data at two taxonomic resolutions also allows us to inspect the effect of methodological choices on results. We hope this research will motivate future research in cultivated milkweed and soil arthropod communities.

Our research objectives include: 1. Evaluate differences in taxonomic composition and diversity, abundance, body size distribution, and biomass of surface-active and soil-dwelling arthropod communities under cultivated milkweed and three regionally common land uses; 2. Compare results from samplings of surface-active versus soil-dwelling arthropod communities; and 3. Assess the effect of taxonomic resolution in analyses by analyzing surface-active samples at the order level and at the genus level for beetles. We hypothesize that arthropod diversity will relate to land use intensity, with low diversity in corn plots, intermediate diversity in hay and milkweed, and high diversity in forest. We expect body size distributions to differ among land uses and that less intensive land uses (such as milkweed and forest) will have the highest total biomasses. We also hypothesize that surface-active and soil-dwelling arthropods results will differ, but that analyses run at the order and genus level will reflect similar trends.

2. Methods

2.1. Site description and experimental design

We conducted our research at Borderview Farm, located in Alburgh, VT (45.010210, −73.307624; Appendix S1) in August 2018 (for soil arthropods) and July 2019 (for general soil tests). Weather conditions in northwestern Vermont in the summer of 2018 were abnormally hot and dry, and in 2019 were slightly warmer and drier than average (Lawrimore, 2016). For instance, July-August high and low temperature averages were 29.9°C/18.2°C in 2018, compared to 28.6 °C/16.5°C in 2019, and 27.3°C/16.2°C in the ten previous years. Additionally, average precipitation rates in May-August were low in 2018 (7.1 cm/month), compared to 2019 (9.4 cm/month) and previous years (10.7 cm/month).

Borderview began growing milkweed in 2016 and has approximately 0.16 km^2 (40 acres) of milkweed in production. Borderview also grows conventional silage corn (hereafter "corn") and a mix of perennial forage grasses and legumes, which we define here as "hay." Corn and hay are the two most common crop types by area in Vermont (USDA NASS, 2021), and within the region these are the most likely land uses to convert to milkweed. A 300 acre patch of forest borders Borderview on its west and south sides (Appendix S1). These conditions enabled us to sample fields (within 1 km) of milkweed, corn, hay, and forest. All treatments were situated on the same general soil type, Benson rocky silt loam (coarse-silty, mixed, nonacid, mesic Typic Haplaquepts) (NRCS and USDA, 1959).

Historical land management practices varied considerably among the study fields. The milkweed field was tilled and planted in the summer of 2016. Between 2016 and 2018 (the time of this study), it did not receive fertilizers, herbicides, pesticides, or further tillage. Previous to conversion to milkweed, this field was planted with no-till corn for 3 years, and was an alfalfa hay crop prior to that. We sampled in corn and hay fields that had typical management schemes seen throughout the state. The corn field was continuously planted with corn since 2015, and received yearly spring tillage (deep disk) and treatments of fertilizers, herbicides, and pesticides. As a corn silage system, the whole plant is harvested once a year at the end of the season. The hay field was planted since around 2005, was fertilized yearly, and contained a mix of grasses and legumes including orchardgrass (*Dactylis glomerata* L.), red clover (*Trifolium pratense*), white clover (*Trifolium repens*), timothy grass (*Phleum pratense*), and meadow fescue (*Festuca pratensis*). The hay field was harvested three times a season, around every 30–40 days from late May to September. The forest location contained mostly Northern hardwood species (Wharton et al., 2003) and has not been logged since at least 1985 (Google Earth Pro Version 6.2.1.601, 1985). Like much of Vermont's forests, this forest patch was likely open pasture land between 1750 and 1900 and transitioned back to forest since agricultural abandonment around 1900 (Foster, 1992).

We established one 100 m transect per land use in neighboring fields of milkweed, corn, hay, and forest. Along each transect, we collected data on soil health, and sampled every 10 m (10 transect sites per land use; Appendix S1) for surface-active and soil-dwelling arthropods. We chose this design, where we sampled in single fields rather than in a replicated field design, because finding multiple sites around New England with nearby milkweed, corn, hay and forest land uses was not feasible, and would have presented further confounding factors including soil type, geography, and management style. This is exacerbated by the fact that milkweed is a new crop with limited area in production, and thus it would have been difficult to find enough replicates of milkweed in which to sample.

2.2. Soil health tests

In July 2019, we collected soil samples to test broad soil conditions. We collected soil in 2019 rather than in 2018 (at the time of the arthropod sampling) due to the availability of funding. We collected three randomly positioned soil samples from each land use, pooled them, and had them analyzed with the Comprehensive Assessment of Soil Health Test (Cornell University Soil Health Lab, Ithaca, NY). This soil test assesses a variety of physical, chemical, and biological soil characteristics, including aggregate stability, extractable phosphorous, organic matter, and soil respiration (Appendix S2). The test then determines each attribute on a scale of 0–100, with 100 indicating the most healthy soil conditions. This test then computes a final soil score on a scale of 0–100 (Moebius-Clune, 2016).

2.3. Arthropod sampling

We collected arthropods between 13 and 18 August 2018 using two methods: pitfall traps and the Berlese funnel method. We sampled in August, rather than earlier in the summer season, due to logistical constraints and because at this time the crops were near or at full maturity. Pitfall traps are collection cups (95 mm diameter lid, 120 mm deep) placed in the soil with their lids level to the surface (Southwood and Henderson, 2009). This method captures surface-active organisms that are trapped in the cups as they move across the soil surface. Importantly, pitfall traps more accurately describe organism *activity* than organism presence. We deployed pitfall traps with soapy water as a collection fluid. We set out four pitfall trap subsamples every 10 m along the 100 m transects (in a square formation, with 0.5 spaces between each cup; Appendix S1). The pitfall traps were active for 24 h and were deployed twice, over two consecutive days in non-rainy weather. There were no trap losses. Therefore, we had a total of 40 subsamples per day and per land use (total 320 pitfall traps).

The Berlese funnel method targets soil-dwelling organism *abundance*. For this method, we took three soil cores (5 cm diameter, 10 cm deep) every 10 m along the 100 m transect (0.5 m apart, in a line formation; Appendix S1). Therefore, we took 30 soil cores (subsamples) per land use (total 120 soil cores). We extracted arthropods by placing collected soil in a funnel apparatus and exposing it to a 60 Watt light bulb for 24 h (Southwood and Henderson, 2009). Arthropods avoid the heat and dryness caused by the light and crawl downward through the funnel, ultimately falling into a collection cup. We refer to arthropods collected with pitfall traps as surface-active arthropods and arthropods collected with the Berlese funnel method as soil-dwelling arthropods.

2.4. Arthropod identification

We first classified all arthropods to morphospecies. For some arthropods, we keyed individuals to family (spiders, Hemipterans), genus (ants, harvestmen spiders, beetles), or species (certain crickets and beetles). Other arthropods we could not adequately identify past order, such as for many springtails and mites. Within broader taxonomic classes, there were sometimes clear further separations based on morphological structures including body structure and color, for which we assigned the individuals as separate morphospecies. We keyed all arthropods collected, excluding primarily aerial species (e.g., Diptera). We used Dindal (1990) to identify arthropods to order level, and Evans (2014) and Bousquet (2010) to identify beetles to genus level. Online sites bugguide.net (Iowa State University, 2021) and iNaturalist.org (iNaturalist, 2021) also guided identification.

We used taxonomic differentiations (not morphospecies) for diversity analyses. We analyzed arthropods at two taxonomic scopes and resolutions: order level for all arthropods (surface-active and soil-dwelling), and genus level for surface-active beetles. Other studies have determined order level to be sufficient for discerning differences in arthropod communities (Jerez-Valle et al., 2014). Additionally including beetle genera allows us to inspect diversity at a finer resolution and compare results between these two resolutions. We specifically chose beetles because they were diverse in many of our samples and we had the expertize to identify this group to the genus level. It should be noted that other arthropod groups, like mites, may have been more diverse than beetles if we had identified them to a finer taxonomic resolution. We identified 20 of 24 beetle morphospecies to genus, representing 98% of the total number of beetles collected. To indicate the degree to which our sampling efforts captured the assembly of present arthropods, we include species accumulation curves for surface-active arthropod orders and beetle genera, and soil-dwelling arthropod orders in Appendix S4.

2.5. Body size measurements

We used morphospecies for our size distribution analysis because this grouping more accurately represented the distinct morphological groups and corresponding body sizes represented in our samples. To quantify body size, we measured the length (mm), width (mm), and weight (mg) of at least 10 individuals in each morphospecies within each land use type for surface-active and soil-dwelling arthropods. This allowed us to specifically examine and account for potential size differences between land uses (Chown and Gaston, 2010; Warzecha et al., 2016). We then used the mean of those 10 or more individuals to estimate the measurements of all unmeasured individuals. For unmeasured arthropods, if there were fewer than 10 individuals of that morphospecies in the land use, we applied the mean measurement of that morphospecies from all land uses.

Arthropods captured in the pitfall traps were generally large enough that we could sufficiently measure them with a common ruler (1 mm precision) and a scale (1 mg precision). Arthropods extracted with Berlese funnels were much smaller and needed increased precision to acquire accurate size measurements, so we used a camera attached to a compound microscope to capture photos of these specimens. While we made slides for some arthropods to improve identification, for size measurements we placed arthropods in a small petri dish, which were held in a special slide insert for holding petri dishes. Using image analysis with the software Zen (ZEISS; Oberkochen, Germany), we measured specimen width and length with a distance function (precision of 0.01 μm; calibrated with the microscope magnification).

For hexapods and arachnids (excluding mites), we measured length from anterior of the head to the posterior of the abdomen, and for myriapods, we measured length from the anterior of the head to the posterior of the last body segment. For mites we measured length from the anterior of the gnathosoma (excluding extended palps and chelicera) to the posterior of the idiosoma, excluding mouthparts (Mesostigmata and Prostigmata) or from the anterior of the rostrum to the anterior of the notogaster (Oribatida). For width we measured the widest part of the arthropods' bodies.

In order to acquire fresh weight measurements for the soil-dwelling arthropods (which were too light to be weighed on a scale), we calculated weight using order-specific regression formulas. These formulas took into account either length or length and width, depending on the order. Because some equations corresponded to the dry weight of organisms, we used a conversion equation to convert dry mass to fresh mass. Order-specific equations and dry to fresh mass equations are listed in Appendix S8. We checked the accuracy of these weight calculations by comparing them to the spheroid volume of the arthropods, using the formula for a prolate spheroid ($V = 4/3 * \text{pi} * \text{length}/2 * (\text{width}/2)^2$). Spheroids have been commonly used in invertebrate studies to estimate volume (Parmelee, 1999; Van Ngo et al., 2014), though they are not a perfect calculation for measured volume (Magnusson et al., 2003). We found a close linear relationship between calculated biomass and estimated volume ($R^2 = 0.98$, Appendix S9).

2.6. Statistical analyses

We perform all analyses in R version 4.0.4 (R Core Team, 2021). To assess arthropod composition, we calculated the mean abundance and standard error of each order or genus. We additionally calculated total abundance of all arthropods in each sample. We exclude ants from abundance measurements because pitfall traps inadequately indicate ant abundance due to ants' central foraging behavior (Higgins and Lindgren, 2012). To understand differences in taxonomic diversity, we calculated richness (number of orders or genera) and Shannon's diversity for each sample using the vegan package in R (Oksanen et al., 2007).

We analyzed differences of variables among treatments using linear mixed effects models (lmer function in lme4 package; Bates et al., 2015), and made multiple comparisons among land uses with least square means tests adjusted using the Tukey method (lsmeans package; Lenth, 2016). Each sampling site along the transect (i.e. 10 m, 20 m, 30 m, etc; in which subsamples were nested) was used as the random effect. For pitfall traps, in which we sampled on two consecutive days, we additionally tested using each subsample as a random effect but this resulted in model overfitting, so we did not keep it in the model. To meet statistical test assumptions, we eliminated outliers and transformed data using log or square root functions as needed to achieve a normal distribution and homoscedasticity of residuals (Table 1).

We additionally assessed differences in community composition with non-metric multidimensional scaling (NMDS) (metaMDS function in vegan), and tested significance using an analysis of similarity test with the ANOSIM function in vegan (Oksanen et al., 2007). These analyses were performed separately for each sampling method and taxonomic resolution (surface-active arthropod orders, surface-active beetles genera, and soil-dwelling arthropod orders). We pooled samples within each sampling site along the transect in this analysis to address nesting without needing hierarchical modeling. Therefore, there are 20 data points per land cover for pitfall traps (10 sampling sites along the transect and 2 days of sampling) and 10 points per land cover for the Berlese samples in this analysis.

To analyze body size, we first assessed body size distributions of all arthropods in each land use. To test whether body weight distributions differed among land uses, we used a G-test of goodness of fit using the Desctools package (Signorell et al., 2018). To determine the number of bins to use in this test, we used the Sturges Rule (Bin number $= 1 + 3.3 \log(N)$, where N is the number of observations in each distribution, or in this case the average number of observations in each land use) (Scott, 2009). From this calculation, we used 23 bins for the surface-active arthropods, 14 bins for the surface-active beetles, and 21 bins for the soil-dwelling arthropods. We then calculated the average weight and sum weight (total biomass) for each plot. We further quantified differences of arthropod sizes among treatments by assessing the abundance of arthropods in "small," "medium," and "large" size classes (Cole et al., 2002; Karen et al., 2008). We defined classes by calculating the minimum and maximum log values of body weights for each sample set (order level for surface-active arthropods, genus level for surface-active beetles, and order level for soil-dwelling arthropods). We divided this range into three equally sized bins representing the three size classes, and calculated the abundance of arthropods in each size class for every plot.

We then assessed significant differences of average body weight, total biomass, and abundances within size classes among land uses again using linear mixed effect models with transect site as a random effect. We transformed biomass, average body weight, and abundance within size classes with a square root function to achieve normal distribution and homoscedasticity of residuals (Table 1).

Table 1
Model statistics from ANOVAs, including data transformation of each variable and F-statistics, degrees of freedom, and p-values of each model (significance level indicated with astericks).

		Surface-active arthropods		Surface-active beetles		Soil-dwelling arthropods	
Variable	Data transfor-mation	F $_{(\text{numDF, denDF})}$	P-value	F $_{(\text{numDF, denDF})}$	P-value	F $_{(\text{numDF, denDF})}$	P-value
Species richness	none	$30.6_{(3,36)}$	<0.0001 ****	$28.1_{(3,36)}$	<0.0001 ****	$8.4_{(3,37)}$	0.0002 ***
Shannon's diversity	none	$56.2_{(3,37)}$	<0.0001 ****	$22.7_{(3,37)}$	<0.0001 ****	$11.5_{(3,36)}$	<0.0001 ****
Total abundance	log	$9.8_{(3,34)}$	<0.0001 ****	$20.1_{(3,36)}$	<0.0001 ****	$8.7_{(3,36)}$	0.0002 ***
Biomass	square root	$28.0_{(3,36)}$	<0.0001 ****	$18.6_{(3,35)}$	<0.0001 ****	$7.2_{(3,36)}$	0.0007 ***
Average body size	square root	$41.4_{(3,36)}$	<0.0001 ****	$3.2_{(3,30)}$	0.035 *	$8.1_{(3,36)}$	0.0003 ***
Abundance of small individuals	square root	$11.0_{(3,36)}$	<0.0001 ****	$9.4_{(3,36)}$	0.0001 ***	$2.9_{(3,36)}$	0.046 *
Abundance of medium individuals	square root	$24.5_{(3,36)}$	<0.0001 ****	$11.0_{(3,36)}$	<0.0001 ****	$6.0_{(3,36)}$	0.002 **
Abundance of large individuals	square root	$31.1_{(3,36)}$	<0.0001 ****	$13.0_{(3,36)}$	<0.0001 ****	$3.8_{(3,36)}$	0.017 *

3. Results

3.1. Soil properties

Overall soil scores for corn, hay, milkweed and forest were, respectively, 80, 92, 91, and 95 (Appendix S2). Milkweed plots had relatively lower organic matter and soil respiration values than forest and hay, though higher values than corn. Milkweed plots also had lower surface and subsurface hardness and higher aggregate stability than other land uses. Corn plots had relatively poor values in physical and biological characteristics, but high values for chemical characteristics, such as phosphorus and potassium concentrations.

3.2. Taxonomic composition

We collected 3878 specimens in the pitfall traps, comprising 12 orders. Beetles were the most abundant order, with 1037 specimens. Ants and true spiders were the second and third most abundant orders, with 935 and 594 total specimens, respectively. Within the beetle order, we found 19 beetle genera, with beetles from the *Harpalus* genus making up around half of all beetles collected. In the Berlese funnel traps, we collected 1932 specimens, representing 20 orders. Elongate-bodied springtails (Entomobryomorpha) were the most common order, with 584 collected specimens. Mesostigmata mites, Oribatida mites, and poduromorpha springtails were also relatively abundant, with around 200 specimens collected each.

In the surface-active arthropod sampling, milkweed had significantly more true spiders (Araneae), true bugs (Hemiptera), crickets and grasshoppers (Orthoptera), and Prostigmata mites than corn and forest, and significantly fewer elongate-bodied springtails (Entomobryomorpha) than corn and forest. For most orders, milkweed had similar abundances to hay. Corn plots had a greater number of beetles (Coleoptera) than other land uses, and forest plots had significantly more harvestman spiders (Opiliones) and globular springtails (Symphyleona) than other land uses (Appendix S3.1).

Among surface-active beetle genera, milkweed plots had significantly more individuals from the *Agonum* and *Poecilus* genera (Carabidae family) and the Curculionidae family (weevils) than corn and forest (Appendix S3.2). Corn had significantly more individuals from the *Harpalus* genus (Carabidae) (around 11 individuals sample^{-1}) than other land uses. Beetles from the *Phyllotreta* genus (flea beetles, a potential agricultural pest) were significantly more abundant in corn than other land uses. Hay plots had significantly more individuals from the *Omonadus* genus (Anthicidae). Forest plots had very few beetles.

In the soil-dwelling arthropod samples, milkweed had higher numbers of beetles (Coleoptera), elongate-bodied springtails (Entomobryomorpha), and true bugs (Hemiptera) than other land uses. Forest plots had significantly more Mesostigmata mites (3 sample^{-1}), Oribatida mites (4 sample^{-1}), and psuedoscorpions than all other land uses, and hay plots had significantly more globular springtails (Symphyleona) than other land uses. Corn plots had very few soil-dwelling arthropods (Appendix S3.3).

3.3. Taxonomic diversity and total abundance

All ANOVAs run for diversity and total abundance revealed significant differences between groups (Table 1). In the surface-active arthropod samples, milkweed had greater order richness than corn ($P < 0.001$) and forest ($P = 0.001$), though this difference was relatively small, representing around two extra orders per plot (Fig. 1a). Shannon's diversity values were similar between milkweed and hay ($P = 0.92$), though around 40% greater in milkweed than in corn and forest (both $P < 0.001$) (Fig. 1d). Milkweed had higher individual abundance (10 individuals sample^{-1}) than forest ($P = 0.004$), hay ($P = 0.039$), and corn (<0.0001) (Fig. 1g). Corn had high variance in individual abundance, with many plots having less than 10 individuals and a small number of plots having higher than 35 individuals.

For surface-active beetles, richness of beetle genera was similar

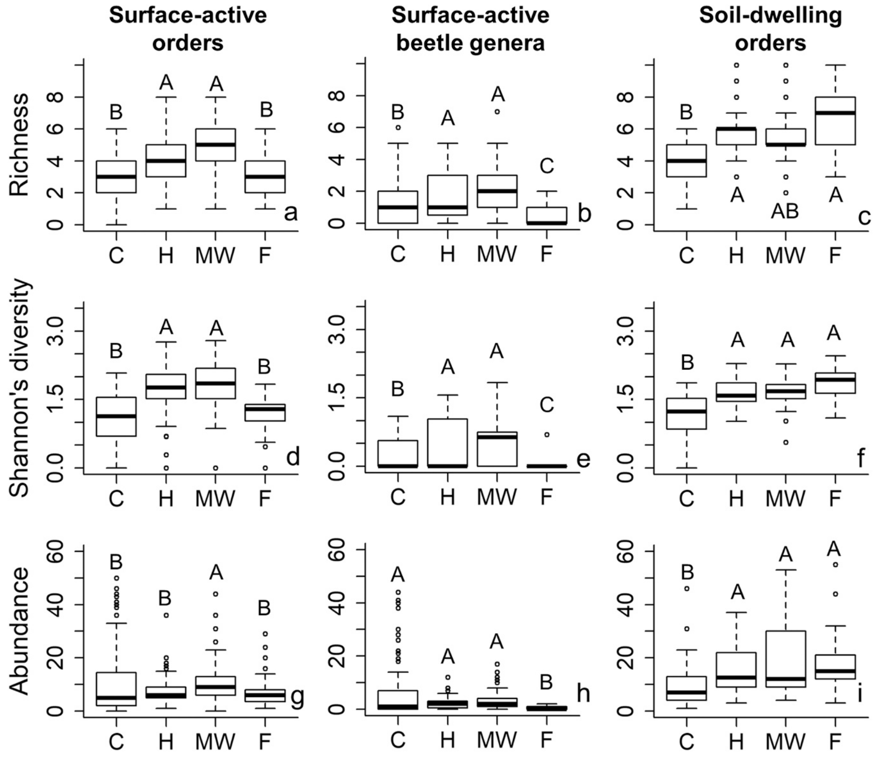

Fig. 1. Taxonomic richness (a–c) and Shannon's diversity (d–f) of orders and beetle genera among land uses, and total abundance of individuals captured in each land use (g–i) (C: corn; H: hay; MW: milkweed; F: forest). "Surface-active" organisms were captured using pitfall traps and "soil-dwelling" organisms were extracted using Berlese funnels. Uppercase letters denote significance: land uses with matching letters are not significantly different.

among milkweed and hay ($P = 0.82$), and slightly lower in corn (Fig. 1b). Forest had the lowest richness of beetle genera (all $P < 0.001$), with on average less than 1 beetle genera for each sample. For Shannon's diversity, hay and milkweed had similar values ($P = 0.79$) and were more diverse than corn and forest (all $P < 0.01$), with forest having the lowest values (Fig. 1e). While some corn plots had high numbers of beetle individuals (Fig. 1h), milkweed, hay, and corn were not significantly different. Forest had significantly fewer beetles than all other land uses (all $P < 0.0001$).

We found a slightly different trend for soil-dwelling arthropods. Richness and Shannon's diversity of orders was similar among hay, milkweed, and forest, while corn mostly had significantly smaller order richness values and Shannon's diversity values than other land uses (Fig. 1c,f). Corn plots similarly had lower abundance than other land uses (all $P < 0.005$), with around 7 individuals compared to around 15 individuals in hay, milkweed, and forest plots (Fig. 1i).

3.4. NMDS analysis of taxonomic composition

There was significant clustering ($P < 0.001$) for surface-active arthropod orders, surface-active beetle genera, and soil-dwelling arthropod orders. For the surface-active arthropod orders (ANOSIM statistic R: 0.6517), the agricultural land uses were most similar to each other, while forest plots were relatively separated (Fig. 2a). For the surface-active beetle genera (ANOSIM statistic R: 0.4424), milkweed separated from hay and corn, but forest plots had high overlap with all land uses (Fig. 2b). Finally, for the soil-dwelling arthropod orders (ANOSIM statistic R: 0.4309), milkweed positioned most closely to hay and forest (Fig. 2c).

3.5. Body size analysis

The distribution of body weight (goodness of fit) significantly differed (all $P < 0.001$) among land uses for each sampling (surface-active arthropods, surface-active beetles, and soil-dwelling arthropods) (Fig. 3a–c). Violin plots for length and width can be found in Appendix S5. ANOVAs revealed significant differences between land uses for all body size analyses except for the analysis of abundance of small soil-dwelling arthropods (Table 1).

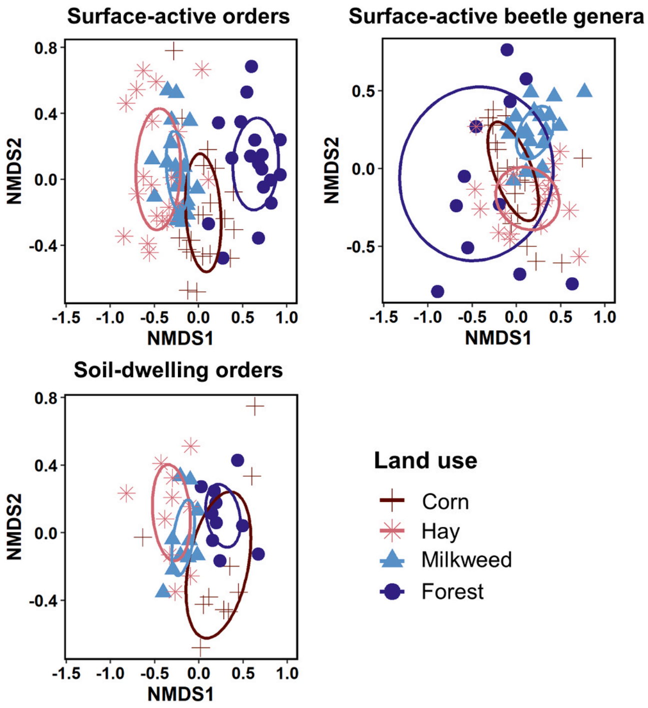

Fig. 2. Nonmetric multidimensional scaling (NMDS) ordination of the taxonomic community for surface-active arthropod orders (a), surface-active beetle genera (b), and soil-dwelling arthropod orders (c). Points represent plots in land uses and ellipses represent 95% confidence intervals.

Surface-active individuals in milkweed plots had an average body weight of 52.9 ± 4.7 mg, which was similar to individuals in corn plots with an average body weight of 58.7 ± 5.6 mg ($P > 0.99$) (Appendix S6). Hay and forest individuals weighed on average 12–13 mg, significantly lower than milkweed (both $P < 0.001$). Accordingly, milkweed and corn plots had similarly high total biomass ($P = 0.98$), and greater biomass than hay and forest (Fig. 3d). Additionally, milkweed and corn had significantly more "large" individuals (over 43.4 mg) than hay or forest and relatively few "small" individuals (under 2.1 mg) (Fig. 3a; Appendix S7). Hay plots tended to have more "small" individuals than other land uses.

We found a similar trend for surface-active beetles, where corn and milkweed had similarly high average body weight (74.4 ± 9.7 and 71.1 ± 7.1 mg; $P = 0.95$; Appendix S6). However, corn had significantly higher total biomass (1684.0 ± 320.7 mg) than all other land uses (all $P < 0.001$; Fig. 3e). Again, corn and milkweed had the highest abundance of "large" beetles (over 21.0 mg), while hay tended to have higher abundances of "medium" (1.4–21.0 mg) and "small" (under 1.4 mg) individuals (Fig. 3b; Appendix S7).

Among soil-dwelling arthropods, milkweed had the highest average body weight (0.92 ± 0.28 mg), followed by hay (0.38 ± 0.13 mg) (between these groups $P = 0.41$; Appendix S6). Corn and forest had significantly smaller average body weight (both less than 0.1 mg) than milkweed (both $P = 0.001$). Similarly, total biomass of soil-dwelling arthropods was largest in milkweed and smallest in corn and forest (Fig. 3f). Milkweed had similar abundances of "large" (over 0.07 mg) and "medium" (0.01–0.07 mg) arthropods to hay and forest (NS), though significantly more "medium" arthropods than corn ($P = 0.002$; Appendix S7). Hay had the highest abundance of "small" (under 0.01 mg) soil-dwelling arthropods, significantly differing from milkweed ($P = 0.03$).

4. Discussion

This case study elucidates differences of surface-active and soil-dwelling arthropod communities in varying land uses, with particular insights on the novel crop, cultivated milkweed. Our use of body size measurements, two sampling methods, and two taxonomic resolutions uncovers complexity within these sites and reflects landscape conditions and functional implications. In general, our findings of relatively diverse communities of both surface-active and soil-dwelling arthropods in our milkweed site, especially as compared to corn, suggest potential positive impacts of this crop for hosting biodiversity.

4.1. Taxonomic and soil differences among land uses

Contextualizing our study system along a spectrum of land use intensity helps interpret our findings. As we hypothesized, for soil-dwelling arthropods we find consistently low arthropod diversity values for corn (high intensity), intermediate diversity for hay (medium intensity), and high diversity in forest (low or no intensity). Arthropod diversity values in milkweed are most similar to those in hay, which is unsurprising considering that, like hay, milkweed is a perennial crop with little tillage needs and, in our study system, received infrequent synthetic inputs. Our study supports many other studies reporting greater diversity of soil arthropods in low intensity versus high intensity systems, including low-till versus high-till systems, perennial versus annual systems, and organic versus conventional systems (Cole et al., 2002; Franco et al., 2016; House and Parmelee, 1985; Kromp, 1999; Tsiafouli et al., 2015).

While, to our knowledge, this is the first study to specifically assess surface-active and soil-dwelling arthropod communities in cultivated

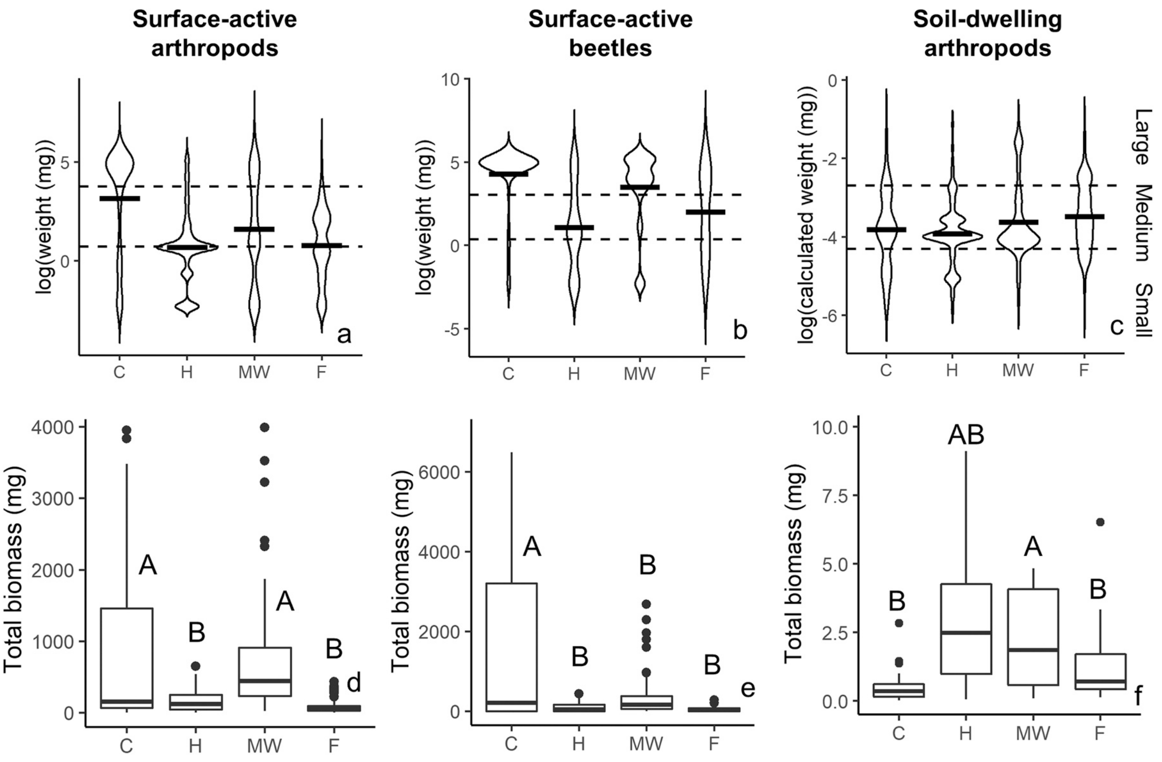

Fig. 3. Body size distribution for the whole community (a–c) and boxplots representing the total biomass (mg) of individuals in each plot (d–f). Black bars on violin plots represent the mean body size of all organisms. Dotted horizontal lines in body size violin plots represent cut-off points for the classification of organisms into "small," "medium," and "large" size classes (see Appendix S7 for more detail). C: corn; H: hay; MW: milkweed; F: forest. Uppercase letters in panels d–f denote significance (land uses with matching letters are not significantly different).

milkweed, other reports on wild growing milkweed corroborate our findings of high biodiversity associated with milkweed. Wild grown milkweed has been associated with 132 species of beetles (Dailey et al., 1978) and a high diversity of pollinators (Southwick, 1983). Milkweed also forms unique associations with certain organisms: due to its toxicity, milkweed attracts specialist herbivores (Zandt and Agrawal, 2004). However, it should be noted that in some ecosystems (such as in Europe), milkweed is an invasive plant that has encroached into forests and can negatively affect arthropod diversity (Kapilkumar et al., 2019). We too found slightly lower diversity of soil-dwelling arthropods in milkweed than in forest, and it is possible that conversion of forest to milkweed could cause negative effects on the soil arthropod community. However, cultivated milkweed in New England largely represents the conversion of cropland like corn and hay to milkweed, and it is not likely that the market for cultivated milkweed will lead to deforestation and subsequent declines in arthropod diversity.

The soil test results (Appendix S2) provide context for land use change and soil arthropod communities, though these tests were not meant to be rigorous examinations of soil conditions. In general, the milkweed site had high soil scores compared to corn, and similar scores to hay. Carbon-related soil health scores, such as organic matter, soil respiration, and active carbon, for milkweed tended to fall between the values for corn and hay, perhaps representing the transition of our milkweed site from an annual system (corn) to a perennial system. Indeed, while our milkweed site transitioned from corn 3 years prior to this study, our perennial hay site had been established for 15 years. Therefore, we likely see higher carbon soil cores in hay because increased time under a perennial system may allow for higher root biomass accumulation and carbon sequestration (Murty et al., 2002; Post and Kwon, 2000). Conversely, physical soil scores like bulk density and aggregate stability were greater in milkweed than in hay, which may be due to frequent use of hay harvesting equipment (3 times a year) and potential associated soil compaction (Glab, 2013). Our soil data were not collected the same year as our soil arthropod data, which makes it difficult to directly relate these results. However, our finding that forest had the highest soil health scores and highest diversity of soil-dwelling arthropods, contrasted with corn having the lowest soil health scores and lowest diversity of soil-dwelling arthropods, may support the idea that soil arthropod diversity can be an effective indicator of soil health (Stork and Eggleton, 1992).

4.2. Body size differences among land uses

Even with geographically proximate sites, size distribution within the arthropod communities notably varied. In general, our whole community size distributions highlight compositional differences between land uses, which are not apparent in the diversity analyses. For instance, while hay and milkweed have similar diversity levels, their distribution of sizes notably differ, with milkweed plots tending to have higher abundance of larger organisms and hay plots having larger abundance of smaller organisms.

Differences in size at the community level are largely driven by interspecific composition and its driving factors, such as resource availability, community dynamics, and environmental pressures. Some research has postulated that smaller arthropods are less vulnerable to disturbance, perhaps due to rapid reproduction cycles (Blake et al., 1994; Chown and Gaston, 2010; Tsiafouli et al., 2015). Our results of soil-dwelling arthropods supported this theory. Our most intensive land use, corn, generally had fewer large and medium-sized arthropods, but similar numbers of small arthropods compared to the other land uses. However, we find the opposite effect for surface-active arthropods, where corn had a high number of large arthropods and beetles and low abundances of medium and small arthropods and beetles. This trend in corn is driven by the dominance of large carabid beetles there, and supported by a number of papers finding that carabid beetles are well adapted to intensive land use (Birkhofer et al., 2017; Schweiger et al., 2005), perhaps due to the higher tolerance of these species to synthetic applications. We further hypothesize that we find low numbers of small surface-active arthropods under corn due to the poor physical soil properties here (likely a result of frequent soil cultivation) (Brennan et al., 2006; Cole et al., 2008; Tsiafouli et al., 2015).

Our biomass results show high biomass of surface-active arthropods in corn and milkweed and high biomass of soil-dwelling arthropods in milkweed. Our finding of relatively lower arthropod biomass in forest than in the agricultural sites is surprising considering that land use intensity tends to reduce soil fauna biomass (Höfer et al., 2001; Yin et al., 2020). However, our biomass results do not seem to be driven by organism density (abundance) as they are in other studies (Yin et al., 2020). Instead, biomass in our system appears closely related to the average weight of individuals in each land use (particularly the presence of large bodied individuals in corn and milkweed) (see Fig. S3d–f and Appendix S6).

These biomass results have implications for ecosystem functioning, including the metabolic potential of each community (Brown et al., 2004; Saint-Germain et al., 2007). For instance, high arthropod biomass within a community could relate to higher rates of vegetation consumption or decomposition, with associated implications for pest control and soil carbon. To better relate community biomass to ecosystem functions, it would be important to do a more in-depth analysis of functional traits, for example finding the biomass of individuals within diet classes (i.e. predators, herbivores, detritivores).

4.3. *Aboveground versus belowground trends*

As we hypothesized, community dynamics differed between sampling of surface-active (aboveground) and soil-dwelling (belowground) arthropods. We found that diversity of soil-dwelling arthropods more closely mirrored the expectation that diversity declines with increasing land use intensity (Tsiafouli et al., 2015). However, for surface-active arthropods, forest plots had lower diversity than milkweed and hay, with similar values to corn. This contradicts empirical evidence poised in the literature that belowground diversity is less sensitive to environmental changes than aboveground diversity (Birkhofer et al., 2017).

Differences between surface-active and soil-dwelling arthropod diversity suggest that differing factors may be at play. Diversity is the product of the complex interactions of a wide range of variables, including soil chemical and physical conditions, biological food web dynamics, disturbance regimes, biomass quantity and quality (Birkhofer et al., 2012; Tsiafouli et al., 2015; Wardle, 2006). Honing in on which of these factors most impact surface-active versus soil-dwelling arthropods would require a systematic study of drivers and diversity. Here, we hypothesize that diversity of soil-dwelling arthropods is driven more heavily by soil disturbance, which destroys the habitat of less mobile soil animals (House and Parmelee, 1985; Kromp, 1999). This explains why corn had the lowest diversity values, as it is tilled annually. Forest, on the other hand, may have the greatest diversity of soil-dwelling arthropods because it had no recent disturbance, allowing a rich community to develop and persist there. Diversity of surface-active arthropods, we hypothesize, is driven by land cover factors, such as plant cover (Meloni et al., 2020) and canopy structure (Henneron et al., 2017). Thus, forest plots may have fewer surface-active arthropods because the dominant plant type there is large trees, with minimal understory plant life. Corn plots, similarly, had high amounts of exposed soil and little understory vegetation.

4.4. *Taxonomic focus and resolution*

Analyzing surface-active samples at the order level for all specimens and genus level for beetles broadened our understanding of our study system while offering insights into the effects of taxonomic grouping in research. For the most part, as we hypothesized, results from the order and beetle genera levels were similar, showing high diversity in milkweed and hay. However, forest plots had very low beetle abundance and genera diversity. This result is not necessarily surprising, as other studies have also found lower beetle abundance or diversity in forests compared to agricultural regions (Méndez-Rojas et al., 2021; Schneider et al., 2016). Still, this result highlights a potential limitation of studies that focus on certain taxonomic groups (e.g. spiders or beetles) to determine differences (Cole et al., 2002; Kapilkumar et al., 2019; Karen et al., 2008). While using beetles in our analysis alone may indicate that forest plots had low diversity, combining that analysis with our other sample sets shows us that the diversity in forest plots is made up of other arthropods, namely arachnids, and also tends to be concentrated belowground. Thus, when choosing taxonomic groups to use in analyses, researchers should ensure those groups sufficiently represent the community or can effectively address the study's purpose.

Running analyses at the order level for all arthropods and genus level for beetles also provides some insight into the topic of taxonomic sufficiency, a research topic aimed at determining what taxonomic resolution is "sufficient" to detect differences between communities (Terlizzi et al., 2009). Identifying organisms to higher taxonomic resolutions requires increasing costs and time requirements, and thus researchers often have to make tradeoffs between efficiency and detail (Bennett et al., 2014; Rosser, 2017; Timms et al., 2013). We found that analyzing data on surface-active arthropods at both the order and genus level demonstrated similar patterns, supporting many studies that have found that coarser taxonomic resolutions effectively convey community differences (Terlizzi et al., 2009; Timms et al., 2013). However, we acknowledge the number of potential limitations in using taxonomically coarse data, such as not capturing within-taxon differences or collecting taxonomic data that is so coarse it hinders functional trait assignments (Jones, 2008). Additionally, it is important to note that many studies that use more detailed taxonomic data often choose to focus on a subset of the community (i.e. focusing only on beetles, as we have done here). As discussed above, this presents its own potential challenges and biases.

4.5. *Conclusions and call for future research*

Milkweed cultivation is a unique opportunity in the Northeastern USA and Southeastern Canada with potentially multifaceted benefits. While agronomic aspects of milkweed production are still being honed (Darby et al., 2019), preliminary research suggests management practices, such as tillage, fertilization, and herbicide use common in other cropping systems in the region, are unlikely to provide production and economic benefit. Therefore, milkweed cultivation will likely remain a relatively low intensity crop, with associated benefits to soil biodiversity and soil health. Additionally, as a larval host plant, milkweed serves a critical role in the conservation of monarch butterflies, a species which has experienced steep population declines over the past two decades (Pleasants and Oberhauser, 2013; Zaya et al., 2017). With the development of viable markets, milkweed could become a rotational crop providing both economic and ecological benefits.

This study should act as a call for further research on cultivated milkweed and biodiversity. We suggest that future studies include additional sampling fields or repetition across other soils to better predict effects. Such research will be more feasible if milkweed production becomes more regionally widespread. As we look to develop agricultural systems that bolster ecological function and conservation while supporting long-term production success, milkweed has unique potential for such multi-faceted benefits and should compel future attention and research.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107749.

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