Suitability of native milkweed (*Asclepias*) species versus cultivars for supporting monarch butterflies and bees in urban gardens

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Public interest in ecological landscaping and gardening is fueling a robust market for native plants. Most plants available to consumers through the horticulture trade are cultivated forms that have been selected for modified flowers or foliage, compactness, or other ornamental characteristics. Depending on their traits, some native plant cultivars seem to support pollinators, specialist insect folivores, and insect-based vertebrate food webs as effectively as native plant species, whereas others do not. There is particular need for information on whether native cultivars can be as effective as true or "wild-type" native species for supporting specialist native insects of conservation concern. Herein we compared the suitability of native milkweed species and cultivars for attracting and supporting one such insect, the iconic monarch butterfly (*Danaus plexippus*), as well as native bees in urban pollinator gardens. Wild-type *Asclepias incarnata* (swamp milkweed) and *Asclepias tuberosa* (butterfly milkweed) and three additional cultivars of each were grown in a replicated common garden experiment at a public arboretum. We monitored the plants for colonization by wild monarchs, assessed their suitability for supporting monarch larvae in greenhouse trials, measured their defensive characteristics (leaf trichome density, latex, and cardenolide levels), and compared the proportionate abundance and diversity of bee families and genera visiting their blooms. Significantly more monarch eggs and larvae were found on *A. incarnata* than *A. tuberosa* in both years, but within each milkweed group, cultivars were as colonized to the same extent as wild types. Despite some differences in defense allocation, all cultivars were as suitable as wild-type milkweeds in supporting monarch larval growth. Five bee families and 17 genera were represented amongst the 2436 total bees sampled from blooms of wild-type milkweeds and their cultivars in the replicated gardens. Bee assemblages of *A. incarnata* were dominated by Apidae (*Bombus, Xylocopa* spp., and *Apis mellifera*), whereas *A. tuberosa* attracted relatively more Halictidae (especially *Lasioglossum* spp.) and

Megachilidae. Proportionate abundance of bee families and genera was generally similar for cultivars and their respective wild types. This study suggests that, at least in small urban gardens, milkweed cultivars can be as suitable as their parental species for supporting monarch butterflies and native bees.

Suitability of native milkweed (*Asclepias*) species versus cultivars for supporting monarch butterflies and bees in urban gardens

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Abstract

Public interest in ecological landscaping and gardening is fueling a robust market for native plants. Most plants available to consumers through the horticulture trade are cultivated forms that have been selected for modified flowers or foliage, compactness, or other ornamental characteristics. Depending on their traits, some native plant cultivars seem to support pollinators, specialist insect folivores, and insect-based vertebrate food webs as effectively as native plant species, whereas others do not. There is particular need for information on whether native cultivars can be as effective as true or "wild-type" native species for supporting specialist native insects of conservation concern. Herein we compared the suitability of native milkweed species and cultivars for attracting and supporting one such insect, the iconic monarch butterfly (*Danaus plexippus*), as well as native bees in urban pollinator gardens. Wild-type *Asclepias incarnata* (swamp milkweed) and *Asclepias tuberosa* (butterfly milkweed) and three additional cultivars of each were grown in a replicated common garden experiment at a public arboretum. We monitored the plants for colonization by wild monarchs, assessed their suitability for supporting monarch larvae in greenhouse trials, measured their defensive characteristics (leaf trichome density, latex, and cardenolide levels), and compared the proportionate abundance and diversity of bee families and genera visiting their blooms. Significantly more monarch eggs and larvae were found on *A. incarnata* than *A. tuberosa* in both years, but within each milkweed group, cultivars were as colonized to the same extent as wild types. Despite some differences in defense allocation, all cultivars were as suitable as wild-type milkweeds in supporting monarch larval growth. Five bee families and 17 genera were represented amongst the 2436 total bees sampled from blooms of wild-type milkweeds and their cultivars in the replicated gardens. Bee assemblages of *A. incarnata* were dominated by Apidae (*Bombus, Xylocopa* spp., and *Apis mellifera*), whereas *A. tuberosa* attracted relatively more Halictidae (especially *Lasioglossum* spp.) and Megachilidae. Proportionate abundance of bee families and genera was generally similar for cultivars and their respective wild types. This study suggests that, at least in small urban gardens, milkweed cultivars can be as suitable as their parental species for supporting monarch butterflies and native bees.

Introduction

Burgeoning interest in ecological landscaping to support pollinators, birds, and other urban wildlife is fueling an enthusiastic and active plant movement (Kendle & Rose, 2000; Tallamy, 2008; Jones, 2019; USFS, 2020; USFWS, 2020) and a robust market for native plant species in the nursery, landscape, and gardening trades (Hanson, 2017; ASLA, 2018; Curry, 2018). Native plants can be defined as those that share an evolutionary history with regional insects and other organisms, whereas non-native or exotic plants evolved someplace other than where they have been introduced (Wilde et al., 2015). A compelling ecological argument for prioritizing the locally native flora over otherwise desirable (e.g., non-invasive) exotic species is its greater capacity to support local biodiversity, particularly of co-adapted native insect herbivores that are critical food for higher-order consumers including the many species of terrestrial birds that rear their young partly or wholly on insects (Tallamy & Shropshire, 2009; Burghardt, Tallamy & Shriver, 2009; Narango, Tallamy & Marra, 2018). Native plants also support numerous species of pollen-specialist native bees (Fowler, 2016).

Besides promoting plants of local provenance, the horticultural industry has introduced many native plant cultivars, natural variants of native species that are deliberately collected, selected, cross-bred, or hybridized for desirable traits; e.g., disease resistance, plant stature, leaf color, floral display, or extended bloom period, that can be maintained through propagation (Wilde et al., 2015). Although use of cultivars is generally discouraged in ecological restoration projects (Lesica & Allendorf, 1999; Kettenring et al., 2014), they are attractive to consumers seeking novel plants that combine the attributes of natives and ornamentals, and open the door to new introductions and vast market potential (Hanson, 2017; Curry, 2018). Indeed, a survey of nurseries in the Mid-Atlantic region, probably representative of the industry overall, found that only 23% of native plant taxa being marketed are true or “wild type”, the rest being available only as cultivated forms (Coombs & Gilchrist, 2017).

Native plant cultivars are not without controversy, however, even for managed landscapes and gardens. Some environmental organizations decry them, arguing that their mass-marketing and use will diminish the genetic diversity of flora in urban ecosystems that are already degraded by preponderance of exotic ornamental plants, further reducing their capacity to adapt to change, support wildlife, or provide other ecosystem services (Wild Ones, 2013). Cultivar traits that could potentially affect pollinator visitation include conversion of anthers and pistils to petals (“double flowered”), color, size, and shape of flowers, floral density, and possibly plant stature (Comba et al., 1999; Corbet et al., 2001; Ricker, Lubell & Brand, 2019). While some floral traits that humans may find attractive in native cultivars, e.g., double flowers or an unusual color, may decrease the quantity, quality, and accessibility of nectar and pollen, making those plants unattractive or of little value to pollinators (Comba et al., 1999; Garbuzov, Alton & Ratnieks, 2017; Mach & Potter, 2018), other native plant cultivars, and many non-natives, do provide high-quality nectar and pollen and can be equally or more attractive to pollinators as native plant species (Masierowska 2006, Salisbury et al., 2015; Mach & Potter, 2018; Ricker, Lubell & Brand, 2019). Thus, the value of native cultivars for pollinators must be evaluated on a case-by-case basis (Ricker, Lubell & Brand, 2019).

Compared to studies focused on pollinators, little work has addressed the question of whether native plant cultivars are the ecological equivalent to their parent species in supporting native insect folivores. Breeding for traits that change a plant's form, foliage color, floral display, or phytochemistry could alter cues used by specialist insects in host recognition or acceptance, perhaps to the extent that the insect no longer recognizes or accepts the cultivar as food (Baisden et al., 2018). Alternatively, because there may be tradeoffs in plants' allocation of resources to defense or growth, selection for traits such as enhanced floral display may make cultivars more palatable to herbivores by reducing their investment in defenses (Herms & Mattson, 1992). Limited research to date suggests the extent to which that may happen depends on the herbivore in question and the particular characteristics of the cultivar that distinguish it from the parent species (Wilde, Gandhi & Colson, 2015). Some cultivar traits, e.g., leaf variegation or leaves altered from green to red or purple, seem to change host suitability for some insects, whereas selection for other traits seems to make little difference insofar as host use by particular herbivores or biodiversity of folivorous insects supported by those plants (Tencazar & Krischik, 2007; Baisden et al., 2018; Poythress & Affolter, 2018).

The monarch butterfly (*Danaus plexippus*) is arguably the most well-known and beloved native North American insect (Gustafsson et al., 2015). Every fall, hundreds of millions of monarch butterflies make their long-distance journey south from the United States and Canada to overwintering sites in Mexico and California. Both the eastern and western North American migratory populations are in serious decline (Brower et al., 2012; Malcolm, 2018; Rendón-Salinas, Pelton et al. 2019) fueling concern that it may face extirpation unless habitat conservation and restoration efforts are enacted on a continental scale. Planting milkweeds (*Asclepias* spp.), the monarch's obligate larval host plants, is a key part of the international conservation strategy to return this iconic butterfly to sustainable status (Thogmartin et al., 2017; Monarch Joint Venture, 2020; US Fish and Wildlife Service, 2020). Restoring sufficient milkweed to ensure a stable monarch population will likely require contributions from all land use sectors including urban and suburban areas (Thogmartin et al., 2017; Johnston et al., 2019). In cities and towns, initiatives such as the Million Pollinator Garden Challenge, the Monarch Waystation Program, The National Wildlife Federation's Butterfly Heroes program, and Mayor's Monarch Pledge are underway, with myriad gardens being planted in backyards, schoolyards, parks, and other public and private places (Phillips, 2019). Milkweed flowers produce abundant nectar and are highly attractive to native bees (Robertson, 1891; Macior, 1965; Baker & Potter, 2018) so urban butterfly gardens can also play a role in supporting their biodiversity. Such gardens also provide opportunities for urban citizens to connect with nature, helping to foster a wider interest in conservation issues (Goddard, Dougill & Benton, 2010; Lepczyk et al., 2017; Bellamy et al., 2017).

Native plant cultivars, including milkweeds selected for novel floral display, longer blooming duration, compact growth form, and other consumer-attractive traits, are increasingly available in the wholesale nursery trade and at local garden centers (Baumle, 2018) so it is important to determine if such plants have equivalent value as native species if used for ecological gardening. Different species of milkweeds present a spectrum of palatability across the monarch's host range (Erickson, 1973; Schroeder, 1976; Baker & Potter, 2018). Milkweed cultivars within a single parental species group may offer a similar spectrum. In this study, we used the high-profile system of milkweeds, monarch butterflies, and bees to test the hypothesis that commercial cultivars provide equivalent ecological benefits as wild-type milkweeds in the context of small urban gardens.

Materials & Methods

Garden study site

Six replicated gardens (1.22 x 9.75 m) were established in public areas of the Arboretum State Botanical Garden of Kentucky, Lexington, in May 2018. Patches of open, low-maintenance grassland were sprayed with glyphosate to kill existing vegetation, tilled, and covered with weed barrier cloth. Each garden was subdivided into eight randomized 1.22 × 1.22 m plots, one for each of eight milkweed types which included *Asclepias incarnata* (swamp milkweed) and *Asclepias tuberosa* (butterfly milkweed) grown from seedlings produced from commercial open-pollinated seed production fields and hereafter called "wild type" for convenience, and three additional cultivars of each species including *A. incarnata* 'Cinderella', 'Ice Ballet', and 'Soulmate', and *A. tuberosa* 'Blonde Bombshell', 'Gay butterflies' and 'Hello Yellow', produced via controlled pollination or tissue culture (Fig. 1, Table S1). The milkweeds were purchased from various producers (American Meadows, Shelburne, VT; Centerton Nurseries, Bridgeton, NJ; Prairie Moon, Winona, MN) as bare root 2-year old plants which were started in a greenhouse. Four plants of a single type (16–30 cm height, depending on species and cultivar) were transplanted 0.6 m apart within each plot. Each garden was then covered with dark brown hardwood mulch (5 cm depth). We replaced a few of the less-vigorous milkweeds with healthier greenhouse-grown transplants in May 2019 at the start of the second growing season.

Monarch colonization of wild-type milkweeds and cultivars in gardens

Milkweeds in each garden were monitored for monarch eggs and larvae twice monthly from June to September 2018 and May to August 2019. At each visit all plants were inspected by turning over all leaves, and also examining all stems and flowering portions of the plant. Eggs and larvae were left in place after counting.

Physical and defensive characteristics of wild-type milkweeds and cultivars

Bloom period was assessed in the field for each milkweed type. Plant height and canopy width were measured after bloom when plants had reached maturity. Six leaves (2 each from the upper, middle, and lower thirds of the plant canopy, per milkweed type) were collected from each garden in July 2018, frozen at -80°C, and lyophilized. Cardenolide analysis followed methods of Wiegrebe & Wichtl (1993) and Malcolm & Zalucki, (1996). Briefly, the samples were extracted in methanol, centrifuged, washed in methanol, and dried in a nitrogen evaporator at 60°C. Dried extracts were resuspended in acetonitrile and filtered through a 0.45 µm luer-lock syringe filter into a 1 ml autosampler vial ready for HPLC analysis. Samples analyses were performed on a Waters gradient HPLC system with WISP autosampler, 600E pump, 996 diode array detector and Millennium[32]® chromatography software. Cardenolides were detected at 218.5 nm and identified by their symmetrical spectra between 205 and 235 nm and a λmax of between 214 and 224 nm. Cardenolide concentration for each peak (µg/g sample DW) was calculated from a calibration curve with the external cardenolide standard digitoxin (Sigma, St Louis, Missouri). Only cardenolide peaks reported by Millennium software as consistently pure were considered for analysis.

Trichome densities and latex exudation were compared among milkweeds by methods of Agrawal & Fishbein (2006). Four upper canopy leaves from each replicate (24 total per plant type) were collected in June 2019, leaf discs (28 mm^2) were cut about 2 cm from their tips, and trichomes on adaxial and adaxial surfaces were counted under a binocular microscope. Latex exudation was sampled in the field by cutting the tips (0.5 cm) off intact leaves (24 total per plant type), collecting the exuding latex into pre-weighed tubes with a filter paper wick, and weighing the samples on a microbalance.

Monarch larval performance on wild-type milkweeds and cultivars

Growth and survival of monarch larvae was tested in the greenhouse in July 2019. This trial included two year-old rootstock of the same milkweed species and cultivars in the gardens except for *A. tuberosa* 'Blonde Bombshell' which was excluded because of poor regeneration and market unavailability. All plants were grown in 5.6 liter pots, using a soil and bark mix (SunGro, Quincy, MI), and were 30-60 cm tall. Temperature was regulated between 20-27°C and no artificial light was used. Newly-molted second instars were placed on plants (one per plant; 10 replicates each) and confined by placing a white fine-mesh bag (25 x 40 cm) over each plant. Potential positional bias was minimized by shuffling the plants from top to bottom within each replicate once per day. Larvae were left in place for 7d and then evaluated for amount of weight gained and larval instar attained.

Bee assemblages of wild-type milkweeds and cultivars

We collected samples of 50 or more bees from blooms of each milkweed type in at least four and in most cases all six of the replicated gardens. Because of sparse blooming of certain milkweed types (mainly *A. tuberosa* straight species and 'Hello Yellow') in one or two of the plots, it was not possible to collect a full sample from every garden. Bees were collected on multiple visits during peak bloom using aerial nets or by knocking them into plastic containers containing 70% EtOH. Bee samples were washed with water and dish soap, rinsed, then dried using a fan–powered dryer for 30–60 min and pinned. Specimens were identified to genus (Packer, Genaro & Sheffield, 2007), with honey bees and bumble bees taken to species (Williams et al., 2014).

Data analyses

We used separate two-way analyses of variance (ANOVA) for a randomized complete block design to compare numbers of monarch eggs and larvae in gardens, larval performance, and plant characteristics between all milkweed types, and within milkweed species. Two-tailed Dunnett's tests were used when the *F*-statistic was significant to test for differences among individual cultivars and their parental milkweed species.

Bee genus richness and diversity (Simpson 1-D; Magurran 2004) were similarly compared. Statistical analyses were performed with Statistix 10 (Analytical Software 2013). Data are reported as means ± standard error (SE).

Results

Monarch colonization of wild-type milkweeds and cultivars in gardens

Each of the six gardens attracted monarchs, with eggs and larvae found throughout the 2018 and 2019 growing seasons (238 and 207 total individuals, respectively). Monarch immature life stages were first found in the gardens in May, peaking in August and persisting into September. Significantly more eggs and larvae were found on *A. incarnata* than *A. tuberosa* in 2018 ($F_{7,47}$ = 5.25, $P < 0.001$) and 2019 ($F_{6,41}$ = 6.29, $P < 0.001$) but within species, there were no differences in extent of colonization of the wild types versus their cultivars in either year (Table 1). The *A. tuberosa* cultivar 'Blonde Bombshell' was excluded in 2019 due to poor regeneration of the in-ground plants and market unavailability for replacements.

Defensive and physical characteristics of wild-type milkweeds and cultivars

Expression of defensive characteristics differed among milkweed types (Table 2). There was no overall significant difference in latex expression between the two milkweed species, but *A. tuberosa*, as a group, had relatively more trichomes and higher cardenolide concentrations (Table 2). Within the *A. incarnata* group, 'Cinderella' had significantly higher latex expression than the wild types, and 'Ice Ballet' had the highest number of trichomes and highest cardenolide concentrations. Within the *A. tuberosa* group 'Gay Butterflies' and 'Hello Yellow' had significantly higher latex expression than the wild type.

Asclepias incarnata, as expected, were taller than *A. tuberosa* (Table S2). Plant stature was similar within the *A. incarnata* group except for cultivar 'Soulmate' which had a wider canopy than the wild type. Within *A. tuberosa*, 'Gay Butterflies' and 'Hello Yellow' were taller and wider than the wild type. All of the milkweeds bloomed in June and July (Table S2).

Larval performance on of wild-type milkweeds and cultivars

Monarch larvae grew and developed on all milkweeds tested (Table 1). Growth and development were faster overall on *A. tuberosa* than on *A. incarnata*, but within groups was similar on wild types and their respective cultivars.

Bee assemblages of garden milkweeds

Five families and 17 genera were represented amongst the total of 2436 bees sampled from milkweed blooms in the replicated garden plots (Table 3). Bee genus diversity was similar within the *A. incarnata* group ($F_{3,15} = 1.74$, $P = 0.2$, Table 3). Bee assemblages of *A. incarnata* were dominated by Apid bees (Fig. 2), particularly bumble bees (*Bombus* spp.), carpenter bees (*Xylocopa* spp.), and honey bees (*Apis mellifera*). Representation of particular families and genera was similar among the four types except for 'Soulmate' which attracted proportionately few *Bombus* spp. compared to the wild type ($\chi^2 = 29.5$, $P < 0.001$).

Asclepias tuberosa attracted a somewhat more even distribution of bee families and genera, with proportionately more Halictidae and Megachilidae compared to the *A. incarnata* group, and each cultivar attracting diverse bee genera in varying proportions (Table 1, Fig. 3). Although *A. tuberosa* 'Blonde Bombshell' attracted bees from 11 different genera, most (71%) of them were Halictidae, genus *Lasioglossum*, accounting for that cultivar having lower genus diversity than the wild type ($F_{3,15} = 5.82$, $P = 0.007$).

Discussion

A major challenge to scaling up the use of native species in landscaping and gardening is providing plants that are both ecologically functional and profitable for the horticulture industry (Wilde, Ganghi & Colson, 2015). Native plants are mainly introduced into urban ecosystems through a market system that satisfies consumer preferences for ornamental traits. Consequently, many native plant species have been selected or bred for extended flowering, novel color, size, or morphology of flowers or foliage, compactness, or other aesthetic characteristics, with frequent new cultivar introductions (Wilde, Ganghi & Colson, 2015). Depending on their traits, some native plant cultivars seem to support specific folivorous insects, or insect-based food webs, as effectively as native plant species, whereas others do not (e.g., Tencazar & Krischik, 2007; Baisden et al., 2018; Poythress & Affolter, 2019; Ricker, Lubell & Brand, 2019). There is particular need for information on whether or not cultivars can support native insects of conservation concern.

Among such insects, none approaches the power of the monarch butterfly as a catalyst for public interest in ecological gardening (Gustafsson et al., 2015). Our results suggest that, at least in urban pollinator gardens, cultivars of *A. incarnata* and *A. tuberosa*, two of the most widely-sold garden-friendly native milkweeds (Baker & Potter, 2018), are as suitable as their respective parental species for attracting and supporting monarch butterflies. Over two growing seasons, we found similar numbers of naturally-occurring eggs and larvae on cultivars and straight species within each group. Despite some differences in plant defensive characteristics (trichomes, latex, and cardenolides), larval growth, development, and survival were similar on milkweeds within each group. Monarch larvae are capable of dealing with a range of milkweed defenses (Dussourd & Eisner, 1987; Agrawal & Fishbein, 2006). It is not unexpected, therefore, that cultivation at least within *A,incarnata* and *A. tuberosa* does not result in changes in defense that are too severe for monarch larvae to overcome.

Shared evolutionary history with plants has led to widespread host specificity in phytophagous insects (Bernays & Graham, 1988). Many Lepidoptera have narrow host ranges, often restricted to a single genus (Dyer et.al., 2007), so a plant breeder selecting for modified plant phenotypes could potentially alter the cues such insect specialists rely upon to recognize their hosts. Butterflies, in general, use a combination of visual, olfactory, and gustatory cues to find and accept host plants (Renwick & Chew, 1994). Monarchs move extensively between habitat patches, but the relative distances over which they use vision or olfaction to locate milkweeds or nectar sources is uncertain (Zalucki, Parry & Zalucki, 2016).

Monarch females foraging in natural habitat tend to lay more eggs on taller, more isolated milkweed plants than on shorter, less accessible ones (Zalucki & Kitching, 1982; Zalucki, Parry & Zalucki, 2016), and the same patterns occur in butterfly gardens (Baker & Potter, 2018; 2019). The relatively short stature of all cultivars of *A. tuberosa* (Table S2) compared to *A. incarnata* may account, in part, for why we found fewer eggs and larvae on the former species in both years despite them both being suitable as larval food (Erikson, 1973). Shorter milkweeds may go unnoticed by the butterflies because they are less visually apparent and accessible than taller milkweeds, especially when surrounded by non-host plants (Baker & Potter, 2019).

Some other butterfly species form a visual search image for host plants with a particular leaf shape that facilitates host-finding in the field (Benson, Brown & Gilbert, 1975; Rausher, 1978; Dell'Aglio, Lasada & Jiggins, 2016), but it is not known if monarchs do this. The estimated 100 milkweed species native to North America vary in leaf size and shape (Woodson, 1954), and several studies suggest that those with narrow leaves (e.g., *A. verticillata*) are less preferred for oviposition (Baker & Potter 2018, Pocius et al., 2018). All native cultivars used in our study had leaves seemingly similar to their parental species, but if plant breeders were to select for cultivars having modified leaf shape, color, or variegation, such changes could potentially affect monarchs' visual perception of them as hosts.

Native bee populations are declining (Cameron et al., 2011; Koh et al., 2016) and millions of urban pollinator gardens are being planted to help their plight (Phillips, 2019). Milkweed flowers are long-lived, produce copious amounts of nectar (Wyatt & Broyles, 1994), and are highly attractive to native bees, honey bees, butterflies, and other nectar-feeding insects (Fishbein & Venable, 1996; MacIvor et al., 2017 Baker & Potter, 2018). Because milkweed pollen is enclosed within pollinia and is probably inaccessible as food, nectar is the only reward that milkweeds offer to their pollinators (Wyatt & Broyles, 1994). In the present study, large-bodied, eusocial Apidae dominated the bee assemblages of *A. incarnata* whereas *A. tuberosa* attracted proportionately more Halictidae, Megachilidae, and other relatively small native bees. Both patterns are consistent with an earlier study in which only wild-type milkweeds were compared (Baker & Potter, 2018). Unlike garden plants wherein cultivar selection has reduced or eliminated floral rewards for pollinators (Garbuzov, Alton & Ratnieks, 2017; Erickson et al., 2019), all of the native milkweed cultivars we evaluated were bee-attractive and visited by similar bee assemblages as their parental species.

Conclusions

Restoration ecologists, conservation groups, and U.S. federal and state agencies are promoting increased use of native plants in landscaping and gardening to help support biodiversity in urbanized areas. A major challenge to that goal is availability of native plants that satisfy requirements for ecological function, cost-effective production, and desirable ornamental characteristics with consumer appeal. Breeding, marketing, and use of native plant cultivars is widespread and growing in the horticulture industry. This study suggests that, at least in small gardens, native milkweed cultivars can be as suitable as their parental species for attracting and supporting monarch butterflies and native bees. Although probably not appropriate for use natural areas where maintaining a reservoir of genetic variability is important for plant population resilience, use of native milkweed cultivars in pollinator gardens can help support the urban public's contribution to monarch and native bee conservation. For urban gardens, planting several species of native milkweeds, regardless of whether they are wild types or native cultivars, plus a variety other plants to provide nectar and pollen throughout the growing season, is probably the best strategy for helping to support monarchs, bees, and other pollinators.

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The authors declare there are no competing interests.

Author Contributions

AB, CR, and DP conceived and performed the field and greenhouse experiments. SM designed and supervised the cardenolide analyses. AB and DP analyzed the data and wrote the manuscript. AB, CR, and DP prepared figures and/or tables. All authors reviewed drafts of the paper and approved the final draft.

Data Availability

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher. Bee voucher specimens are stored in the University of Kentucky Insect Collection.

Supplemental Information

Supplemental information for this article can be found online at:

References

Agrawal AA, Fishbein M. 2006. Plant defense syndromes. *Ecology* **87(sp7)**:S132–S149 DOI: 10.1890/0012-9658(2006)87[132:PDS]2.0.CO;2

Analytical Software. 2013. Statistix v. 10. Tallahassee, FL

ASLA. 2018. ASLA Survey: Demand high for residential landscapes with sustainability and active living elements. https://www.asla.org/NewsReleaseDetails.aspx?id=53135.

Baker AM, Potter DA. 2018. Colonization and usage of eight milkweed (*Asclepias*) species by monarch butterflies, bees, and other insect herbivores in urban garden settings. *Journal of Insect Conservation* **22**:405–418 DOI: 10.1007/s10841-018-0069-5

Baker AM, Potter DA. 2019. Configuration and location of small urban gardens affect colonization by monarch butterflies. *Frontiers in Ecology and Evolution* **7**:474. https://doi.org/10.3389/fevo.2019.00474

Baisden EC, Tallamy DW, Narango DL, Boyle E. 2018. Do cultivars of native plants support insect herbivores? *HortTechnology* **28**:596–606 DOI: 10.21273/HORTTECH03957-18

Baumle K. 2018. Building the #Milkweedmovement. Green Profit Magazine. https://www.greenprofit.com/Article/?articleid=24164

Bellamy CC, van der Jagt APN, Barbour S, Smith M, Moseley D. 2017. A spatial framework for targeting urban planning for pollinators and people with local stakeholders: A route to healthy, blossoming communities? *Environmental Research* **158**:255–268 DOI: 10.1016/j.envres.2017.06.023

Benson W, Brown K, Gilbert L. 1975. Coevolution of plants and herbivores: Passion flower butterflies. *Evolution* **29**:659–680 DOI:10.2307/2407076

Bernays EA, Graham M. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* **69**:886–892 www.jstor.org/stable/1941237

Brower LP, Taylor OR, Williams EH, Slayback DA, Zubieta RR, Ramirez MI. 2012. Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? *Insect Conservation and Diversity* **5**:95–100 DOI: 10.1111/j.1752-4598.2011.00142.x

Burghardt KT, Tallamy DW, Shriver WG. 2009. Impact of native plants on bird and butterfly biodiversity in suburban landscapes. *Conservation Biology* **23**:219–224 DOI: 10.1111/j.1523-1739.2008.01076.x

Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF, Griswold TL. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences* **108(2)**:662–667 DOI: 10.1073/pnas.1014743108

Comba L, Corbet SA, Barron A, Bird A, Collinge S, Miyazaki N, Powell M. 1999. Garden flowers: Insect visits and the floral reward of horticulturally-modified variants. *Annals of Botany* **83**:73–86 DOI: 10.1006/anbo.1998.0798

Coombs G, Gilchrist D. 2017. Native and invasive plants sold by the Mid-Atlantic nursery industry. A baseline for future comparisons. _http://1x848d9mftq5g9wx3epiqa1d-wpengine.netdna-ssl.com/wp-content/uploads/2018/03/Native-and-Invasive-Plants-Report-Public-Version.pdf

Corbet SA, Bee J, Dasmahapatra K, Gale S, Gorringe E, La Ferla B, Moorhouse T, Trevail A, Van Bergen Y, Vorontsova M. 2001. Native or exotic? Double or single? Evaluating plants for pollinator-friendly gardens, *Annals of Botany* **87**:219–232 DOI: 10.1006/anbo.2000.1322

Curry CJ. 2018. Using nativars. *Greenhouse Production*. http://magazine.greenhousemag.com/article/july-2018/production-pointers-using-nativars.aspx

Dell'Aglio DD, Lasada ME, Jiggins CD. 2016. Butterfly learning and the diversification of plant leaf shape. *Frontiers in Ecology and Evolution* **4**(81) DOI: 10.3389/fevo.2016.00081

Dussourd DE, Eisner T. 1987. Vein-cutting behavior: insect counterploy to the latex defense of plants. *Science* **237**:898-901

Dyer LA, Singer MS, Lill JT, Stireman JO, Gentry GL, Marquis RJ, Ricklefs RE, Greeney HF, Wagner DL, Morais HC, Diniz IR, Kursar TA, Coley PD. 2007. Host specificity of Lepidoptera in tropical and temperate forests. *Nature*. 2007;448(7154):696-699. DOI:10.1038/nature05884

Erickson JM. 1973. The utilization of various *Asclepias* species by larvae of the monarch butterfly, *Danaus plexippus*. *Psyche* **80**:230-244.

Erickson E, Adam S, Russo L, Wojcik V, Patch HM, Grozinger CM. 2019. More than meets the eye? The role of annual ornamental flowers in supporting pollinators. *Environmental Entomology* **49**: 178–188 DOI: 10.1093/ee/nvz133

Fishbein M, Venable DL. 1993. Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology* 77:1016–1073. DOI: 10.2307/2265576

Fowler J. 2016. Specialist Bees of the Northeast: Host Plants and Habitat Conservation. *Northeastern Naturalist* **23**:305–320 DOI: 10.2307/26453772

Garbuzov M, Alton K, Ratnieks F. 2017. Most ornamental plants on sale in garden centres are unattractive to flower-visiting insects. *PeerJ*, **5(e3066)**:1–17. DOI: 10.1111/1365-2435.12178

Goddard MA, Dougill AJ, Benton TG. 2010. Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution* **2**:90–98 DOI: 10.1016/j.tree.2009.07.016

Goulson D, Nicholls E, Botias C, Rotheray EL. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* **347**:1255957

Gustafsson KM, Agrawal AA, Lewenstein BV, Wolf SA. 2015. The monarch butterfly through time and space: the social construction of an icon. *BioScience* **65**:612–622 DOI: 10.1093/biosci/biv045

Hall DM, Camilo GR, Tonietto RK, Ollerton J, Ahrne K, Arduser M, Ascher JS, Baldock KCR, Fowler R, Frankie G, Goulson D, Gunnarsson B, Hanely ME, Jackson JI, Langellotto G, Lowenstein D, Minor ES, Philpott SM, Potts SG, Sirohi MH, Specak EM, Stone GN, Threlfall CG. 2017. The city as a refuge for insect pollinators. *Conservation Biology* **31**:24–29 DOI: 10.1111/cobi.12840

Hanson J. 2017. Nativars versus natives. The need for both. *Nursery Management*. https://www.nurserymag.com/article/natives-vs-nativars-the-need-for-both/

Haribal M, Renwick JAA. 1998. Differential postalignment oviposition behavior of monarch butterflies on *Asclepias* species. *Journal of Insect Behavior* **11**:507–538 DOI: 10.1023/A:1022363329446

Hennig EI, Ghazoul J. 2012. Plant-pollinator interactions within the urban environment. *Perspectives in Plant Ecology, Evolution, and Systematics* **13**:137–150 DOI: 10.1007/s11252-011-0202-7

Herms DA, Mattson WJ. 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* **67**:283–333

Johnston MK, Hasle EM, Klinger KR, Lambruschi MP, Lewis AD, Stotz DF, Winter AM, Bouman MJ, Redlinski I. 2019. Estimating milkweed abundance in metropolitan areas under existing and user-defined scenarios. *Frontiers in Ecology and Evolution* **7**:210 DOI: 10.3389/fevo.2019.00210

Jones R. 2019. The native plant movement. Nursery Management July 2019; https://www.nurserymag.com/article/the-native-plant-movement/

Kendle AD, Rose JE. 2018. The aliens have landed! What are the justifications for 'native only' policies in landscape plantings? *Landscape and Urban Planning* **47**:19–31 DOI: 10.1016/S0169-2046(99)00070-5

Kennedy CEJ, Southwood TRE. 1984. The number of insects associated with British trees a re-analysis. *Journal of Animal Ecology* **53**:455–478. DOI:10.2307/4528

Kettenring KM, Mercer KL, Adams CR, Hines J. 2014. Application of genetic diversity–ecosystem function research to ecological restoration. *Journal of Applied Ecology* **51**:339–348 DOI: 10.1111/1365-2664.12202

Koh I, Lonsdorf EV, Williams NM, Brittain C, Isaacs R, Gibbs J, Ricketts TH. 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Science USA* **113(1)**:140–145 DOI: 10.1073/pnas.1517685113

Lepczyk CA, Aronson MFJ, Evans KL, Goddard MA, Lerman SB, MacIvor JS. 2017 Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *BioScience* **67**:799–807 DOI: 10.1093/biosci/bix079

Lesica P, Allendorf FW. 1999. Ecological genetics and the restoration of plant communities: Mix or Match? *Restoration Ecology* **7**:42–50 DOI: 10.1046/j.1526-100X.1999.07105.x

Levy JM, Connor EF. 2004. Are gardens effective in butterfly conservation? A case study with the pipevine swallowtail, *Battus philenor*. *Journal of Insect Conservation* **8**:323–330 DOI: 10.1007/ss10841-004-0796-7

Mach BM, Potter DA. 2018. Quantifying bee assemblages and attractiveness of flowering woody landscape plants for urban pollinator conservation. *PLoS ONE* **13(12)**: e0208428 https://journals.plos.org/plosone/article/authors?id=10.1371/journal.pone.0208428

Macior LW. 1965. Insect adaptation and behavior in *Asclepias* pollination. *Bulletin of the Torrey Botanical Club*, **92**:114–126.

MacIvor JS, Roberto AN, Sodhi DS, Onuferko DM, Cadotte MW. Honey bees are the dominant diurnal pollinator of native milkweed in a large urban park. *Ecology and Evolution* 2017;7:8456–8462. DOI: 10.1002/ece3.3394

Majewska AA, Altizer S. 2019. Exposure to non-native tropical milkweed promotes reproductive development in migratory monarch butterflies. *Insects* **10(8)**:253 DOI: 10.3390/insects10080253

Malcolm SB. 2018. Anthropogenic impacts on mortality and population viability of the monarch butterfly. *Annual Review of Entomology* **63**:277–302.

Malcolm SB. Zalucki. MP. 1996. Milkweed latex and cardenolide induction may resolve the lethal plant defence paradox. *Entomologia experimentalis et applicata* **80**:193–196

Marinelli J. 2016. Native, or not so much? National Wildlife Federation. https://www.nwf.org/Magazines/National-Wildlife/2016/JuneJuly/Gardening/Cultivars

Masierowska M. 2006. Floral reward and insect visitation in ornamental deutzias (*Deutzia* spp.), Saxifragaceae sensu lato. *Journal of Apicultural Research* **45**: 13–19.

Missouri Botanical Garden. 2020. Plant finder. https://www.missouribotanicalgarden.org/plantfinder/plantfindersearch.aspx

Monarch Joint Venture. 2020. https://monarchjointventure.org/

MonarchWatch. 2020. Monarch Waystation Program. https://www.monarchwatch.org/waystations/

Narango DL, Tallamy DW, Marra PP. 2018. Nonnative plants reduce population growth of an insectivorous bird. *Proceedings of the National Academy of Sciences* **115(45):**11549–11554 DOI: 10.1073/pnas.180925911510.1073/pnas.1809259115

National Pollinator Garden Network. 2020. Million pollinator garden challenge. http://millionpollinatorgardens.org/

Nevison K. 2016. The role of native cultivars in the ecological landscape: evaluating insect preferences and nectar quality in phlox and its cultivars. https://www.ecolandscaping.org/01/native-plants/the-role-of-native-cultivars-in-the-ecological-landscape-evaluating-insect-preferences-and-nectar-quality-in-phlox-and-its-cultivars/

Packer L, Genaro JA, Sheffield CS. 2007. The bee genera of eastern Canada. *Canadian Journal of Arthropod Identification*. No. 3.

Pelton EM, Schultz CB, Jepson SJ, Black SH, Crone EE (2019) Western monarch population plummets: Status, probable causes, and recommended conservation actions. *Frontiers in Ecology and Evolution* 7(258). DOI: 10.3389/fevo.2019.00258

Phillips M. 2019. The Million Pollinator Garden Challenge meets its mark, 2015-2018. http://millionpollinatorgardens.org/wp-content/uploads/2019/02/Million-Pollinator-Garden-Challenge-Report-FINAL-FOR-WEB-022519v3.pdf

Pocius VM, Debinski DM, Pleasants JM, Bidne KG, Hellmich RL. 2018. Monarch butterflies do not place all of their eggs in one basket: oviposition on nine Midwestern milkweed species. *Ecosphere* **9(1)**:e02064 DOI: 10.1002/ecs2.2064

Poythress JC, Affolter JM. 2018. Ecological value of native plant cultivars versus wild-type native plants for promoting hemipteran diversity in suburban areas. *Environmental Entomology* **47**:890–901 DOI: 10.1093/ee/nvy057

Rausher MD. 1978. Search image for leaf shape in a butterfly. *Science* **200**:1071–1073 https://www.jstor.org/stable/1746197

Rendón-Salinas E, Fajardo-Arroyo A, Tavera-Alonso G. 2015. Forest surface occupied by monarch butterfly hibernation colonies in December 2014. World Wildlife Fund. https://c402277.ssl.cf1.rackcdn.com/publications/768/files/original/REPORT_Monarch_Butterfly_colonies_Winter_2014

Renwick JAA, Chew FS. 1994 Oviposition behavior in Lepidoptera. *Annual Review of Entomology* **39**: 377–400 DOI: 10.1146/annurev.en.39.010194.002113

Ricker JG, Lubell JD, Brand MH. 2019. Comparing insect pollinator visitation for six native shrub species and their cultivars. *HortScience* **54**:2086–2090 DOI: 10.21273/HORTSCI14375-19

Robertson C. 1891. Flowers and insects, Asclepiadaceae to Scrophulariaceae. *Transactions of the Academy Sciences of St. Louis* **5**:569–598.

Salisbury A, Armitage J, Bostock H, Perry J, Tatchell M, Thompson K. 2015. Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should we plant native or exotic species? *Journal of Applied Ecology* **52**:1156–1164 DOI: 10.1111/1365-2664.12499

Satterfield DA, Maertz JC, Altizer D. 2015. Loss of migratory behaviour increases infection risk for a butterfly host. *Proceedings of the Royal Society B* **282**:20141734 DOI: 10.1098/rspb.2014.1734

Satterfield DA, Hunter MA, Flockhart DTT, Hobson KA, Noris DR, Streit H, deRoode JC, Altizer S. 2018. Migratory monarchs that encounter resident monarchs show life-history differences and higher rates of parasite infection. *Ecology Letters* **21**:1670–1680 DOI: 10.1111/ele.13144

Schroeder LA. 1976. Energy, matter and nitrogen utilization by the larvae of the monarch butterfly Danaus plexippus. *Oikos* **27**:259–264

Tallamy DW. 2008. Bringing nature home. Timber Press, Portland OR

Tallamy DW, Shropshire KJ. 2009. Ranking lepidopteran use of native versus introduced plants. *Conservation Biology* **23**:941–947. DOI: 10.1111/j.1523-1739.2009.01202.x

Tencazar EG, Krischik VA. 2007. Effects of new cultivars of ninebark on feeding and ovipositional behavior of the specialist ninebark beetle, *Calligrapha spiraeae* (Coleoptera: Chrysomelidae). *HortScience* **42**:1396–1399 DOI: 10.21273/HORTSCI.42.6.1396

Thogmartin WE, Wiederholt R, Oberhauser K, Drum RG, Diffendorfer JE, Altizer S, Taylor OR, Pleasants J, Semmens D, Semmens B, Erickson R, Libby K, López-Hoffman L. 2017. Monarch butterfly population decline in North America: identifying the threatening processes. *Royal Society Open Science* **4**:170760 DOI: 10.1098/rsos.170760

USFWS. 2020. Save the monarch butterfly. United States Fish and Wildlife Service. https://www.fws.gov/savethemonarch/

USFS. 2020. The monarch butterfly in North America. United States Forest Service. https://www.fs.fed.us/wildflowers/pollinators/Monarch_Butterfly/

Wheeler J. 2018. Tropical milkweed – a no-grow. https://xerces.org/blog/tropical-milkweed-a-no-grow

Wilde HD, Gandhi KJK, Colson G. 2015. State of the science and challenges of breeding landscape plants with ecological function. *Horticultural Research* **69**:1–8 DOI: 10.1038/hortres.2014.69

Williams PH, Thorp RW, Richardson LL, Colla SR. 2014. Bumble Bees of North America: An Identification Guide. Princeton University Press, Princeton, NJ

Wiegrebe H, Wichtl M. 1993 High-performance liquid chromatographic determination of cardenolides in *Digitalis* leaves after solid-phase extraction. *Journal of Chromatography* **630**:402–407 DOI: 10.1016/0021-9673(93)80478-Q

Wild Ones. 2013. Nativars: Where do they fit in? Wild Ones J. Nov/Dec 2013 issue; https://rivercitygrandrapids.wildones.org/wp-content/uploads/sites/21/2018/03/Nativars-Statement.pdf

Woodson RE Jr. 1954. The North American species of *Asclepias* L. *Annals of the Missouri Botanical Garden* **41**:1–211 DOI: 10.2307/2394652

Wyatt R, Broyles SB. 1994. Ecology and evolution of reproduction in milkweeds. *Annual Review of Ecology and Systematics* **25**:423–441 DOI: 10.1146/annurev.es.25.110194.002231

Xerces Society 2020.

Zalucki MP, Kitching RL. 1982. Dynamics of oviposition in *Danaus plexippus* (Insecta: Lepidoptera) on milkweed, *Asclepias* spp. *Journal of Zoology* **198**:103–116 DOI: 10.1111/j.1469-7998.1982.tb02063.x

Zalucki MP, Brower LP, Malcolm SB. 1990. Oviposition by *Danaus plexippus* in relation to cardenolide content of three *Asclepias* species in the southeastern U.S.A. *Ecological Entomology* **14**: 231–240 DOI: 10.1111/j.1365-2311.1990.tb00804.x

Zalucki MP, Parry HR, Zalucki JM. 2016. Movement and egg laying in Monarchs: To move or not to move, that is the equation. *Austral Ecology* **41**: 154–167 DOI: 10.1111/aec.12285

Figure legends

Figure 1. Native milkweed straight species and cultivars as they appeared in the field in 2019. Left column, *Asclepias incarnata*: 1a. wild type, 1b. 'Cinderella', 1c. 'Ice Ballet', 1d. 'Soulmate'. Right column, *Asclepias tuberosa*: 2a.wild type, 2b. 'Blonde Bombshell', 2c. 'Gay Butterflies', 2d. 'Hello Yellow'.

Figure 2. Relative proportions of bee families (a) and genera (b) collected from *A. incarnata* wild type and cultivars.

Figure 3. Relative proportions of bee families (a) and genera (b) collected from *A. tuberosa* wild type and cultivars.

Figure 1

Native wild-type milkweed and cultivars as they appeared in the field in 2019.

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Left column, *Asclepias incarnata*: 1a.Wild type, 1b. 'Cinderella', 1c. 'Ice Ballet', 1d. 'Soulmate'. Right column, *Asclepias tuberosa*: 2a. Wild type, 2b. 'Blonde Bombshell', 2c. 'Gay Butterflies', 2d. 'Hello Yellow'.

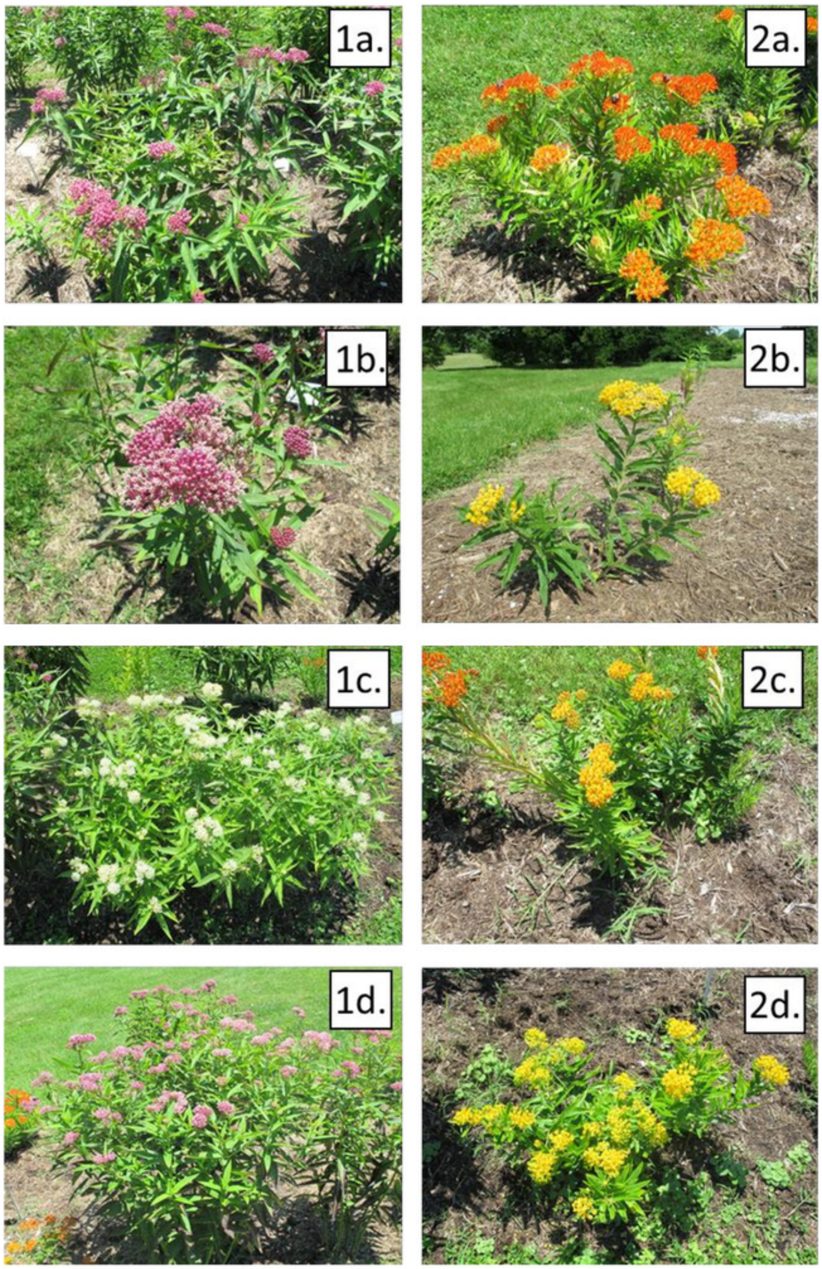

Figure 2

Relative proportions of bee families (a) and genera (b) collected from *A. incarnata* wild type and cultivars.

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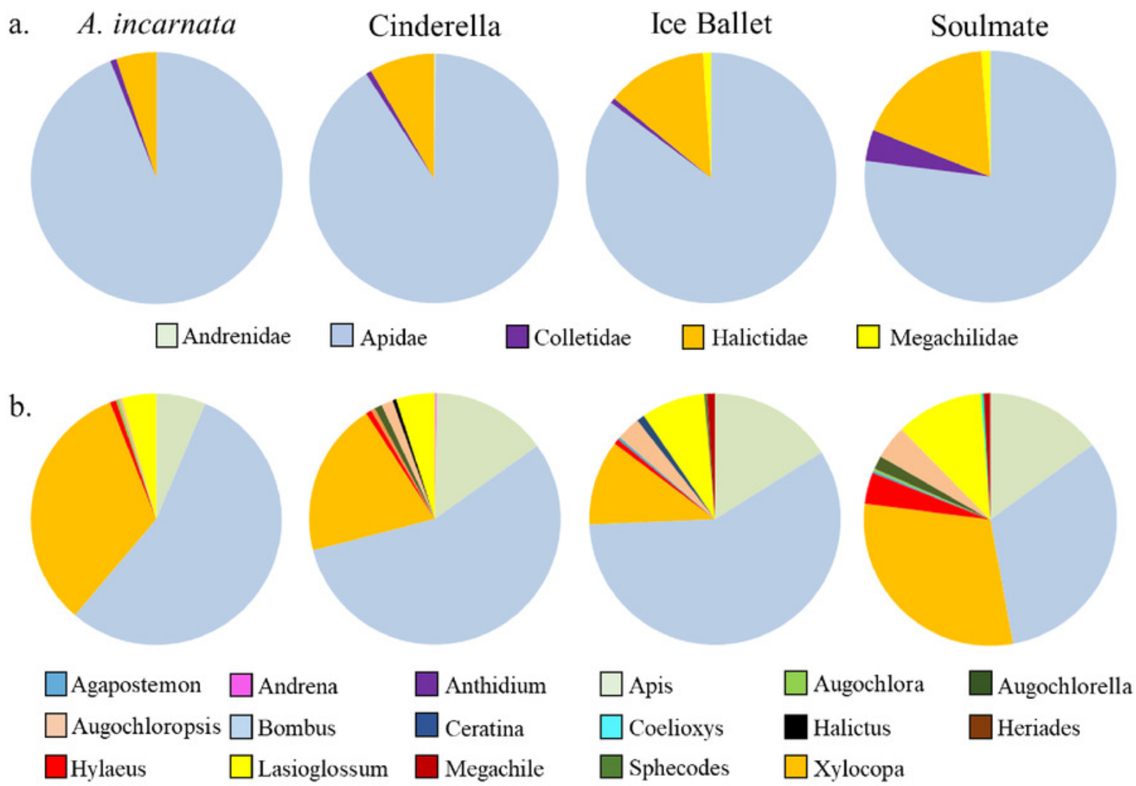

Figure 3

Relative proportions of bee families (a) and genera (b) collected from *A. tuberosa* wild type and cultivars.

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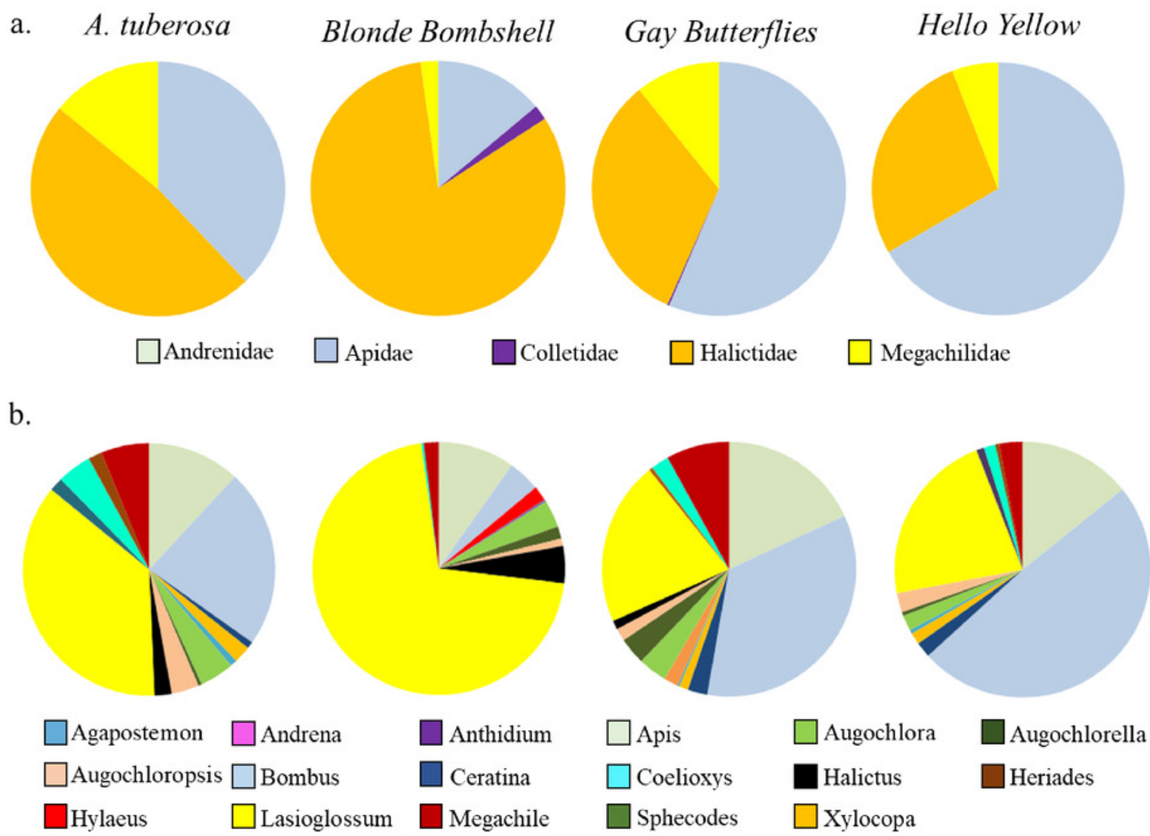

Table 1 (on next page)

Monarch colonization of wild-type milkweed and cultivars in replicated outdoor gardens, and larval performance on those milkweeds in the greenhouse, showing within-species similarity.

Data are means ± SE for each milkweed type. [1]Eggs and larvae were more abundant on *A. incarnata* than *A. tuberosa* in 2018 ($F_{7,47} = 5.25$, $P < 0.001$) and in 2019 ($F_{6,41} = 6.29$, $P < 0.001$) [2]Newly-molted second instars (n = 10) were reared individually on separate plants

[3]Larval weight differed significantly among milkweed types ($F_{6,48} = 12.42$; $P < 0.001$) and was greater on *A. tuberosa*, as a group, than on *A. incarnata* (contrasts, $t = 8.1$; $P < 0.001$)

[4]Larval instar differed significantly among milkweed types ($F_{6,48} = 7.95$; $P < 0.001$) and was greater on *A. tuberosa*, as a group, than on *A. incarnata* (contrasts, $t = 6.65$; $P < 0.001$)

[5]Blonde Bombshell was excluded in 2019 due to poor regeneration in the gardens and market unavailability for the greenhouse trial

Table 1. Monarch colonization of wild-type milkweed and cultivars in replicated outdoor gardens, and larval performance on those milkweeds in the greenhouse, showing within-species similarity.

	Eggs and larvae on milkweeds in gardens[1]			Larval performance after 7 d on plants in the greenhouse[2]		
Species and cultivar	2018	2019		Weight (mg) attained[3]	Instar attained[4]	No. live (of 10)
A. incarnata						
Wild type	7.7 ± 2.6	7.3 ± 1.0		436 ± 81	3.7 ± 0.2	9
'Cinderella'	11.7 ± 3.4	11.0 ± 1.6		392 ± 43	3.5 ± 0.2	10
'Ice Ballet'	7.7 ± 3.0	13.3 ± 3.5		417 ± 42	3.3 ± 0.2	9
'Soulmate'	8.7 ± 2.4	12.3 ± 2.4		386 ± 59	3.6 ± 0.3	9
$F_{3,15}$	0.80	1.08	$F_{3,24}$	0.14	0.52	
P	0.51	0.39	*P*	0.94	0.67	
A. tuberosa						
Wild type	1.7 ± 0.8	2.2 ± 0.6		1122 ± 184	4.6 ± 0.2	9
'Blonde Bombshell'[5]	0.5 ± 0.3	–		–	–	
'Gay Butterflies'	1.8 ± 0.6	3.3 ± 1.8		1175 ± 155	4.8 ± 0.2	8
'Hello Yellow'	1.2 ± 0.6	2.2 ± 0.9		739 ± 70	4.3 ± 0.2	10
$F_{3,15\ [2,10]}$	1.33	0.35	$F_{2,15}$	3.2	1.55	
P	0.30	0.71	*P*	0.07	0.24	

Data are means ± SE for each milkweed type.

[1]Eggs and larvae were more abundant on *A. incarnata* than *A. tuberosa* in 2018 ($F_{7,47} = 5.25$, $P < 0.001$) and in 2019 ($F_{6,41} = 6.29$, $P < 0.001$)

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Table 2(on next page)

Defensive characteristics of native wild-type milkweeds and cultivars

Data are means ± SE for each milkweed type. [1]amount exuded from cut leaves (n = 24 per plant type, 4 per garden) *denotes significant within-species difference from straight species by 2-tailed Dunnett's test.

Table 2. Defensive characteristics of native wild-type milkweeds and cultivars

	Latex (mg exuded)[1]	Trichomes per 28 mm[2]	Cardenolides (µg/g)
Natives			
A. incarnata			
Straight species	1.4 ± 0.2	97 ± 13	4.6 ± 1.8
'Cinderella'	3.4 ± 0.8*	93 ± 14	4.9 ± 2.8
'Ice Ballet'	1.1 ± 0.2	131 ± 13*	18.5 ± 6.3*
'Soulmate'	1.1 ± 0.2	92 ± 14	12.2 ± 3.4
	$F_{3,35} = 11.2$	$F_{3,67} = 3.1$	$F_{3,15} = 2.3$
	$P < 0.001$	$P = 0.03$	$P = 0.01$
A. tuberosa			
Straight species	0.7 ± 0.2	212 ± 17	392 ± 93
'Blonde Bombshell'	–	–	489 ± 148
'Gay Butterflies'	2.1 ± 0.4*	202 ± 27	684 ± 535
'Hello Yellow'	2.3 ± 0.3*	153 ± 21	498 ± 296
	$F_{2,31} = 14.4$	$F_{2,64} = 2.6$	$F_{3,14} = 0.25$
	$P < 0.001$	$P = 0.08$	$P = 0.86$

Data are means ± SE for each milkweed type.

[1]amount exuded from cut leaves (n = 24 per plant type, 4 per garden)

*denotes significant within-species difference from straight species by 2-tailed Dunnett's test.

1

Table 3(on next page)

Bee assemblages of two species of native milkweeds and their cultivars in replicated gardens (WT, Wild Type; CN, 'Cinderella'; IB, 'Ice Ballet'; SM, 'Soulmate'; BB, 'Blonde Bombshell', GB, 'Gay Butterflies', HY, 'Hello Yellow').

Table 3. Bee assemblages of two species of native milkweeds and their cultivars in replicated gardens (WT, Wild Type; CN, 'Cinderella'; IB, 'Ice Ballet'; SM, 'Soulmate'; BB, 'Blonde Bombshell', GB, 'Gay Butterflies', HY, 'Hello Yellow').

	A. incarnata and cultivars				*A. tuberosa* and cultivars			
	WT	CN	IB	SM	WT	BB	GB	HY
Andrenidae								
Andrena sp.	0	1	0	0	0	0	0	0
Apidae								
Apis mellifera	16	60	47	52	27	31	79	29
Bombus bimaculatus	0	12	0	2	6	1	5	9
B. griseocollis	137	213	165	110	41	9	117	75
B. impatians	0	1	5	0	4	3	29	16
B. pensylvanicus	0	0	0	1	0	0	0	0
Ceratina sp.	0	0	0	0	2	0	11	4
Xylocopa virginica	82	80	32	104	5	0	5	3
Colletidae								
Hylaeus sp.	2	3	2	14	0	6	1	0
Halictidae								
Agapostemon sp.	0	2	1	1	2	1	8	1
Augochlora sp.	1	0	0	1	10	11	16	4
Augochlorella sp.	0	4	0	6	1	5	15	1
Augochloropsis sp.	1	6	9	15	8	3	7	5
Halictus sp.	0	2	3	0	5	15	5	0
Lasioglossum sp.	11	20	24	39	83	224	91	45
Sphecodes sp.	0	0	1	0	0	0	0	0
Megachilidae								
Anthidium sp.	0	0	0	0	4	0	2	2
Coelioxys sp.	0	0	0	1	10	1	10	3
Heriades sp.	0	0	0	0	4	0	0	1
Megachile sp.	0	0	3	3	14	6	35	6
Total bees sampled	250	404	291	346	227	317	398	203
Genus richness	5	7	8	9	10	11	8	13
Mean genus diversity (SE)	0.59 (0.04)	0.61 (0.08)	0.63 (0.03)	0.74 (0.04)	0.74 (0.11)	0.46 (0.07)	0.75 (0.02)	0.83 (0.02)

1