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Common milkweed gardens increase occupancy by monarch butterflies and other specialist herbivores towards an urban centre

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Abstract

1. Specialised species interactions are likely vulnerable to urbanisation because fragmented habitat patches within cities are often smaller and more isolated than natural habitat. As a result, semi-natural habitat and key resources are sometimes deliberately maintained in cities to support biodiversity (e.g., pollinator gardens), but the effectiveness of these efforts is often unclear.
2. We studied four specialised herbivores (monarch butterflies, milkweed leaf miner flies, milkweed aphids and milkweed weevils) of the ruderal plant common milkweed (*Asclepias syriaca*) to test the predictions that (1) herbivore occupancy of milkweed stands and stems declines towards urban areas and (2) milkweed maintained in urban gardens ameliorates this potentially negative effect of urbanisation.
3. We surveyed 1848 stems in 119 common milkweed stands across an urban–rural gradient in Ontario, Canada, and fit occupancy of stands and individual stems to mixed-effects models to estimate the effects of urbanisation, stand size and stand type (maintained vs. unmaintained) on milkweed occupancy by the four herbivores. The effects of urbanisation, stand size and type varied among herbivore species.
4. Unexpectedly, stand and stem occupancy by monarchs and leaf miners, and stem occupancy by aphids (but neither for weevils) increased towards urban areas, and the presence of milkweed maintained in urban gardens was largely responsible for this. The presence of maintained common milkweed stands may boost occupancy by several specialist herbivores in urban areas.
5. We recommend encouraging urban residents and municipal organisations to plant and maintain common milkweed and other critical host plants to provide habitat for these specialist herbivores.

KEYWORDS
conservation biology, conservation gardening, entomology, habitat restoration, herbivory, landscape ecology, patch dynamics, plant ecology, species interactions, urban ecology

Graydon J. Gillies and Rishona Vemulapalli should be considered joint first author.

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INTRODUCTION

Habitat destruction and fragmentation are major causes of biodiversity loss (Fahrig, 2003) and these might have the greatest impact on specialist species (Matthews et al., 2014). For instance, species that engage in specialist or obligatory interactions (e.g., mutualism, parasitism, predation) depend on other species who may also be subject to the effects of fragmentation and may consequently be more vulnerable than generalist species to habitat fragmentation or other anthropogenic activity, such as urbanisation (Devictor et al., 2008). Thus, it is vital to understand how specialists respond to habitat fragmentation and how the impacts of fragmentation are mediated and potentially ameliorated. Studies that examine how species interactions respond to urbanisation are sparse and generally focus on plant–pollinator interactions or generalist interactions, while studies that investigate how habitat modifications affect specialist species interactions across urban–rural gradients are even rarer.

Urbanisation fragments habitat, often leaving behind small and isolated habitat remnants that are separated by a potentially hostile matrix of human-built areas (Brady et al., 2009; Liu et al., 2016). The effects of urban fragmentation on species persistence can be anticipated through metapopulation theory (Parris et al., 2018). Classic metapopulation theory posits that individual habitat patches are linked by dispersal between patches, so that whether a species is present in a metapopulation of patches is dictated by the balance between extinction from occupied patches and recolonisation of these unoccupied patches (Levins, 1969). Urbanisation reduces the number, size, connectivity and quality of habitat patches (Liu et al., 2016), thereby potentially increasing extinction from occupied patches and reducing recolonisation of vacant patches, and ultimately reducing patch occupancy and possibly causing a species to become extinct from the whole metapopulation ("metapopulation collapse"; Hanski, 1994). Generalist species may be more resistant to metapopulation collapse because they can use a broader range of resources and habitats or do not rely on the presence of any other particular species (Ockinger et al., 2010). Species that participate in specialist interactions, in contrast, may be more vulnerable to the effects of fragmentation, as a decline in the abundance or presence of one partner species may tip the scales towards metapopulation collapse for the other. A global meta-analysis revealed that arthropod abundance and richness often declines with urbanisation, with Lepidoptera that specialise on host plant species among the most sensitive and therefore candidate indicators of ecosystem health (Fenoglio et al., 2020).

To counteract the effects of urban habitat fragmentation on biodiversity, conservation initiatives aim to restore habitat and promote species interactions in urban environments, but evidence for the effectiveness of these efforts is either mixed or entirely absent. Moreover, the available evidence is primarily focused on plant-pollinator interactions. For example, a survey in Zürich, Switzerland found that greater floral abundance and green space were associated with increased bee visitation to gardens, parks, and ruderal green spaces, but did not parse the effects of intentionally planted gardens (i.e., restored habitat) compared to other types of urban habitat (Hennig & Ghazoul, 2012). Green corridors are another type of habitat modification that is generally thought to promote habitat connectivity, but a survey in Toronto, Canada, unexpectedly found lower pollinator diversity and richness in a green corridor (Breitbart et al., 2023). Even fewer studies examine how restored habitat supports other plant–insect interactions, such as herbivory, across gradients of urbanisation (Miles et al., 2019). However, Hordley and Fox (2024) found that leaving grass to grow longer increased the abundance and richness of grass-eating butterflies in gardens across Great Britain, particularly in urban environments.

Common milkweed (*Asclepias syriaca* L., Asclepiadaceae, hereafter "milkweed") is host to a suite of specialist herbivores that have adapted to tolerate its toxic latex sap (Birnbaum & Abbot, 2018). Among these specialists is the monarch butterfly *Danaus plexippus*, classified as endangered by the Committee on the Status of Endangered Wildlife in Canada (Bériault & Packer, 2010) and the IUCN Red List (Walker, 2022). Some studies attribute the decline of monarch butterflies to reduced habitat availability (Pelton et al., 2019; Zaya et al., 2017). While milkweed occurs commonly in disturbed habitats including roadsides, rural fields and other ruderal habitats (hereafter called "unmaintained" stands), homeowners and conservationists are increasingly compelled to plant and/or maintain milkweed in gardens (hereafter "maintained" stands), usually to intentionally provide host plants for monarch butterflies and native pollinators (Landis, 2014). Conservation initiatives such as The Butterflyway Project (David Suzuki Foundation, 2022) encourage citizens to plant pollinator gardens to support biodiversity and reconnect with nature in urban areas (Goddard et al., 2010; Miller, 2005). Maintaining milkweed in urban areas likely increases habitat availability and connectivity, thereby reducing extinction and enhancing colonisation by herbivore species (Baker & Potter, 2018; Schultz & Crone, 2005). Furthermore, there have been some efforts to understand how structural attributes of milkweed stands might promote species interactions, but this work is narrowly focused on monarch butterflies (e.g., Baker & Potter, 2018, 2019; Klinger et al., 2024; Pitman et al., 2018). Generally, this work has demonstrated that monarchs more frequently occupy milkweed stands with larger plants but lower stem density, as well as stands with a greater diversity of other floral resources.

Here, we aim to (1) understand variation in occupancy of milkweed stands by specialist herbivores across the urban–rural gradient and (2) assess whether and how gardens support increased occupancy. Miles et al. (2022) found evidence that abundance in milkweed stands by multiple specialist milkweed herbivores unexpectedly increased towards urban areas and speculatively attributed this to the "urban saturation hypothesis", which proposes that if host plant abundance declines towards urban centres but herbivores decline at a slower rate, then the proportion of individual hosts occupied by herbivores will be higher in urban areas as herbivore individuals distribute themselves across fewer available patches of suitable habitat. An alternative but not mutually exclusive hypothesis, not investigated by Miles et al. (2022), is that urban areas contain patches of attractive, high-quality habitat that ameliorate any negative effects of urbanisation that would otherwise reduce herbivore abundance. Pollinator

gardens might play this role. For instance, Cutting and Tallamy (2015) found that oviposition on milkweed in residential gardens was greater than on milkweed in natural stands, but did not compare occupancy in these gardens across an urbanisation gradient or by other specialist herbivores. To more comprehensively understand how garden milkweed supports specialist herbivores across an urban–rural gradient, we surveyed the occupancy of common milkweed by four specialised insect herbivores (monarchs, milkweed leaf miners, aphids, milkweed weevils) in both "maintained" gardens and "unmaintained" natural stands across an urban–rural gradient in Ontario, Canada.

In this study, we test the hypothesis that urbanisation inhibits interactions between milkweed and its specialised herbivores but that milkweed gardens partially ameliorate this negative effect. We predict that:

1. Urbanisation decreases both stand occupancy (whether a stand is occupied by at least one individual) and stem occupancy (the proportion of stems occupied within a stand) by specialist milkweed herbivores. If gardens ameliorate the negative effect of urbanisation, we expect a stronger decline in occupancy (among unmaintained stands) when maintained stands are excluded from analysis. Should there be an urban saturation effect (as suggested by Miles et al., 2022), we expect to find that occupancy increases with urbanisation for both maintained and unmaintained stands.
2. In urban areas, maintained stands (i.e., milkweed in gardens) will have greater herbivore occupancy than unmaintained stands. Compared to unmaintained stands, stems in maintained stands may be larger, providing more and better resources or being more noticeable for colonising adults.
3. Greater stand size increases occupancy because species are more likely to colonise and less likely to go extinct from larger stands.
4. Stems that are larger, have more leaves, and are surrounded by a lower density of other stems will have greater occupancy by specialist herbivores, and these structural variables might explain differences in occupancy between maintained and unmaintained stands.

METHODS

Study system

Common milkweed is a useful study system because the plant is conspicuous and its specialist herbivores (or the diagnostic tissue damage they inflict) are readily identified. Milkweed is also common in ruderal, disturbed habitat across gradients of urbanisation. The four specialist common milkweed herbivores that we surveyed are monarch butterflies *Danaus plexippus* (Linnaeus, 1758), milkweed leaf miner flies *Liriomyza asclepiadis* (Spencer, 1969), milkweed aphids *Aphis nerii* (Boyer de Fonscolombe, 1841), *A. asclepiadis* (Fitch, 1851) and *Myzocallis asclepiadis* (Monell, 1879) and milkweed weevils *Rhyssomatus lineaticollis* (Say & T., 1824). Although adult monarch butterflies can use nectar from many species, the larvae feed exclusively on the milkweed leaves where adults most often lay their eggs on the lower surface (Prysby, 2004). Milkweed leaf miner fly is the only known leaf miner species on *A. syriaca*, and their larvae feed between the upper and lower epidermal leaf layers leaving behind characteristic mining tracks (Agrawal, 2017). At least three species of specialist "milkweed aphid" feed on *A. syriaca* sap (Smith et al., 2008) and are often observed in large clusters (Mach et al., 2023). Milkweed weevil *R. lineaticollis* is the only weevil known to feed on *A. syriaca*, leaving behind distinctive 2–4 cm longitudinal stem scars (Fordyce, 2000).

Field survey

We surveyed 119 stands of milkweed along an urban–rural gradient in eastern Ontario, Canada, from 11 July 2023 to 5 August 2023. This period encompasses the peak flowering period in this region (Finch, 2025). Further, Miles et al. (2022) found little difference in general abundance patterns across urban gradients in Ontario between early and late seasons, suggesting the exact timing of the survey period should have little influence on herbivore occupancy patterns in our study. From the city of Kingston, Ontario, our survey region extended north to the Rideau Lakes township, south to Wolfe Island and west to Kingsford in Hastings County, spanning ~70 km latitudinally and ~50 km longitudinally and covering a total area of ~2600 km^2 (Figure 1). We located unmaintained stands by visiting the coordinates of research-grade observations of common milkweed on iNaturalist (inaturalist.org) and searching habitat along roadsides or other ruderal areas. To locate maintained (garden) stands of milkweed, we contacted regional gardening organisations and searched haphazardly chosen neighbourhoods to find gardens that contained milkweed. In total, we sampled 35 maintained stands and 84 unmaintained stands.

We defined a stand of milkweed as a cluster of stems separated from other clusters by at least 10 m but usually much more (Matter, 1996). To minimise spatial autocorrelation, we only surveyed stands located at least 100 metres apart, though the distance between most stands far exceeded this minimum. We classified milkweed stands as "maintained" if they were planted, tended to, or intentionally left to grow in an ornamental garden, usually on private properties or in public "pollinator gardens" in urban parks, or as "unmaintained" if they were found occurring naturally, with no evidence of human intervention, usually in rural fields, along roads, in vacant lots, or other ruderal habitat. In stands of >20 stems, we haphazardly selected at least 20 individual stems to sample. We sampled all stems in stands with ≤20 stems. Overall, we surveyed between 1 and 29 stems per stand (mean ± sd = 15.3 ± 7.0 stems) for a total of 1848 stems.

At each stand, we counted the total number of individual stems, estimating this number for stands of >1000 stems. Although milkweed spreads clonally through underground rhizomatic roots, the above-ground stem was the unit of observation in our study because stem number represents the resources available to milkweed herbivores. If stems split into shoots beneath the ground, we counted each emergent stem separately but stems with above-ground branching were considered a single stem. For small stands, we measured total stand

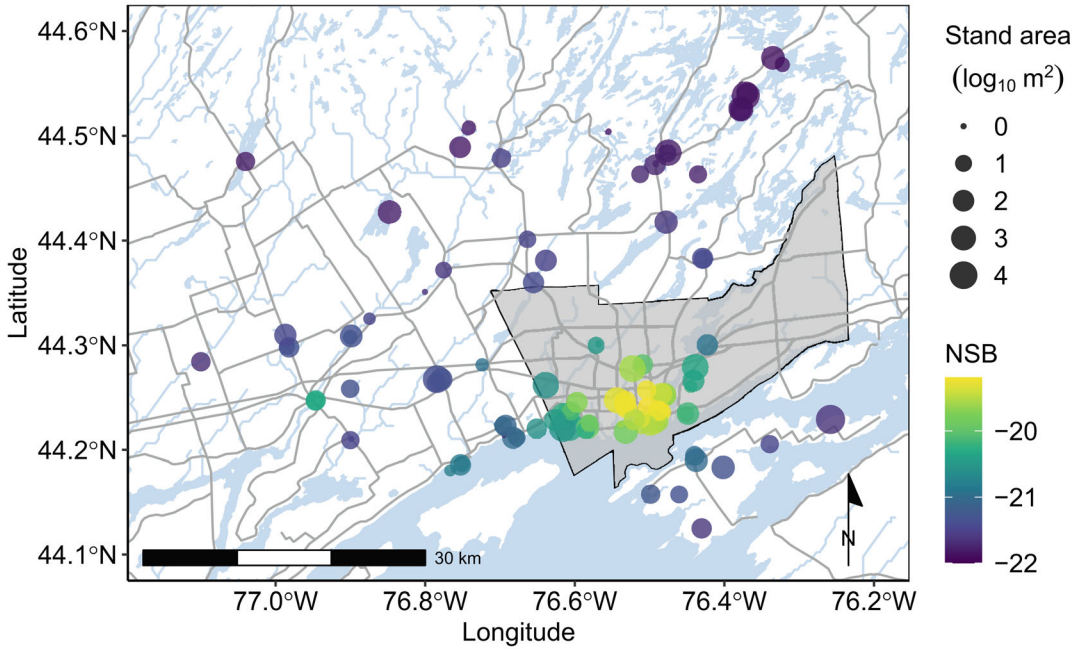


FIGURE 1 Locations of 119 common milkweed stands surveyed in and around Kingston, Canada. Point size is scaled by $\log_{10}$ stand area (m^2; with $0 = 1\ m^2$). Points are coloured by night-sky brightness (NSB), ranging from rural (dark purple) to urban (yellow) stands. Indicated are the municipal boundary of Kingston (shaded grey area), major roadways (grey), and rivers and lakes (blue). Shapefiles from the City of Kingston, Natural Earth, Lehner and Grill (2013) and Messager et al. (2016).

area using a metre stick. For the smallest stands, consisting of one or a few clustered stems, the minimum measured stand size was 1 m^2. To measure the area of large stands, we recorded latitude and longitude coordinates with a Garmin GPSMAP 65S every ~10 paces around the perimeter of the stand and calculated stand area using QGIS (v. 3.32.1; QGIS Development Team, 2024). For each set of coordinates, we outlined the stand perimeter and calculated area with the *field calculator* tool.

At each surveyed stem, we noted the presence of each herbivore or its diagnostic damage. For monarch butterflies, we counted (i) the number of eggs, easily identified by their translucent white colour and longitudinal ridges and (ii) the number of larvae, identified by their distinctive yellow, white and black stripes. We did not find chrysalises on any plants, likely because larvae tend to wander from milkweed plants to more secluded locations to pupate (Fisher et al., 2020). We recorded the presence of weevil stem scars, aphids and leaf miner scars, as well as the number of leaves with leaf miner scars as a proxy for their abundance. We also measured stem height, leaf number and counted the number of stems within a 1-metre radius of each focal stem (hereafter "focal density").

To quantify urbanisation at each stand, we used night sky brightness (NSB; Sutton et al., 2001; Pun & So, 2012). While urbanisation has been measured using several variables such as human population density, the coverage of impermeable surfaces and spectral measures of vegetation coverage (Murray-Stoker et al., 2025), we required an integrative measure that best reflected the impact of humans on the distribution of common milkweed and its specialist herbivores. NSB is closely associated with many metrics of urbanisation (Mellander et al., 2015; Zheng et al., 2022) and correlates strongly with distance to the city centre in the area around Kingston, Ontario (Dawson et al., 2025). Percent impervious surface is also commonly used but is highly zero-inflated in our study area because many types of urban habitat contain no impervious surface. As a result, this measure might not capture residential and suburban development as effectively as NSB. We first obtained sky-quality metre scores (SQM, mag/arcsec^2) for each stand by cross-referencing coordinates of each site on a light pollution map with an adequately high resolution of 1000 m (Falchi et al., 2016). Zenith sky brightness generally ranges from 16 mag/arcsec^2 for the brightest skies to 22 mag/arcsec^2 for the darkest skies. Across the stands of milkweed we sampled, SQM scores ranged from 19.19 mag/arcsec^2 to 22.00 mag/arcsec^2. We multiplied the SQM scores by −1 to yield NSB, which is higher for brighter urban skies than darker rural skies (see Table S1 for descriptive statistics of all covariates).

Analysis

We performed all analyses using R (v. 4.3.1; R Core Team, 2025). We first categorised the occupancy of stands by each herbivore as a binary variable ("stand occupancy"; 1 indicating at least one individual of an herbivore species present) and the number of sampled stems occupied vs. not occupied by each herbivore as a binomial variable ("stem occupancy").

Potential predictors of species-specific occupancy included NSB, stand type (maintained or unmaintained), and two predictors of stand size: stand area (m^2) and stem abundance. Because both stand size predictors were highly colinear ($r = +0.88$, Table S2), we used principal components analysis (PCA) to generate one axis (PC1) to represent stand size (see Colautti et al., 2010). PC1 accounted for 94.0% of variance in the $\log_{10}$-transformed stand size variables. Factor loadings indicated that PC1 correlated positively with both $\log_{10}$ stand area (+0.71) and $\log_{10}$ stem abundance (+0.71). We scaled all predictors using the *scale* function in R to allow comparison of regression coefficients.

Binary stand occupancy may be influenced by sample size. The probability of finding an herbivore on at least one stem increases with the number of stems sampled. As a result, a positive effect of stand size on occupancy may simply represent a positive correlation between stand size and sample size. Among the stands we sampled, however, sample size correlated only weakly with PC1 ($r = +0.17$) or NSB ($r = +0.26$).

Because almost all maintained stands (31 of 35) occurred in urban areas (defined as greater than median NSB), we used two approaches to parse the effect of stand type on occupancy from the effect of NSB. First, to understand the impact of urbanisation on stand and stem occupancy, we fit both stand occupancy (binary) and stem occupancy (binomial) to a model with scaled NSB and stand size (scaled PC1) but not stand type for each herbivore. Then, for each herbivore, we repeated this analysis using only the 84 unmaintained stands. We expected that repeating the analysis without the 35 maintained stands would reduce the coefficient of regression for occupancy over NSB if maintained stands increase occupancy towards the urban end of the rural–urban gradient. That is the absolute difference in the regression coefficient for NSB (b_{NSB}) between the model fit to all the data and the model fit only to the unmaintained stands would be greater than zero ($\Delta b_{obs} > 0$). However, removing the 35 maintained stands from the analyses could weaken the regression coefficient simply by reducing sample size. To verify that removing maintained stands had an effect above and beyond reducing sample size, we conducted a randomisation test: For each herbivore, we fit the model with a random subset of 35 stands removed, estimated the partial regression coefficient for NSB (b_{NSB}) and calculated the difference between b_{NSB} for all the data and b_{NSB} for the randomly thinned data (Δb_{rand}). We repeated this randomisation 1000 times and calculated the proportion of runs where $\Delta b_{rand} > \Delta b_{obs}$. This is analogous to a *p*-value for the significance of Δb_{obs}. We report this p_{rand} as approximate because each run of 1000 random simulations gives a slightly different result. The second approach we used to understand the effect of stand type on occupancy was to restrict our analysis to only urban stands (above median NSB of −20.30). With these data, we fit both measures of occupancy to GLMs with stand type (maintained vs. unmaintained; $n_{stand} = 59$, $n_{stem} = 971$) and stand size as predictors.

To assess the factors that predict occupancy at the stem level within stands, we fit binary stem-level occupancy (for each herbivore) to binomial GLMs with stem height, leaf number, and focal density as fixed effects and stand ID as a random effect. We then fit GLMs to assess whether these structural variables, as well as stand size (PC1), differed between maintained and unmaintained stands. We repeated this and all above analyses instead fitting abundance as the response variable for species for which we had counts of the number of herbivores on each plant sampled (monarchs and leaf miners) using negative binomial GLMs for stand abundance to address overdispersion and Poisson GLMs for stem abundance (Table S6).

We fit each model using the *glmmTMB* function from the glmmTMB package (v. 1.1.8; Brooks et al., 2017), performed type II tests of significance using the *Anova* function in the car package (v. 3.1–2; Fox & Weisberg, 2019), and acquired regression coefficients using the *summary* function.

RESULTS

Stand occupancy across NSB

Binomial GLMs predicted a significant increase in stand occupancy by monarchs from 59.9% in rural stands (low NSB) to 86.9% in urban areas (high NSB, holding stand size constant at its median value) and an increase from 55.3% to 86.0% by leaf miners (Figure 2a,b; Table 1). Stand occupancy increased non-significantly from 4.1% to 17.6% for aphids and decreased non-significantly from 29.8% to 24.8% for weevils (Figure 2c,d). Stand occupancy increased significantly with stand size (PC1) for leaf miners, aphids and weevils and non-significantly for monarchs.

Removing maintained stands from the analysis reduced the unexpectedly positive effects of NSB on stand occupancy. The randomisation confirmed that this reduction in regression coefficients for NSB was larger than the change caused by the removal of 35 random stands. Removing maintained stands significantly reduced the positive regression coefficients for monarchs ($\Delta b_{obs} = +0.44$, $p_{rand} = 0.001$), leaf miners ($\Delta b_{obs} = +0.26$, $p_{rand} < 0.001$) and aphids ($\Delta b_{obs} = +0.51$, $p_{rand} = 0.018$) and significantly increased the negative regression coefficient for weevils ($\Delta b_{obs} = -0.035$, $p_{rand} < 0.001$) (Table 2).

Stem occupancy across NSB

Stem occupancy for monarchs increased significantly from 15.1% in rural stands to 30.1% in urban stands (at median stand size) but declined with increasing stand size (Figure 2e). Stem occupancy increased significantly from 0.69% to 3.0% for aphids and from 19.0% to 28.6% for leaf miners but declined non-significantly from 6.2% to 3.7% for weevils (Figure 2f–h). Stand size did not predict stem occupancy for leaf miners, aphids or weevils.

Removing maintained stands significantly reduced the positive regression coefficient for monarchs ($\Delta b_{obs} = +0.34$, $p_{rand} < 0.001$) and leaf miners ($\Delta b_{obs} = +0.31$, $p_{rand} < 0.001$), increased the negative effect of NSB for weevils ($\Delta b_{obs} = -0.30$, $p_{rand} = 0.047$) but did not significantly change the effect of NSB for aphids ($\Delta b_{NSB} = +0.28$, $p_{rand} = 0.16$) (Table S3).

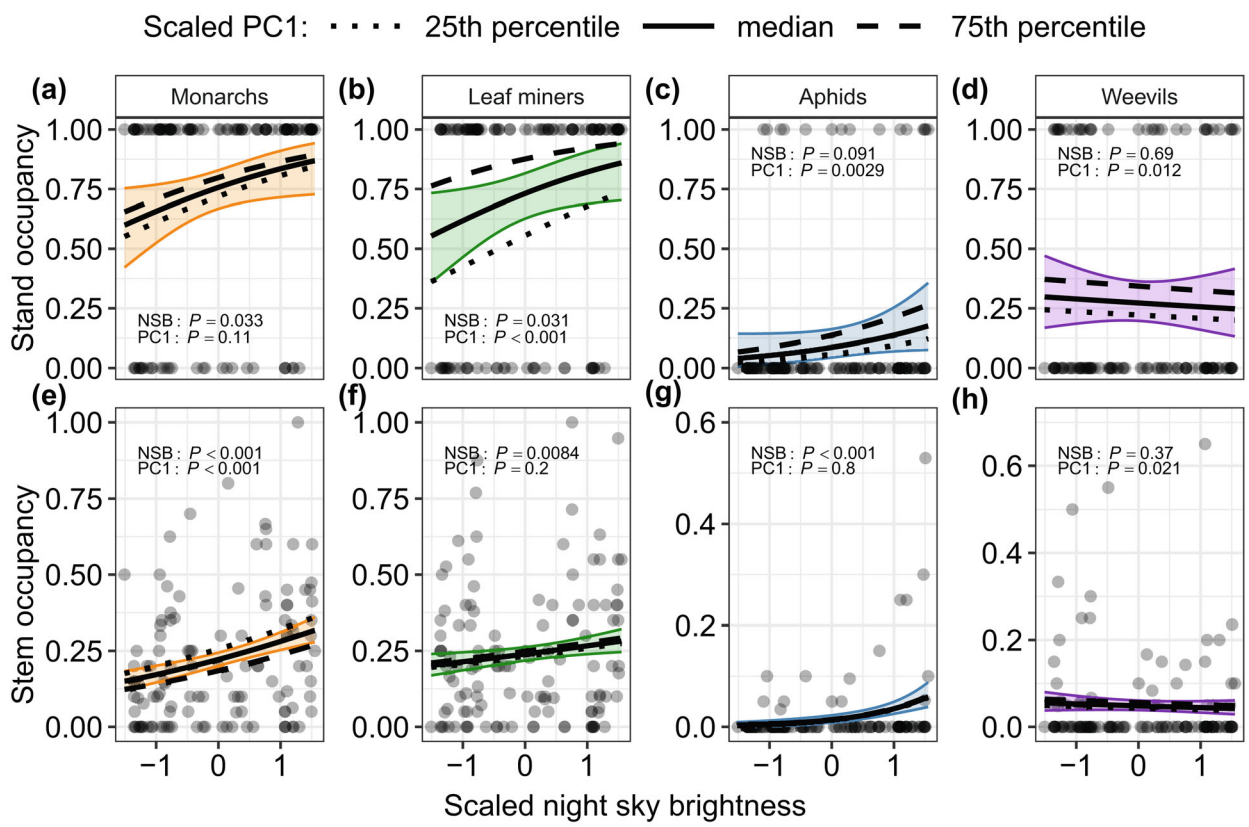


FIGURE 2 Variation in occupancy of common milkweed stands (upper row) and stems (bottom row) across an urbanisation gradient (scaled night sky brightness, NSB) for (from left to right) monarch butterflies (orange), milkweed leaf miner flies (green), aphids (blue) and milkweed stem weevils (purple). Dotted, solid and dashed lines show model-predicted occupancy when stand size (PC1) is held constant at the 25th, 50th and 75th percentiles. Confidence bands represent 95% confidence intervals at median PC1. *p*-values are shown for both predictors.

Stand types in urban areas

In urban areas, stand occupancy was significantly greater in maintained stands than in unmaintained stands for monarchs (97% > 64%, respectively; $p = 0.01$; Figure 3a) and aphids (26% > 4%; $p = 0.041$; Figure 3c) and was nearly significant for leaf miners (87% > 61%; $p = 0.057$; Figure 3b). Stand occupancy was lower in maintained stands for weevils, but this was not significant (23% < 36%; $p = 0.25$; Figure 3d). Leaf miners were significantly more likely to occupy larger stands, while stand size did not predict occupancy for any other herbivore (Table 2).

Stem occupancy in urban areas was greater in maintained stands than unmaintained stands for monarchs (35.0% ± 20.3% sd > 16.0% ± 22.7%; $p < 0.001$), leaf miners (33.1% ± 25.6% > 16.3% ± 20.7%; $p < 0.001$), and aphids (4.9% ± 11.6% > 0.89% ± 4.7%; $p = 0.013$; Figure 3e–g). In contrast, weevils tended to occupy a greater proportion of stems in unmaintained stands compared to maintained stands (6.2% ± 13.2% > 2.5% ± 5.9%; $p < 0.001$; Figure 3h) (see Table S4 for occupancy rates). Greater stand size was associated with lower stem occupancy for monarchs, but not for leaf miners, aphids or weevils. Supplementary analyses showed that in urban areas, monarchs and leaf miners also exhibited greater abundance on stems in maintained stands than stems in unmaintained stands, and monarchs had greater abundance on stems occurring in larger stands (Table S7).

In maintained stands, stems were on average 27.6% taller than unmaintained stands ($n = 1848$, df = 1, $\chi^2 = 150.09$, $b = -19.62$, $p < 0.001$), had 14.9% more leaves ($n = 1848$, df = 1, $\chi^2 = 36.00$, $b = -3.01$, $p < 0.001$) and 78.5% higher focal density ($n = 1848$, df = 1, $\chi^2 = 266.37$, $b = -1.48$, $p < 0.001$) (Figure S1). Stand size (PC1) did not differ significantly between maintained and unmaintained stands across the entire study region ($n = 119$, df = 1, $\chi^2 = 0.96$, $b = -0.27$, $p = 0.33$) or within urban areas ($n = 59$, df = 1, $\chi^2 = 0.23$, $b = -0.17$, $p = 0.63$).

Stem-level predictors within stands

Across all 1848 stems sampled, stem occupancy by monarchs and leaf miners increased with stem height and leaf number, and leaf miner occupancy decreased with increasing focal stem density (Table 3). None of these predictors influenced stem occupancy for aphids or weevils. Further, the abundance of both monarchs and leaf miners on stems increased with stem height and leaf number but decreased with increasing focal stem density (Table S8).

TABLE 1 Binomial GLM analysis of the effects of urbanization (night sky brightness; NSB) and multivariate stand size (PC1) on occupancy of 119 common milkweed stands and 1848 stems by specialist herbivores in and around Kingston, Canada.

Response variable	Herbivore	Predictor	*b*	χ^2	*p*
Stand occupancy (all stands)	Monarchs	**NSB**	**0.49**	**4.54**	**0.033**
		PC1	0.38	2.53	0.11
	Leaf miners	**NSB**	**0.52**	**4.64**	**0.031**
		PC1	**1.51**	**19.27**	**<0.001**
	Aphids	NSB	0.52	2.85	0.091
		PC1	**0.83**	**8.89**	**0.0029**
	Weevils	NSB	−0.083	0.16	0.69
		PC1	**0.53**	**6.31**	**0.012**
Stand occupancy (unmaintained stands)	Monarchs	NSB	0.050	0.032	0.86
		PC1	0.45	3.25	0.071
	Leaf miners	NSB	0.26	0.59	0.44
		PC1	**1.78**	**17.53**	**<0.001**
	Aphids	NSB	0.017	0.0009	0.98
		PC1	**0.86**	**5.46**	**0.019**
	Weevils	NSB	−0.048	0.026	0.87
		PC1	**0.65**	**7.22**	**0.0072**
Stem occupancy (all stands)	Monarchs	**NSB**	**0.32**	**28.89**	**<0.001**
		PC1	**−0.36**	**23.67**	**<0.001**
	Leaf miners	**NSB**	**0.14**	**6.95**	**0.0084**
		PC1	0.077	1.68	0.20
	Aphids	**NSB**	**0.96**	**21.05**	**<0.001**
		PC1	0.048	0.063	0.80
	Weevils	NSB	−0.093	0.80	0.37
		PC1	**0.24**	**5.36**	**0.021**
Stem occupancy (unmaintained stands)	Monarchs	NSB	−0.026	0.061	0.81
		PC1	**−0.27**	**7.31**	**0.0068**
	Leaf miners	NSB	−0.17	3.57	0.059
		PC1	0.12	2.75	0.097
	Aphids	**NSB**	**0.68**	**4.10**	**0.043**
		PC1	0.071	0.063	0.80
	Weevils	NSB	0.21	2.28	0.13
		PC1	**0.27**	**6.05**	**0.014**

Note: All predictors are scaled and have 1 degree of freedom. The regression coefficients (*b*) are in log-odds units and chi-squared tests of significance are presented for each predictor. The bold values indicates $p < 0.05$.

DISCUSSION

Effects of urbanisation and stand type

We predicted that common milkweed would be occupied by progressively fewer of its specialised herbivores towards urban areas but instead found the opposite for monarchs, leaf miners, and aphids (Figure 2), as well as an increase in abundance towards urban centres for monarchs and leaf miners (Methods S2) – a pattern that appears to be caused at least in part by the presence of maintained milkweed (gardens) in urban environments. Other evidence for habitat restoration across urbanisation gradients affecting herbivory, particularly for specialist species, is rare. One study found a decline in insect herbivory on several *Quercus* species towards urban centres, but did not measure herbivore occupancy or abundance, and these urban trees don't represent habitat restoration per se (Moreira et al., 2019). Other work has demonstrated higher herbivore abundance in urban areas (Andrade et al., 2017; Dale & Frank, 2017; Shrewsbury & Raupp, 2000; Speight et al., 1998) despite general expectations that herbivore abundance should decline as urbanisation increases (Miles et al., 2019). In particular, Miles et al. (2022) found a positive effect of urbanisation on overall milkweed herbivore abundance towards

TABLE 2 Binomial GLM analyses of the effects of stand type (maintained vs. unmaintained; ST) and multivariate stand size (PC1) on stand and stem occupancy of 59 urban common milkweed stands in and around Kingston, Canada.

Response variable	Herbivore	Predictor	*b*	χ^2	*p*
Stand occupancy (urban stands)	Monarchs	**ST**	**2.80**	**6.57**	**0.010**
		PC1	0.12	0.15	0.70
	Leaf miners	ST	1.32	3.62	0.057
		PC1	**0.82**	**4.49**	**0.034**
	Aphids	**ST**	**2.27**	**4.16**	**0.041**
		PC1	0.30	0.41	0.52
	Weevils	ST	0.69	1.32	0.25
		PC1	0.49	2.85	0.091
Stem occupancy (urban stands)	Monarchs	**ST**	**1.25**	**46.25**	**<0.001**
		PC1	**−0.38**	**12.47**	**<0.001**
	Leaf miners	**ST**	**0.73**	**19.28**	**<0.001**
		PC1	0.025	0.083	0.77
	Aphids	**ST**	**1.22**	**6.19**	**0.013**
		PC1	−0.42	2.28	0.13
	Weevils	**ST**	**−1.11**	**10.97**	**<0.001**
		PC1	0.19	1.75	0.19

Note: The regression coefficients (*b*) are in log-odds units and chi-squared tests of significance are presented for each predictor. Positive stand type coefficients represent greater occupancy in maintained stands. The bold values indicates $p < 0.05$.

several urban centres in southern Ontario, Canada. This involved species-specific increases for monarchs and leaf miners but the expected negative effect for weevils. They speculate that this pattern may be caused by lower patch density in urban environments necessitating herbivores be distributed across fewer milkweed stands and consequently increasing per-stand abundance (i.e., "urban saturation"), but our findings suggest that the relation between urbanisation and occupancy may instead be caused by the presence of gardens.

Our results indicate that the urbanisation gradient in stand and stem occupancy we detected for specialist herbivores monarchs and leaf miners, and stand occupancy for aphids, is caused primarily by the presence of maintained stands (gardens), with little other net effect of urbanisation on occupancy by these herbivores once the effect of gardens is accounted for. If the urban saturation hypothesis explained increasing occupancy and abundance by herbivores towards urban areas, we would have expected to find these occupancy patterns regardless of whether maintained stands were included in our analysis. Thus, there seems to be qualities inherent to garden habitat that support greater occupancy regardless of the spatial distribution of habitat in the urban landscape. Aphids, however, still occupied more stems in urban areas once gardens were excluded from the analysis. This positive effect of urbanisation on aphid stem occupancy even after removing maintained stands could still be explained by the urban saturation hypothesis. Alternatively, some evidence suggests increased impervious surfaces in urban areas lead to decreased water absorption and higher amino acid concentrations in urban plants, which could promote occupancy by aphids and other sap-sucking herbivores (Miles et al., 2019; White, 1984, 2009). Interestingly, the exclusion of maintained stands from the analysis resulted in a significantly higher regression coefficient for weevils, suggesting that weevils may tend to avoid gardens in urban areas. Miles et al. (2022) did not account for variation in stand type (i.e., maintained vs. unmaintained stands) despite including a variety of stand types in their survey, leaving the possibility that the positive effect of urbanisation on abundance they detected is a consequence of urban milkweed gardens.

We predicted that the occupancy of milkweed plants by specialist herbivores would be influenced by characteristics of the milkweed stands and the milkweed plants themselves within stands. The effects of these plant-and-stand attributes might partially explain differences in occupancy between maintained and unmaintained stands. First, stand occupancy was associated with greater stand size for leaf miners, aphids and weevils (but not monarchs), regardless of whether maintained stands were included in the analysis (Table 1). However, PC1 did not differ between maintained and unmaintained stands, suggesting it is unlikely that differences in stand size between stand types explain why maintained stands were more frequently occupied. For monarchs, stem occupancy was lower in larger stands. This result does not necessarily indicate that larger stands support fewer monarchs but may instead suggest that, even if stand size increases stand occupancy, stem occupancy doesn't keep pace with increasing stand size. This may also explain why leaf miners and aphids have greater stand occupancy but not stem occupancy as stand size increases. Larger stands may increase the likelihood of patch colonisation or reduce the chance of extinction, increasing the likelihood of stand occupancy, but may not have any effect on the proportion of stems that are occupied.

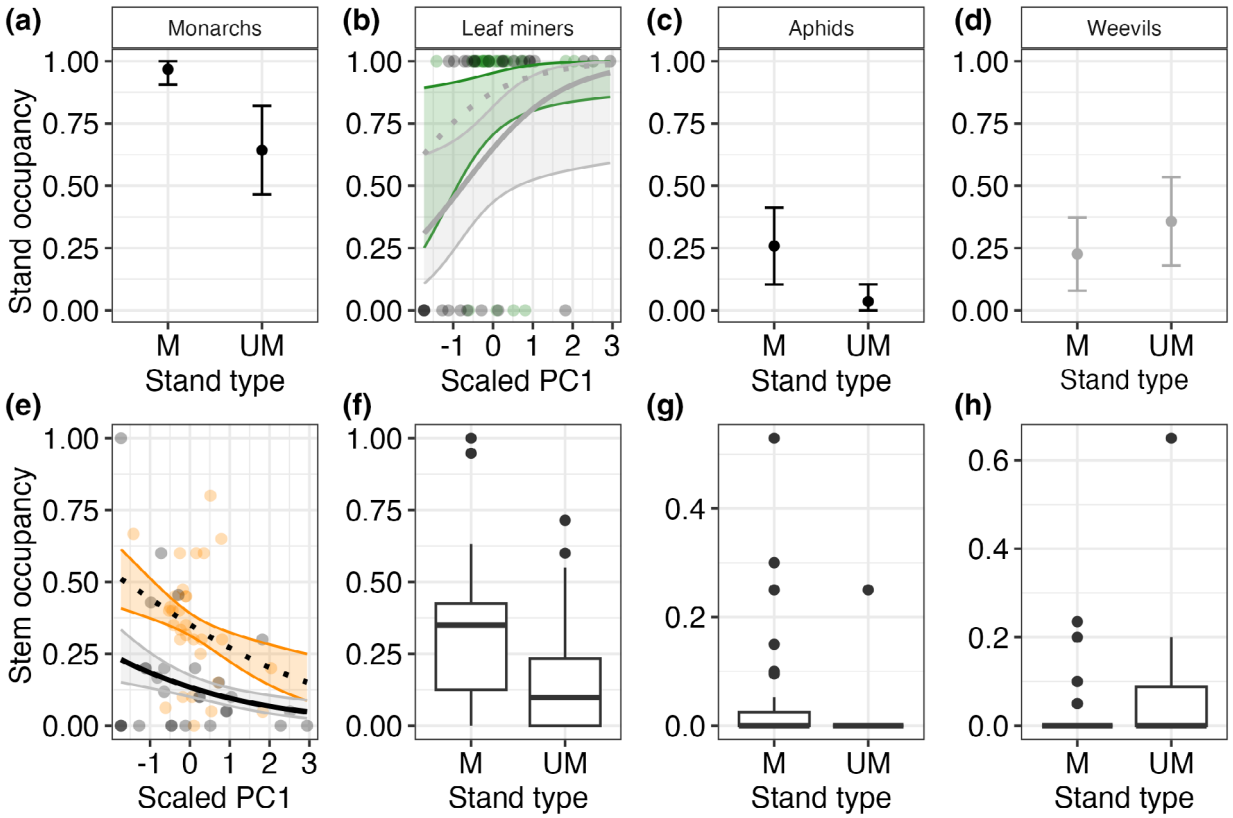


FIGURE 3 Variation in stand occupancy (top row) and stem occupancy (bottom row) between maintained (M) and unmaintained (U) stands and with stand size (PC1) within urban areas (NSB > median NSB). Points in panels (a, c, d) indicate the proportion of stands occupied in urban areas with error bars representing 95% confidence intervals. Stand occupancy by leaf miners (b) and stem occupancy by monarchs (e) was significantly predicted by stand size (PC1), and as such stand type is indicated by line type and ribbon colour (dotted/coloured = maintained, solid/grey = unmaintained). Panels (f–h) show stem occupancy (proportion of stems occupied in each stand) as box plots. The centre line is the median; top and bottom edge are the 75- and 25-percentiles, respectively, and the whiskers extend to 1.5 interquartile distances from the median or the maximum and minimum points, whichever is less. Black dot plots, lines, and box plots indicate significant differences between stand types, while grey indicates non-significant differences between stand types (panels b and d).

TABLE 3 Binomial GLM analysis of the effects of stem characteristics (stem height, leaf number and surrounding density of con-specific stems) on herbivore occupancy within stands of common milkweed in and around Kingston, Canada.

Response variable	Herbivore	Predictor	*b*	χ^2	*p*
Stem occupancy	Monarchs	**Height**	**0.22**	**7.48**	**0.0063**
		Leaf number	**0.17**	**5.66**	**0.017**
		Focal density	−0.11	1.63	0.20
	Leaf miners	**Height**	**0.51**	**31.66**	**<0.001**
		Leaf number	**0.25**	**11.21**	**<0.001**
		Focal density	**−0.36**	**13.30**	**<0.001**
	Aphids	Height	0.025	0.011	0.92
		Leaf number	0.23	2.57	0.11
		Focal density	−0.47	2.22	0.14
	Weevils	Height	0.27	2.44	0.12
		Leaf number	−0.33	2.30	0.13
		Focal density	−0.016	0.012	0.92

Note: All predictors are scaled and have 1 degree of freedom. The regression coefficient (*b*) in log-odds units and chi-squared tests of significance are presented for each predictor. All models include stand ID as a random effect. The bold values indicates $p < 0.05$.

Although the effect of stand size was inconsistent, monarch and leaf miner occupancy correlated positively with plant vigour. Within stands, both herbivores tended to occupy taller stems with more leaves, both traits that were more pronounced in maintained than unmaintained stands. It is possible that both herbivores preferentially select maintained stands of milkweed because they provide better host resources. This is supported by observations that monarchs preferentially oviposit on more vigorous milkweed stems (Cutting & Tallamy, 2015). Other unmeasured features of gardens may also benefit particular species, such as greater floral diversity (Marín et al., 2020) yielding greater and/or more consistent nectar availability for ovipositing monarchs. Interestingly, our randomisation tests (Table S3) and stand-type models (Table 2) indicate that gardens may have lower weevil occupancy than unmaintained stands. It is possible that the higher occurrence of weevils on unmaintained stems reflects some aspect of garden habitat that is detrimental to their survival or reproduction such as less leaf litter for overwintering compared to unmaintained stands (Marín et al., 2020).

Implications for conservation

Gardening for wildlife, especially butterflies and other pollinators, has become increasingly popular. Taking our data at face value, it seems that this is justified for at least some of the specialist herbivores of milkweed, including the endangered monarch butterfly. Milkweed in gardens was more frequently occupied by monarchs, aphids and leaf miners compared to unmaintained stands, leading us to suggest that milkweed be planted in conjunction with other plant species that provide resources for insect diversity. Our results are supported by work indicating that adult female monarchs prefer to oviposit on milkweed in gardens (Cutting & Tallamy, 2015).

Definitive support for the efficacy of milkweed gardens requires following the fate of individuals in garden vs. ruderal habitat. While we found higher occupancy by monarch eggs and larvae in garden stands, it remains possible that this could be counterbalanced by lower survival to adulthood; hence, pollinator gardens might be "ecological traps" (Robertson & Hutto, 2006). As a post-hoc analysis, we fit our monarch butterfly stand-type model with the occupancy by only eggs and only larvae (rather than occupancy by either) and found that the relation between stem occupancy and stand-type remains positive and significant for eggs and larvae separately (Table S5) suggesting that there is no reversal of the "garden effect" between at least these two life history stages. We were not able to track the fate of pupating larvae because they tend to abandon milkweed plants at this stage (Fisher et al., 2020). Our results provide no insight into the fate of the other milkweed herbivores.

If herbivores in urban gardens do not suffer decreased success, people should be encouraged to plant more milkweed in their yards across the urban landscape to support these specialised species interactions, including the endangered monarch butterfly. Unfortunately, there remains much public resistance to planting milkweed largely due to aesthetic reasons, perceived labour for care and maintenance, or misconceptions that the species is invasive (Davis & Stoyko, 2022). Furthermore, planting milkweed is an example of ecological gardening that not only provides nectar for pollinator species but also provides forage for other herbivores. Planting species with the intention of them being eaten and damaged by herbivores is an interesting component of ecological gardening that warrants consideration by all gardeners. Gardening remains a powerful tool and productive form of public engagement in conservation that proves economically viable and important for supporting both insect and plant biodiversity (Segar et al., 2022), and here we have provided some empirical support for the idea that conservation gardening is an effective tool for supporting wildlife in urban ecosystems.

AUTHOR CONTRIBUTIONS

Graydon J. Gillies: Conceptualization; methodology; software; data curation; investigation; validation; formal analysis; funding acquisition; visualization; writing – review and editing. **Rishona Vemulapalli:** Conceptualization; methodology; software; data curation; investigation; validation; formal analysis; visualization; writing – original draft. **Christopher G. Eckert:** Supervision; resources; project administration; writing – review and editing; conceptualization; funding acquisition; methodology; formal analysis.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code for the project can be found at DOI: https://doi.org/10.5281/zenodo.15713253 (Gillies et al., 2025). https://doi.org/10.5281/zenodo.15713254.

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REFERENCES

Agrawal, A. (2017) *Monarchs and milkweed: a migrating butterfly, a poisonous plant, and their remarkable story of coevolution*. Princeton, NJ: Princeton University Press.

Andrade, R., Bateman, H.L. & Kang, Y. (2017) Seasonality and land cover characteristics drive aphid dynamics in an arid city. *Journal of Arid Environments*, 144, 12–20.

Baker, A.M. & Potter, D.A. (2018) Colonization and usage of eight milkweed (asclepias) species by monarch butterflies and bees in urban garden settings. *Journal of Insect Conservation*, 22(3), 405–418.

Baker, A.M. & Potter, D.A. (2019) Configuration and location of small urban gardens affect colonization by monarch butterflies. *Frontiers in Ecology and Evolution*, 7, 496401.

Bériault, K. & Packer, L. (2010) COSEWIC assessment and status report on the Monarch, *Danaus plexippus*, in Canada. Committee on the status of endangered wildlife in Canada.

Birnbaum, S.S.L. & Abbot, P. (2018) Insect adaptations toward plant toxins in milkweed–herbivores systems – a review. *Entomologia Experimentalis et Applicata*, 166(5), 357–366.

Brady, M.J., McAlpine, C.A., Miller, C.J., Possingham, H.P. & Baxter, G.S. (2009) Habitat attributes of landscape mosaics along a gradient of matrix development intensity: matrix management matters. *Landscape Ecology*, 24(7), 879–891.

Breitbart, S., Tomchyshyn, A., Wagner, H.H. & Johnson, M.T.J. (2023) Urbanization and a green corridor influence reproductive success and pollinators of common milkweed. *Urban Ecosystems*, 26(1), 31–43.

Brooks, M.E., Brooks, M.E., Kristensen, K., Benthem, K.J., Magnusson, A., Berg, C.W. et al. (2017) GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378.

Colautti, R.I., Eckert, C.G. & Barrett, S.C.H. (2010) Evolutionary constraints on adaptive evolution during range expansion in an invasive plant. *Proceedings. Biological Sciences*, 277(1689), 1799–1806.

Cutting, B.T. & Tallamy, D.W. (2015) An evaluation of butterfly gardens for restoring habitat for the monarch butterfly (lepidoptera: Danaidae). *Environmental Entomology*, 44(5), 1328–1335.

Dale, A.G. & Frank, S.D. (2017) Warming and drought combine to increase pest insect fitness on urban trees. *PLoS One*, 12(3), e0173844.

David Suzuki Foundation. (2022) The butterflyway project. Available from: https://davidsuzuki.org/take-action/act-locally/butterflyway/ [Accessed 16th December, 2024].

Davis, A. & Stoyko, J. (2022) Barriers to native plantings in private residential yards. *Land*, 12(1), 114.

Dawson, K., Maunder, K.G., Eckert, L., Kraml, M.M., Dean-Moore, C., Joslin, L. et al. (2025) Viral-induced flower colour breaking reveals that turnip mosaic virus infection prevalence increases with urbanization in the invasive mustard *Hesperis matronalis*. *International Journal of Plant Sciences*, 737468. Available from: https://doi.org/10.1086/737468

Devictor, V., Julliard, R. & Jiguet, F. (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos (Copenhagen, Denmark)*, 117(4), 507–514.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 487–515.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C.C.M., Elvidge, C.D., Baugh, K. et al. (2016) Supplement to: the new world atlas of artificial night sky brightness. GFZ data services. Available from: https://dataservices.gfz-potsdam.de/panmetaworks/showshort.php?id=escidoc:1541893 [Accessed 8th March, 2025].

Fenoglio, M.S., Rossetti, M.R. & Videla, M. (2020) Negative effects of urbanization on terrestrial arthropod communities: a meta-analysis. *Global Ecology and Biogeography: A Journal of Macroecology*, 29(8), 1412–1429.

Finch, J. (2025) Latitudinal variation in phenology and reproduction among seed sources of *Asclepias syriaca* L. (common milkweed). *The Great Lakes Botanist*, 63(3–4): 56–74. Available from: https://doi.org/10.3998/glbot.7730

Fisher, K.E., Hellmich, R.L. & Bradbury, S.P. (2020) Estimates of common milkweed (*Asclepias syriaca*) utilization by monarch larvae (*Danaus plexippus*) and the significance of larval movement. *Journal of Insect Conservation*, 24(2), 297–307.

Fordyce, J.A. (2000) Specialist weevil, *Rhyssomatus lineaticollis*, does not spatially avoid cardenolide defenses of common milkweed by ovipositing into pith tissue. *Journal of Chemical Ecology*, 26(12), 2857–2874.

Fox, J. & Weisberg, S. (2019) *An R companion to applied regression*. Thousand Oaks CA: Sage. Available from: https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Gillies, G.J., Vemulapalli, R. & Eckert, C.G. (2025) Common milkweed gardens increase occupancy by monarch butterflies and other specialist herbivores towards an urban centre. *Zenodo*. Available from: https://doi.org/10.5281/ZENODO.15713254

Goddard, M.A., Dougill, A.J. & Benton, T.G. (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology & Evolution*, 25(2), 90–98.

Hanski, I. (1994) A practical model of metapopulation dynamics. *The Journal of Animal Ecology*, 63(1), 151–162.

Hennig, E.I. & Ghazoul, J. (2012) Pollinating animals in the urban environment. *Urban Ecosystems*, 15(1), 149–166.

Hordley, L.A. & Fox, R. (2024) Wildlife-friendly garden practices increase butterfly abundance and species richness in urban and arable landscapes. *The Science of the Total Environment*, 929(171503), 171503.

Klinger, K.R., Hasle, A.F. & Oberhauser, K.S. (2024) Characteristics of urban milkweed gardens that influence monarch butterfly egg abundance. *Frontiers in Ecology and Evolution*, 12, 1444460.

Landis, T.D. (2014) Monarch waystations: propagating native plants to create travel corridors for migrating monarch butterflies. *Native Plants Journal*, 15(1), 5–16.

Lehner, B. & Grill, G. (2013) Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems: global river hydrography and network routing. *Hydrological Processes*, 27(15), 2171–2186.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15(3), 237–240.

Liu, Z., He, C. & Wu, J. (2016) The relationship between habitat loss and fragmentation during urbanization: an empirical evaluation from 16 world cities. *PLoS One*, 11(4), e0154613.

Mach, B.M., Long, W., Daniels, J.C. & Dale, A.G. (2023) Aphid infestations reduce monarch butterfly colonization, herbivory, and growth on ornamental milkweed. *PLoS One*, 18(7), e0288407.

Marín, L., Martínez-Sánchez, M.E., Sagot, P., Navarrete, D. & Morales, H. (2020) Floral visitors in urban gardens and natural areas: diversity and interaction networks in a neotropical urban landscape. *Basic and Applied Ecology*, 43, 3–15.

Matter, S.F. (1996) Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation. *Oecologia*, 105(4), 447–453.

Matthews, T.J., Cottee-Jones, H.E. & Whittaker, R.J. (2014) Habitat fragmentation and the species–area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. *Diversity and Distributions*, 20(10), 1136–1146.

Mellander, C., Lobo, J., Stolarick, K. & Matheson, Z. (2015) Night-time light data: a good proxy measure for economic activity? *PLoS One*, 10(10), e0139779.

Messager, M.L., Lehner, B., Grill, G., Nedeva, I. & Schmitt, O. (2016) Estimating the volume and age of water stored in global lakes using a geo-statistical approach. *Nature Communications*, 7, 13603.

Miles, L.S., Breitbart, S.T., Wagner, H.H. & Johnson, M.T.J. (2019) Urbanization shapes the ecology and evolution of plant-arthropod herbivore interactions. *Frontiers in Ecology and Evolution*, 7, 469218.

Miles, L.S., Murray-Stoker, D., Nhan, V.J. & Johnson, M.T.J. (2022) Effects of urbanization on specialist insect communities of milkweed are mediated by spatial and temporal variation. *Ecosphere (Washington, D.C)*, 13(9), e4222.

Miller, J.R. (2005) Biodiversity conservation and the extinction of experience. *Trends in Ecology & Evolution*, 20(8), 430–434.

Moreira, X., Abdala-Roberts, L., Berny Mier y Teran, J.C., Covelo, F., de la Mata, R., Francisco, M. et al. (2019) Impacts of urbanization on insect herbivory and plant defences in oak trees. *Oikos*, 128(1), 113–123.
Murray-Stoker, D., Santangelo, J.S., Szulkin, M. & Johnson, M.T.J. (2025) Comparing approaches to quantify urbanization on a multicontinental scale. *Urban Ecosystems*, 28(2), 1–16.
Ockinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M. et al. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis: habitat fragmentation and life-history traits. *Ecology Letters*, 13(8), 969–979.
Parris, K.M., Amati, M., Bekessy, S.A., Dagenais, D., Fryd, O., Hahs, A.K. et al. (2018) The seven lamps of planning for biodiversity in the city. *Cities (London, England)*, 83, 44–53.
Pelton, E.M., Schultz, C.B., Jepsen, S.J., Black, S.H. & Crone, E.E. (2019) Western monarch population plummets: status, probable causes, and recommended conservation actions. *Frontiers in Ecology and Evolution*, 7, 458330.
Pitman, G.M., Flockhart, D.T.T. & Norris, D.R. (2018) Patterns and causes of oviposition in monarch butterflies: implications for milkweed restoration. *Biological Conservation*, 217, 54–65.
Prysby, M.D. (2004) Natural enemies and survival of monarch eggs and larvae. In: *The monarch butterfly: biology and conservation*, Ithaca: Cornell University Press, pp. 27–38.
Pun, C.S.J. & So, C.W. (2012) Night-sky brightness monitoring in Hong Kong: a city-wide light pollution assessment. *Environmental Monitoring and Assessment*, 184(4), 2537–2557.
QGIS Development Team. (2024) *QGIS geographic information system*. QGIS Association. Available from: https://www.qgis.org
R Core Team. (2025) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/
Robertson, B.A. & Hutto, R.L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87(5), 1075–1085.
Schultz, C.B. & Crone, E.E. (2005) Patch size and connectivity thresholds for butterfly habitat restoration. *Conservation Biology: The Journal of the Society for Conservation Biology*, 19(3), 887–896.
Segar, J., Callaghan, C.T., Ladouceur, E., Meya, J.N., Pereira, H.M., Perino, A. et al. (2022) Urban conservation gardening in the decade of restoration. *Nature Sustainability*, 5(8), 649–656.
Shrewsbury, P.M. & Raupp, M.J. (2000) Evaluation of components of vegetational texture for predicting azalea lace bug, *Stephanitis pyrioides* (Heteroptera: Tingidae), abundance in managed landscapes. *Environmental Entomology*, 29(5), 919–926.
Smith, R.A., Mooney, K.A. & Agrawal, A.A. (2008) Coexistence of three specialist aphids on common milkweed, *Asclepias syriaca*. *Ecology*, 89(8), 2187–2196.
Speight, M.R., Hails, R.S., Gilbert, M. & Foggo, A. (1998) Horse chestnut scale (*Pulvinaria regalis*) (Homoptera: Coccidae) and urban host tree environment. *Ecology*, 79(5), 1503–1513.
Sutton, P., Roberts, D., Elvidge, C. & Baugh, K. (2001) Census from heaven: an estimate of the global human population using night-time satellite imagery. *International Journal of Remote Sensing*, 22(16), 3061–3076.
Walker, A. (2022) *Danaus plexippus* ssp. plexippus, IUCN Red List [Preprint].
White, T.C.R. (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia*, 63(1), 90–105.
White, T.C.R. (2009) Plant vigour versus plant stress: a false dichotomy. *Oikos (Copenhagen, Denmark)*, 118(6), 807–808.
Zaya, D.N., Pearse, I.S. & Spyreas, G. (2017) Long-term trends in midwestern milkweed abundances and their relevance to monarch butterfly declines. *Bioscience*, 67(4), 343–356.
Zheng, Y., He, Y., Zhou, Q. & Wang, H. (2022) Quantitative evaluation of urban expansion using NPP-VIIRS nighttime light and Landsat spectral data. *Sustainable Cities and Society*, 76, 103338.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Descriptive statistics for stand and stem surveys of *Asclepias syriaca* in and around Kingston, Canada.

Table S2. Correlations (Pearson's correlation coefficients) between night sky brightness and stand structural variables across common milkweed stands in Kingston, Canada, and the surrounding region for all surveyed stands (top) and only unmaintained stands (bottom).

Table S3. Randomisation tests to assess whether excluding maintained stands from the analysis results in a greater reduction of the effect of NSB than would be expected from a simple reduction in sample size. For all herbivores the partial regression coefficient for NSB is larger in magnitude for analyses including maintained stands ($n = 119$) than when unmaintained stands are excluded ($n = 84$). Δb_{obs} is the observed difference in b_{NSB} between the regression involving all stands and that involving only unmaintained stands and represents the effect of maintained stands on the regression. p_{rand} is the proportion of Δb values from 1000 models fit to a randomised set of 84 stands (Δb_{rand}) that were greater than or equal in magnitude to Δb_{obs} ($p_{rand} < 0.001$ indicates none of the permutations yielded a slope greater in magnitude than with all stands included).

Table S4. Occupancy rates of common milkweed stands in Kingston, Canada, and the surrounding region at the stand-level (top) and stem-level (bottom).

Table S5. Analyses of the effects of stand type (maintained vs. unmaintained; ST) and stand size (scaled PC1) on stem occupancy by two life stages of *Danaus plexippus* across 59 urban *Asclepias syriaca* stands in and around Kingston, Ontario, Canada, using binomial GLMs with scaled predictors. Positive coefficients represent greater occupancy in maintained stands. The regression coefficient (*b*) in log-odds units and chi-squared tests of significance are presented for each predictor.

Figure S1. Comparison of stand (a–e) and stem (f–h) characteristics between maintained (M) and unmaintained (U) stands of common milkweed across all stands ($n = 119$) in and around Kingston, Canada. Stand characteristics shown are (a) night sky brightness, (b) $\log_{10}$ stand area, (c) $\log_{10}$ stand-wide density, (d) $\log_{10}$ number of stems and (e) PC1 (i.e., stand size), and stem characteristics include (f) focal stem density, (g) stem height and (h) the $\log_{10}$ number of leaves. The center line of each boxplot is the median; top and bottom edge are the 75- and 25-percentiles, respectively, and the whiskers extend to 1.5 interquartile distances from the median or the maximum and minimum points, whichever is less.

Figure S2. Comparison of stand (a–e) and stem (f–h) characteristics between maintained (M) and unmaintained (U) stands of common milkweed in the urban area (greater than median NSB; $n = 59$) in and around Kingston, Canada. Stand characteristics shown are

(a) night sky brightness, (b) $\log_{10}$ stand area, (c) $\log_{10}$ stand-wide density, (d) $\log_{10}$ number of stems and (e) PC1 (i.e., stand size), and stem characteristics include (f) focal stem density, (g) stem height and (h) the $\log_{10}$ number of leaves. The centre line of each boxplot is the median; top and bottom edge are the 75- and 25-percentiles, respectively, and the whiskers extend to 1.5 interquartile distances from the median or the maximum and minimum points, whichever is less.

Table S6. Results from models that fit herbivore stand abundance ($n = 119$) and stem abundance ($n = 1848$) to urbanisation (scaled night-sky brightness; NSB), stand size (scaled PC1) and stand type (ST). Model parameters are scaled have 1 degree of freedom. Positive stand type coefficients indicate greater abundance in maintained stands. Negative binomial error distributions were used to account for overdispersion where necessary. Chi-squared tests of significance are presented for each predictor.

Table S7. Randomisation tests to assess whether excluding maintained stands from the analysis results in a greater reduction of the effect of NSB than would be expected from a simple reduction in sample size. For all herbivores the partial regression coefficient for NSB is larger in magnitude for analyses including maintained stands than when unmaintained stands are excluded. Δb_{obs} is the observed difference in b_{NSB} between the regression involving all stands and that involving only unmaintained stands and represents the effect of maintained stands on the regression. p_{rand} is the proportion of Δb values from 1000 models fit to a randomised set of 84 stands (Δb_{rand}) that were greater than or equal in magnitude to Δb_{obs} ($p_{rand} < 0.001$ indicates none of the permutations yielded a slope greater in magnitude than with all stands included).

Table S8. Poisson GLM analyses of variation in herbivore abundance in response to stem characteristics. Focal density is the number of con-specific stems within 1 m of a sampled stem. Parameters are scaled and have 1 degree of freedom. Chi-squared tests of significance are presented for each predictor.

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