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Decline in common milkweed along roadsides around Ottawa, Canada

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ABSTRACT
Over the past two decades, monarch butterfly populations have been declining. This decline has been partly attributed to the extensive loss of breeding habitat through the reduction of common milkweed (*Asclepias syriaca*, the larval host plant) through herbicides. While the decline of milkweed has been well documented in the US, less is known about its decline in Canada. To take a first step in quantifying its potential decline, we compared roadside milkweed abundance at sites around Ottawa, Ontario, Canada in 2018, to a county-wide estimate of milkweed abundance in 1943 and 1944. We also evaluated the effect of roadside characteristics on milkweed abundance at these sites. Current milkweed density in the Ottawa region is 33–86% lower than it was 75 years ago. We found milkweed at 67% of our 100 sites and found less milkweed at sites with a higher number of lanes in the road adjacent to the roadside. Interestingly, mowing indices were not significant predictors of milkweed abundance. Here we document the first quantitative evidence for milkweed decline over the past 75 years in Canada, which has likely contributed to the decline of breeding monarchs in Canada.

RÉSUMÉ
Les populations de papillons monarques ont décliné au cours des deux dernières décennies. Ce déclin a été en partie attribué à la perte d'habitat de reproduction due à la diminution de l'asclépiade commune (*Asclepias syriaca*, la plante hôte de la larve) en raison de l'utilisation d'herbicides. Alors que le déclin de l'asclépiade a été bien documenté aux États-Unis, ce n'est pas le cas au Canada. Comme première étape de quantification du déclin potentiel de l'asclépiade, nous avons comparé l'abondance d'asclépiade en 2018 en bordure de route à des sites dans les environs d'Ottawa (Ontario, Canada) à une estimation à l'échelle du comté réalisée en 1943 et 1944. Nous avons aussi évalué les effets des caractéristiques des bordures de routes sur l'abondance d'asclépiade. La densité actuelle d'asclépiade dans la région d'Ottawa est de 33 à 86% plus faible qu'il y a 75 ans. Nous avons trouvé de l'asclépiade à 67% de nos 100 sites et nous en avons trouvé moins aux sites avec un plus grand nombre de voies sur les routes adjacentes aux bordures échantillonnées. Il est intéressant de noter que les indices de fauchage n'étaient pas des prédicteurs significatifs de l'abondance d'asclépiade. Nous avons présenté la première quantification du déclin de l'asclépiade au Canada au cours des derniers 75 ans, qui a vraisemblablement contribué au déclin des monarques reproducteurs.

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Introduction

The eastern migratory population of the monarch butterfly (*Danaus plexippus*) overwinters in central Mexico and then migrates to its summer breeding grounds in the northern United States and southern Canada. The decline of this population over the past two decades is well documented (Flockhart et al. 2015; Semmens et al. 2016; Brower et al. 2018). As a result, monarchs in Canada are listed as *Endangered* by COSEWIC (2016) and *Special Concern* under the Species at Risk Act (currently under consideration for status change; Government of Canada 2003). Three main factors are thought to be contributing to this decline: (i) loss of overwintering habitat, (ii) extreme weather conditions at the overwintering grounds and along the migratory corridor, and (iii) reductions of breeding habitat through increased land development and use of glyphosate herbicides on host milkweed plants (Oberhauser and Peterson 2003; Brower et al. 2012; Flockhart et al. 2015). This last potential driver of monarch decline has gained considerable support, and shows a strong correlation with the loss of the monarch's larval host plants across their breeding range (Pleasants 2017; Thogmartin et al. 2017).

The sole larval host plants of the monarch are those in the milkweed genus (*Asclepias* spp.). In particular, common milkweed (*Asclepias syriaca*) is used by over 90% of

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Supplemental data for this article can be accessed here.

monarchs in the summer breeding range of the eastern population (Malcolm et al. 1993). Common milkweed has been declining in the Midwestern U.S. over the past two decades (Pleasants and Oberhauser 2013; Zaya et al. 2017) and has been mostly eradicated from U.S. croplands due to herbicide use (Hartzler 2010; Pleasants and Oberhauser 2013). Researchers estimate that roadsides account for 10–20% of the remaining milkweed in the central U.S. (Pleasants and Oberhauser 2013; Flockhart et al. 2015). This suggests that roadsides could be important in milkweed and monarch persistence. For monarchs, roadsides provide long connected habitats that can also act as corridors between other suitable habitat (Hopwood 2010; Zalucki and Lammers 2010; Kasten et al. 2016; Daniels et al. 2018; Kaul and Wilsey 2019; Knight et al. 2019). However, not all roadsides have equal value for monarchs. Roadsides have been shown to be a source of monarch mortality (McKenna et al. 2001; Alvarez et al. 2019; Kantola et al. 2019) and can be less suitable than other habitats (Kasten et al. 2016; Pitman et al. 2018).

While the decline of common milkweed has been well documented in the Midwestern U.S., the status of the Canadian population is unknown. To the best of our knowledge, there has been no quantification of the decline of the milkweed population in southern and eastern Ontario, which represents the most extensive area of monarch breeding in Canada (COSEWIC 2010). To our knowledge, the first, and only, comprehensive study of milkweed in both roadside and field stands in Ontario and Quebec was undertaken in 1943 and 1944 (Groh and Dore 1945). The purpose of their survey was to describe the distribution and density of milkweed in those areas due to its interest as a possible source of substitutes for rubber and floss – products in short supply during World War II (Figure 1).

Since Groh and Dore's survey, Ontario's human population has increased by 255% (~9,600,000 people; Statistics Canada 2013, 2017), and the province has become much more developed, both in terms of expanding agriculture and urban growth (Fox and Wang 2016; Statistics Canada 2016). Common milkweed was on the Ontario Noxious Weed list from 1990–2014 (*Weed Control Act* 1990) before it was removed based on its ecological significance to the monarch. The Act mandates that plants identified as noxious weeds must be destroyed if they negatively impact agricultural lands. There has also been an increased use of genetically modified crops and associated herbicide use on milkweed over recent decades (Boyle et al. 2019). Therefore, there has likely been a decline in milkweed in Ontario.

Although roadsides can provide habitat for milkweed (Kasten et al. 2016; Pitman et al. 2018; Kaul and Wilsey 2019), disturbances associated with roadsides can negatively impact plant populations in many ways. For example, dust deposition, nitrogen, chemical pollutants and altered pH can modify the soil and water used by roadside plants (Forman and Alexander 1998; Coffin 2007; Snell-Rood et al. 2014). In Iowa, U.S., roadside sites with milkweed had higher soil pH and lower soil density than

Figure 1. Historical milkweed images. (a) A newspaper article from the London Free Press (London, Ontario, Canada) dated Saturday July 8 1944 describing the efforts to collect milkweed to help support war efforts. (b) A picture of a roadside stand from Groh and Dore (1945) with 30,000 stalks per mile in the former Nepean township, Carleton County.

milkweed sites in conservation areas (Kaul and Wilsey 2019). Moreover, the invasion of exotic species (Forman and Alexander 1998; Coffin 2007), roadwork (Spooner et al. 2004), and mowing also alters roadside vegetation (Simard and Benoit 2011). These disturbances lead to systematic changes in the environment as a function of the distance to the edge of the road (i.e., edge effects; Ries et al. 2004) and could reduce the suitability of roadsides as habitat for milkweed.

Common milkweed generally persists in disturbed habitats due to its superior dispersal but inferior competitive abilities (Evetts and Burnside 1975; Sacchi 1987; Borders and Lee-Mäder 2014). However, previous work examining which factors associated with disturbance best predict milkweed occurrence and abundance have found mixed results. For example, some studies have found an impact of adjacent land use type on roadside milkweed density (Hartzler and Buhler 2000; Follak et al. 2018) whereas others have not (Kasten et al. 2016). Other studies show variation in milkweed density across land cover types (Zaya et al. 2017) including roadsides (Pitman et al. 2018; Kaul and Wilsey 2019). Roadsides with non-crop as adjacent land use may be more likely to support higher milkweed occurrence and/or density than adjacent crop areas because non-crop areas lead to less herbicide contamination of roadsides (Kasten et al. 2016) and are more likely to support milkweed populations than crop areas, and therefore provide seed sources for colonization of nearby roadsides (Hartzler and Buhler 2000).

Mowing has also been shown to have varying effects on milkweed at the individual and patch-level (Baum and Mueller 2015; Fischer et al. 2015; Daniels et al. 2018; Dee and Baum 2019; Kaul and Wilsey 2019). Some mowing can have a positive effect on milkweed growth by inducing the sprouting of underground root buds, which can lead to larger colonies (Bhowmik and Bandeen 1976; Bhowmik 1994; Baum and Mueller 2015; Fischer et al. 2015; Zalai et al. 2017). Indeed, mowing has been shown to increase milkweed density in some locations (Daniels et al. 2018). However, this is not always the case (Kaul and Wilsey 2019). The timing (Fischer et al. 2015) and frequency of mowing is also key. Mowing too frequently can affect growth structure (Dee and Baum 2019) and reduce density because plants are not able to regenerate (Baum and Sharber 2012; Daniels et al. 2018).

Recent research suggests that road type can influence milkweed. Greater traffic volume, which is generally associated paved roads and a higher number of lanes, has been shown to decrease the nutritional quality of milkweed (Mitchell et al. 2020). Work done in Austria where *A. syriaca* is invasive indicates that milkweed has a higher preference for local unpaved roads (Follak et al. 2018). The upper soil layer along the road verges of these roads were highly disturbed, as they were mostly associated with gravel mining. Consequently, they provided beneficial growth conditions for *A. syriaca*. In contrast, roadsides of paved roads in this region were generally mown and covered by dense vegetation, which likely increased competition and negatively impacted milkweed establishment and performance (Follak et al. 2018).

In this study, we quantify temporal changes in roadside common milkweed populations around Ottawa, Ontario, Canada between the early 1940s and now, and test the effect of certain roadside characteristics on current milkweed populations. We describe the disturbance level and adjacent land-use of the roadsides based on factors previously shown to potentially influence the suitability of roadsides for milkweed. Specifically, we consider the number and type of lanes in the road adjacent to the roadside, mowing (extent, approximate time since last mowing) and the land-use of the area adjacent to the roadside transect. The number of lanes in the road adjacent to the roadside integrates multiple factors such as usage frequency, traffic volume, higher human population densities, higher pollutant concentrations and herbicide applications (Bernes et al. 2017; Khalid et al. 2018; Zhou et al. 2020), so we included it as a potential predictor of milkweed density.

Material and methods

Study species

Common milkweed (*Asclepias syriaca)* is a flowering perennial herbaceous plant, typically 60–120 cm tall (Bhowmik and Bandeen 1976). It is widespread across the eastern U.S. and can be found in southern Canada from Saskatchewan to New Brunswick (Canadensys 2020; Taylor [date unknown]). Common milkweed can be found across numerous habitats, including roadsides, landfill sites, forest edges, cultivated lands, pastures, gardens, and fields. It will tolerate salt concentrations up to 2500 ppm, pH ranging from 2 to 12, and most soil textures (Evetts and Burnside 1972). It is most prevalent in well-drained, loamy soils and in areas with 30% to full sunlight (Berkman 1949). It propagates through wind-dispersed seeds (Bhowmik and Bandeen 1976) and asexually through its rhizomes (Taylor [date unknown]).

Site selection

In the summers of 1943 and 1944, Groh and Dore (1945) traveled by car and train across Ontario and a small portion of southern Quebec, to survey common milkweed presence and density along entire roadsides and field stands (Figure 1). We use only their surveys of roadside stands in this study. They did so by visual estimation based on prior systematic counts of representative roadside stands and assigned sites to five density grades (Appendix A.; Groh and Dore 1945: Table 1). It is unclear from their study how many roadsides were surveyed to determine the density grades. In total, they estimated milkweed density in 23 counties across southern Ontario. They counted all stalks in a roadside strip (Figure 1(b)) and kept track of the transect length, but not width, which varied. They then kept track of the estimated milkweed density category along each segment of all roads they travelled by writing on National Topographic Series maps. Unfortunately, these maps were not stored in the archives of the National Collection of Vascular Plants of Agriculture and Agrifood Canada, which houses other notes from Groh and Dore's research.

To assess changes in milkweed population in roadsides since then, we measured milkweed abundance along roadsides in the former Carleton County, which is now part of the Regional Municipality of Ottawa-Carleton (Figure 2), from July to September of 2018. We note, as Groh and Dore note in their paper, that the roads around Ottawa were the most comprehensively surveyed due to being in close proximity to their place of work. In 1943 and 1944, Carleton County (approximately 2450 km^2 (Statistics Canada 2013)), was divided into 10 townships. We maintained these borders and treated them like a form of cluster sampling (Wulfsohn 2010). We used a systematic uniform random sampling technique (Wulfsohn 2010) to select 10 sites in each former township at approximate equal distances

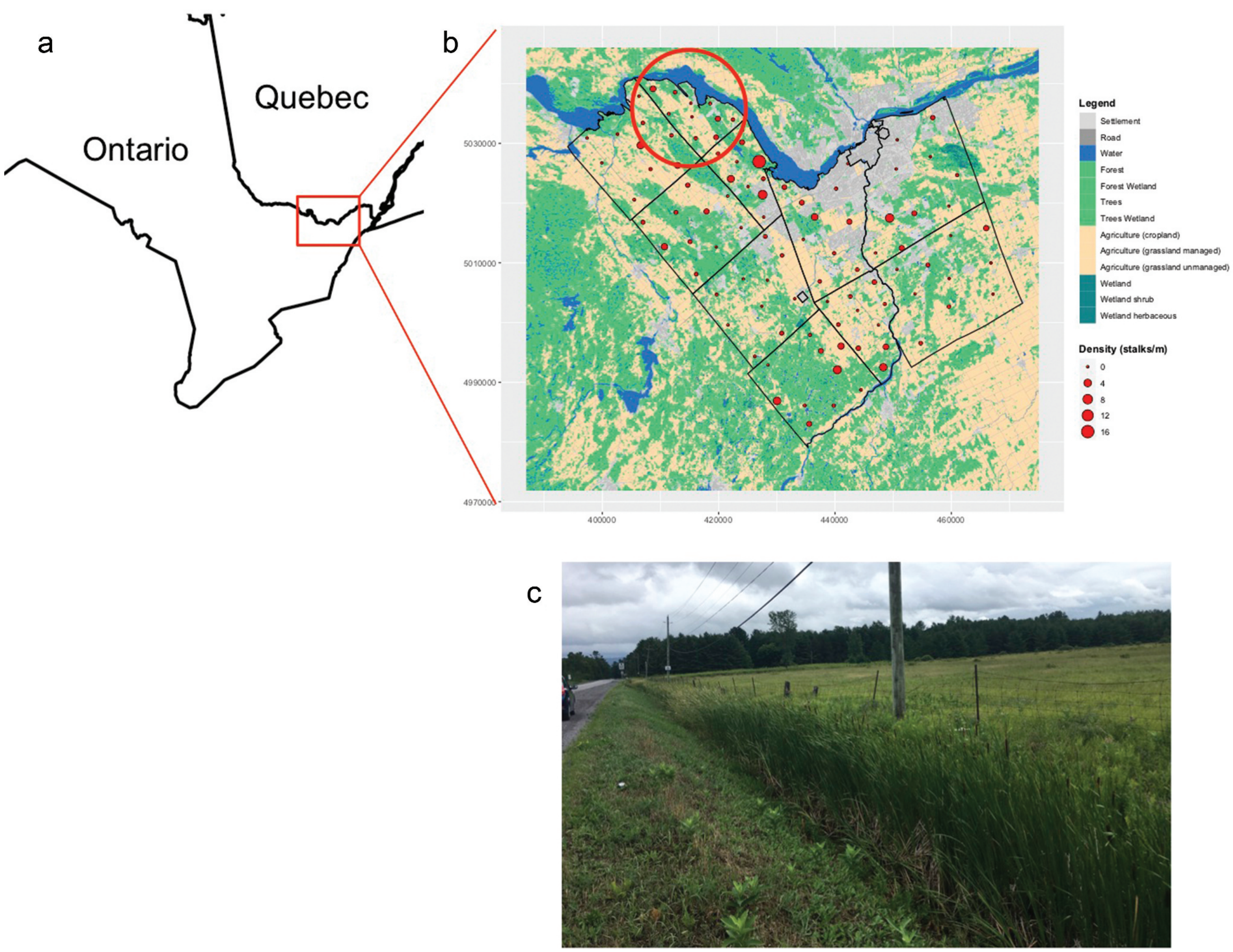

Figure 2. Roadside milkweed surveys in 2018. (a) The study region, former Carleton County, is found in Eastern Ontario and includes the Regional Municipality of Ottawa-Carleton. (b) 100 surveyed roadside sites and their respective milkweed densities (red dots; stalks/m) relative to the 1951 Census boundaries of the ten former townships of Carleton County. Shown in the background is a 2010 land use map from Agriculture and Agri-Food Canada. (c) An example of a roadside site in the former Torbolton township, Carleton County. The township is highlighted by the red circle in panel b.

(3–7 km) from each other (Figure 2(b)). Variation in distance between sites was caused by road placement.

Roads used in the 2018 survey were limited to those that were present at the time of the historical survey. To determine which roads to survey, we compared present-day roads to scanned historical road maps of the 10 townships (dates ranging from 1933 to 1943) obtained from Scholars Geoportal (http://geo2.scholarsportal.info/). We visited 100 sites, each sampled once (Figure 2(b)). Each day of site selection, we aimed to minimize the distance traveled while maximizing the number of sites visited.

Sampling technique

Before arriving at a site, we flipped a coin to decide which side of the road to survey. We did not sample sites that were not safely accessible (e.g., high traffic with small roadside, no safe place to park, private property with no one home to ask for permission). In these cases, we moved the site to the next safest location on that road and sampling occurred there instead.

Each site consisted of a 100-meter-long transect centered on the site coordinates. Similar to a study by Kasten et al. (2016), we used a continuous belt transect sampling method where the width of the transect extended from the road edge (where vegetation began growing) to an obvious outer edge barrier (e.g., fence, wooded area, agricultural field, lawn edge; Figure 2(c)). For transects adjacent to grasslands and some lawns, there was often no clear delineation of where the inner boundary should be placed. In such cases, we measured the roadside width to the telephone poles.

We recorded the total number of milkweed stalks in each transect. This species can have multiple stalks that may be ramets from a single plant (Gleason and Cronquist 1991). It is impossible to distinguish individual genets using our sampling method (Kasten et al. 2016). This species is considered to be unbranched (Minnesota Wildflower Guide (https://www.minnesotawildflowers.info/), accessed October 25 2020) but in extremely rare cases in this region (0.67% of stalks surveyed, Gilmour and Kharouba, unpubl.), a single stalk can have above-ground branching. For these individuals, we counted only a single stalk. The sampling time frame captured milkweed at a time in which it would have been fully grown, thus allowing for easier plant identification and distinction between mowed and non-mowed sites.

At each roadside site, we made seven observations to describe the disturbance level and the adjacent land-use. We recorded the number of adjacent, parallel, lanes in the road adjacent to the roadside and whether they were paved or unpaved. If there was evidence that the roadside had been mowed, we measured the width of the mowing section from the edge of the road to the end of the mowed section, and the height of the grass, which was used to approximate how long it had been since the site was last mowed (e.g., shorter grass = mowed more recently). We took representative measurements of mowed grass height at two random locations within the transect: one for grass growing at a faster rate (taller), and the other for grass growing at a slower rate (shorter). We converted mean grass height into a 'last mowed index' with four levels: 0–20 cm, 21–41 cm, 42–62 cm, > 62 cm (clearly never mowed). We visually identified the land-use of the area adjacent to the roadside transect. If a transect spanned more than one land-use type, we chose the land-use category that covered the majority of the transect. Initially, we identified eight land-use types (Table 1). We later pooled these into broader categories due to low counts of some land-use types. The three broad categories of land-use were: developed, farmland, and undeveloped (Table 1).

Statistical analysis

Historical comparison

We converted the historical county-wide estimate of 1665 stalks/mile for roadside counts in Carleton county (Groh and Dore 1945) to 1.035 stalks/m and used this value as the historical density. For each county, Groh and Dore (1945) summed their site density classifications and divided this sum by the miles of road they covered, producing an approximate county-level estimate of

Table 1. Description of broad land-use categories used in visual surveys of land use adjacent to roadside sites.

Broad land-use	Specific land-use	Frequency	Description
Developed	Residential	5	Houses, parks, lawns, sidewalks, mix of private property and public land
	Urban	9	No public roadside, parking lots, sidewalks, parks, commercial areas
Farmland	Cropland	23	Any form of crop (e.g., soy, corn, berries, fruit trees)
	Pasture	6	Fenced area with short grass regularly maintained/grazed by farm animals
Undeveloped	Grassland	22	Large natural area of undeveloped and non-cropped grasses, little to no tree cover
	Hedgerow	10	Thin strip of trees (e.g., near houses or edge of field)
	Forest edge	21	Forest directly adjacent to roadside
	Wetland	4	Natural area of undeveloped land that is inundated by water

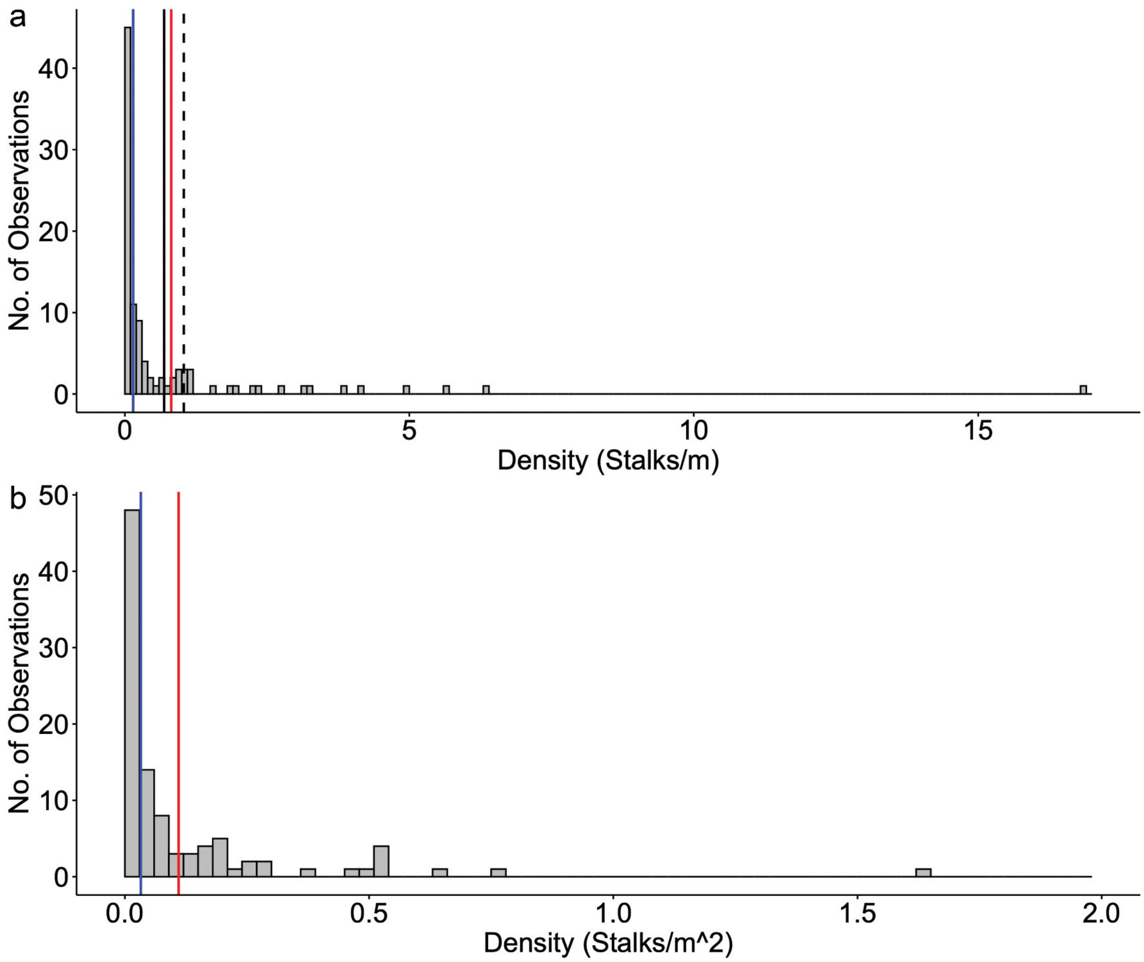

Figure 3. Distribution of roadside milkweed densities in units of stalks/m (a) and stalks/m^2 (b) across sites (n = 100). (a) From left to right, lines shown are current-day median (0.15; blue solid line), current-day weighted average (0.69; black solid line), current-day mean (0.82; red solid line), and historical baseline (1.035; black dashed line). (b) From left to right, lines shown are current-day median (0.033; blue solid line) and current-day mean (0.11; red solid line).

mean density. Based on the concepts of density they established, Groh and Dore (1945) included zeros (i.e., sites with no milkweed) in their estimates of density. As they provided no estimate of variance for the county-level estimate, we could not calculate variance around their estimate of density. To be consistent with historical survey methods, we report current-day density as plants/m length of road surveyed regardless of roadside width. However, to facilitate direct comparisons between our survey and more recent surveys, we also report current-day density as stalks/m^2 to account for varying roadside width.

To compare current-day and historical densities, we took two approaches. First, we used a two-sided one-sample sign test (BSDA package; Arnholt and Evans 2017). We used a non-parametric test because the current-day roadside milkweed density is extremely right-skewed (Shapiro-Wilk test, $W = 0.42$, $P < 0.0001$; Figure 3), and thus the median is more informative of the central tendency of the observations. Second, to better incorporate the lack of information we have about the distribution of historical densities, we calculated a mean of the current density estimates based on the same approach Groh and Dore (1945) used (i.e., a weighted average). Namely, we assigned our site-level density estimates to one of the five corresponding density grades used by Groh and Dore (1945) (Appendix A) and assigned the site an average density based on these grades (Appendix A). We then multiplied the number of sites with each of these averages, summed across five categories to get a total number of estimated stalks and then divided by the total length of our transects (10,000 m). With this mean estimate, we calculated the percentage change in density compared to the Groh and Dore (1945) estimate.

To compare how the distribution of milkweed density has changed across the Ottawa area at a broad scale, we compared current-day and historical rankings of townships. We ranked the historical townships based on their total classification of density (1000–2500; 2500–5000; 5000–1000; > 10,000 stalks/mile as per Figure 7 from Groh and Dore 1945). We note that they included densities from their roadside and field stands in their classification of townships so the change we estimate here reflects an overall change in milkweed density, and not one specific to roadsides. To facilitate a comparison, we summed our estimate of densities (stems/m) across sites to get a township-estimate of density. We compared the township rankings using a Spearman's rank correlation test.

Predictors of current-day milkweed abundance

To determine the roadside characteristics that best predict milkweed abundance (i.e., number of stalks), we analyzed the number of milkweed plants as a function of our six roadside variables. Since milkweed abundance was an overdispersed count (mean:variance = 81.6:203.6) that was also zero-inflated (33% zeros), we used zero-inflated generalized linear models (pscl package; Zeileis et al. 2008) with the negative binomial probability distribution, which has been shown to be the best approach for overdispersed count data (Welsh et al. 2000).

We began with six roadside variables: mowing (factor; mowed or not), type of road (factor; paved or unpaved), last mowed index (ordered factor; four levels), proportion of the site that had been mowed (width mowed/total transect width), the number of lanes in the road adjacent to the roadside (integer), and adjacent habitat type (factor; three levels). We also included day of year and site area as covariates. We included day of year to account for potential differences in the detection of stems over the season due to mowing (i.e., recently mown milkweed stalks with no leaves can blend in with other vegetation) and to better assess the likelihood of mowing frequency (later in the season there is a higher likelihood of greater mowing frequency). We assessed collinearity using variance inflation factors (i.e., correlated if VIF > 5; James et al. 2017) from the car package (Fox and Weisberg 2019). Due to large differences in the scales of our continuous predictor variables, we standardized continuous predictors by subtracting the mean and dividing by the standard deviation.

Model selection followed a backward step-wise approach based on AIC (i.e., Δ AIC > 2; Burnham and Anderson 1998) with the final models being those that were the most parsimonious (i.e., lowest AIC). Using the package DHARMa in R, we validated final models by visually assessing scaled residual plots (Hartig 2019). DHARMa uses a simulation-based approach to produce scaled residuals (between 0 and 1) that are readily interpretable for generalized models (Hartig 2019). We assessed the relative importance of each of the variables retained in the final model based on the difference in AIC with and without the predictor, and by using a χ^2 test. We evaluated the influence of an outlier site (stalk count = 1686) on our results by comparing the final model with and without this site included. All statistical analyses were performed in R 3.5.2 (R Core Team 2018).

Results

Current-day milkweed surveys

The total number of milkweed stalks we counted across all 100 sites was 8157. Milkweed was present at 67 of the 100 sites surveyed (Figure 2). Density across all sites ranged from 0 to 16.86 stalks/m with a mean and median of 0.82 (0.20 SE) and 0.15 stalks/m (95% CI: 0.057, 0.23), respectively (Figure 3). The largest portion (47%) of sites hosted low milkweed density (0.01–1 stalks/m; Figure 2). When only considering sites with milkweed present, median density was 0.37 stalks/m (95% CI: 0.23, 0.79; mean = 1.22 stalks/m (0.24 SE), n = 67). Mean and median stalk density based on site area was 0.11 (0.022SE) and 0.033 stalks/m^2, respectively. There was some spatial clustering of higher density milkweed in the northwestern and southeastern regions of the Greater Ottawa area (Figure 2).

Undeveloped habitat was the most common habitat observed adjacent to the roadside sites (58% of total), with 29% of sites being classified as farmland and 13% classified as developed. 82% of roadsides were mowed to some extent, with the proportion of the total site mowed ranging from 11 to 100% (mean = 60% ± 0.03 SE). Sites were most often adjacent to two-lane roads (93% of the time).

Historical comparison

In 1943 and 1944, milkweed roadside density in Carleton County was 1.035 stalks/m (Groh and Dore 1945; Figure 3). Median density in 2018 (0.15 stalks/m (95% CI: 0.057, 0.23; s = 20, P< 0.0001, n = 100) was 86% (95% CI: 78–94%) lower than in 1943 and 1944 (Figure 3). Using Groh and Dore's (1945) weighted mean approach, mean density in 2018 was 0.69 stalks/m, which represents a 33% decline compared to 1943 and 1944 (Figure 3).

Historical and current-day rankings of township density were not correlated (rho = 0.37, s = 104.2, P = 0.3, n = 10).

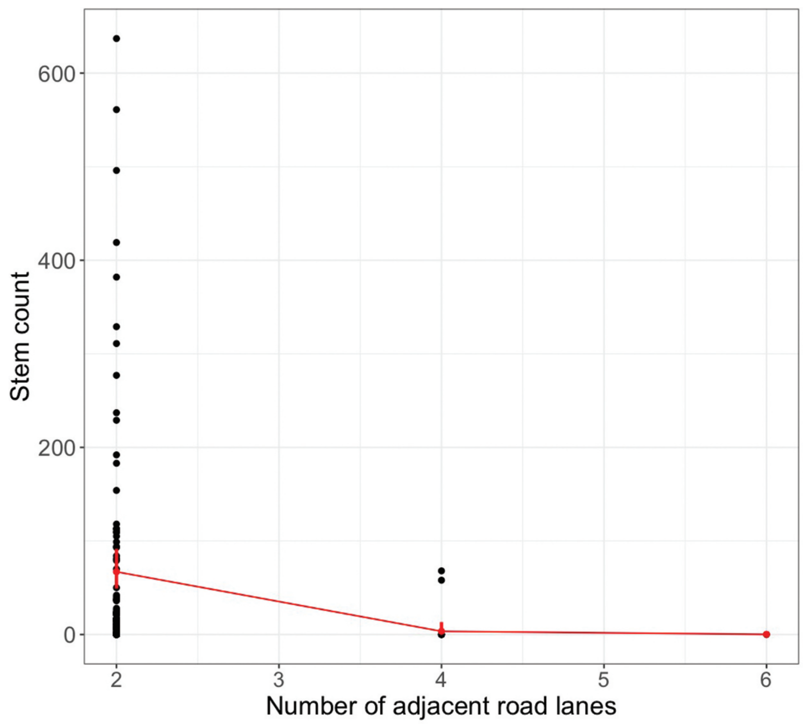

Figure 4. Relationship between milkweed abundance and the number of lanes in the road adjacent to the roadside (n = 99). The solid line represents the best-fit line (on log scale: y = −1.49x−7.18) based on the full zero-inflated negative binomial model fit in Table 2 where all other covariates were held constant and the predicted values are conditioned on the fixed effects only. The error bars represent 95% confidence intervals. The outlier (a two-lane site with 1686 stems) was removed to aid visual interpretation of relationship. There were 93 two-lane, 6 four-lane and 1 six-lane road sites.

Predictors of milkweed abundance

The final model included three predictors: number of lanes in the road adjacent to the roadside, day of year and site area. The number of lanes in the road adjacent to the roadside was the only roadside characteristic with an effect on milkweed abundance (Table 2; Figure 4). Milkweed abundance was higher in sites with fewer lanes in the road adjacent to the roadside (on log scale: $\beta = -1.49$ (0.35SE), Δ AIC = 5.5; Table 2; Figure 4): 1 unit decrease in the number of lanes in the road adjacent to the roadside is expected to increase milkweed abundance by 78%. The effect of road lanes was not affected by the removal of the outlier (Table 2). Site area had a positive effect (on log scale: $\beta = 0.93$ (0.18SE), Δ AIC = 26.7; Table 2) on milkweed abundance, and therefore density (i.e., larger roadsides have greater density). Day of year had a negative effect (on log scale: $\beta = -0.41$ (0.2SE), Δ AIC = 3.8) on milkweed abundance in roadsides (Table 2).

Discussion

Our results suggest there has been a 33–86% decline in milkweed density along roadsides in the Ottawa region over the past 75 years. This decline is not surprising given the trends observed in the U.S. There was a 81% decline in milkweed abundance in agricultural lands in the Midwest from 1999 to 2010 (Pleasants and Oberhauser 2013) and a 68% loss of milkweed across Illinois croplands over the last 20 years (Zaya et al. 2017). Our high-end estimate of decline (86%) is greater than previous studies. This could reflect differences in initial densities between roadsides and agricultural lands or a greater initial density of roadside milkweed given that Groh and Dore's surveys in the early 1940s were done well before the consolidation of small farms and the industrialization of farming, with its rapid increase of herbicide use, in the 1950s and 1960s, and the introduction of glysophate in the 1990s (Timmons 2005). Roadside milkweed may have declined from herbicide sprayed directly for road maintenance or by drift from nearby crop fields (Marrs et al. 1989; Olszyk et al. 2015; Bernes et al. 2017). At the other end of the range of estimated decline, our low-end estimate of decline (33%) is still greater than a previous estimate of decline from roadsides alone (Hartzler 2010: no decline in number of patches in Iowa from 1999–2009).

We also found that the spatial distribution of milkweed density has changed across the Ottawa area, such that some high-density townships are no longer high

Table 2. Results of zero-inflated negative binomial model predicting milkweed abundance with (n = 100 sites) and without outlier site (stalk count = 1686; n = 99 sites). Model terms are listed in order of decreasing influence as measured by the difference in AIC between the full model and a model without the variable. Note that the estimates and standard error are given on the log scale.

	Estimate	SE	df	Δ AIC	X^2	P
Full model			6	0		
-Site area	0.93	0.18	1	26.7	26.4	< 0.0001
-Road lanes	−1.49	0.35	1	5.5	18.05	<0.0001
-Day of year	−0.41	0.17	1	3.8	6.1	0.013
Full model without outlier			6	0		
-Site area	0.81	0.20	1	18.3	17.5	< 0.0001
-Road lanes	−1.38	0.37	1	4.34	14.1	0.0001
-Day of year	−0.41	0.16	1	4.31	6.8	0.009

density, or low-density townships are no longer low. This suggests there has been a spatial shift where milkweed is most abundant and could reflect broader scale land-use changes, like urbanization or agricultural intensification in the area. For example, the total built-up area around Ottawa has increased by 263% from 1971–2011 (737 km^2; census metropolitan area-ecosystem; Statistics Canada 2016) and most of the growth has been via suburbanization (Zhang et al. 2010). However, given that the historical township-level estimates of milkweed abundance incorporated both roadside and field stands, it is unclear which type of land-use change is likely to have been more influential.

Our estimates of current milkweed density in the Ottawa area (mean = 0.11 (0.022SE), median = 0.033 stalks/m^2, when all sites were included) are in the range of recent surveys of common milkweed densities from roadsides in the U.S. They are higher than surveys in the Upper Midwestern U.S. (median = 0.0036 plants/m^2: Kasten et al. 2016) but lower than surveys from Iowa, U.S. (median = 0.1 stems/m^2: Kaul and Wilsey 2019). Our estimate is also lower than a recent survey done in southwestern Ontario (mean = 1.9 (1.1 SD); Pitman et al. 2018). The disparity could be related to sample size (n = 100 vs. n = 9; Pitman et al. 2018), the variation in types of roadsides we visited or other differences between the areas (e.g., climate). Nevertheless, additional estimates of milkweed density are needed to help guide restoration efforts and provide a baseline for future studies.

The number of lanes in the road adjacent to the roadside was a significant predictor of milkweed density. More road lanes were associated with lower milkweed abundance in roadside sites. This is likely because the number of lanes integrates many factors (e.g., usage frequency, traffic volume, herbicide applications (Bernes et al. 2017; Khalid et al. 2018; Zhou et al. 2020). To our knowledge, no one else has tested the influence of number of road lanes on milkweed density. However, related work shows that greater traffic volume can decrease the nutritional quality of milkweed (Mitchell et al. 2020). Declines in milkweed have already been strongly linked to the application of glyphosate herbicides in croplands (Hartzler 2010; Pleasants and Oberhauser 2013; Flockhart et al. 2015). While our results suggest that we need to consider the effect of the size of our roadways on milkweed abundance, we caution that the low number of sites we had adjacent to larger roads and the large variation in stem counts we observed adjacent to smaller roads (Figure 4) could limit our ability to accurately predict milkweed abundance alongside smaller roads especially.

With the exception of number of lanes in the road adjacent to the roadside, milkweed abundance was not well predicted by the proxies of roadside management and surrounding land cover that we measured. This is consistent with recent work in the U.S. that found mowing regimes did not predict milkweed density (Kaul and Wilsey 2019) or age structure (Dee and Baum 2019). However, mowing has been shown to spur milkweed regrowth if timed appropriately (Bhowmik and Bandeen 1976; Bhowmik 1994; Baum and Mueller 2015; Fischer et al. 2015; Zalai et al. 2017) and affect milkweed growth structure (Dee and Baum 2019). Although not measured here directly, mowing frequency may influence milkweed abundance. Indeed, there was a decline in milkweed abundance as the season progressed which may be linked to mowing frequency, as milkweed are exposed to more mowing visits by the end of the season (Daniels et al. 2018). Mowing too frequently can impact successful plant growth, reproduction, seed dispersal, and population persistence and expansion (Baum and Sharber 2012; Daniels et al. 2018; Dee et al. 2018). However, since common milkweed is considered a disturbance-tolerant species, mowing infrequently may benefit milkweed populations by reducing competitors and promoting clonal reproduction (Bhowmik and Bandeen 1976; Daniels et al. 2018). In any case, measuring more direct aspects of human disturbance like mowing frequency will help determine how best to manage roadsides to preserve milkweed populations.

While this study is a good first step towards quantifying temporal changes in milkweed density in Ontario and provides evidence of roadside effects on milkweed densities, our ability to infer the extent of historical change is limited. As is always the case with historical data, there were some constraints to working with the data from Groh and Dore (1945). The sampling methods and sites from the historical survey could not be fully reproduced. Given that no measure of variance was given with their estimate of density, and frequency distributions of the data were not shown, it is uncertain whether the historical data was normally distributed. If the distribution of density was skewed as it was in 2018, then it is not clear how well the estimate of density they report (the mean) was indicative of the central tendency of their data, and thus our high-end estimate of decline may be an overestimate. Consequently, we report that the true decline is likely between 33–86% and report uncertainty intervals along with our high-end estimate of the decline. Groh and Dore (1945) also travelled across Ontario by car and train and, in the Ottawa region, were able to cover nearly every road at the time. They reported a single estimate of density for the entire county, which combined estimates from their car and train surveys. Because we did not revisit sites that were likely visited by train in 1943 and 1944, we may be overestimating the amount of decline that has occurred if sites along railroads have been less affected by human activities. However, much of the old railroad network around Ottawa has been converted to roads limiting our overestimate of the decline.

Conclusion

The loss of milkweed as a threat to monarchs that breed in Canada has mostly been inferred from U.S. studies. Here we document the first quantitative evidence that this decline is also happening in Canada. While there has been a substantial decline in milkweed density along roadsides in the Ottawa region, common milkweed still occurred in 67% of the roadside sites we surveyed, potentially providing breeding habitat for monarchs (Hopwood 2010; Zalucki and Lammers 2010; Daniels et al. 2018; Kaul and Wilsey 2019; Knight et al. 2019).Future studies should expand the resurveys beyond Ottawa, extend the survey area to include non-roadside habitats as a reference, and measure the frequency of mowing.

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Appendix A.

Density grades used in the estimation of historical and current stem density of roadsides. Reproduced from Table 1 from Groh and Dore (1945)

Density grades	Range (stalks per mile)	Range (stalks per meter)	Average (stalks per mile)	Average (stalks per meter)
Absent	0–50	0–0.031	0	0
Poor	50–700	0.031–0.43	300	0.19
Sparse	700–3000	0.43–1.86	1500	0.93
Medium	3000–8000	1.86–4.97	5000	3.11
Good	>80,000	>4.97	10,000	6.21