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RESEARCH ARTICLE

Traffic patterns, more than adjacent land use, influence element content of roadside forbs for insect pollinators

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Abstract

1. Roadsides are targeted for restoration of pollinator-friendly plants. Yet, roads are sources of macronutrient, micronutrient and heavy metal pollution that may contaminate roadside plants. Adjacent landscape features such as railroads and agriculture provide additional macronutrient and heavy metal pollution that may exacerbate traffic effects. However, we lack perspective on how roads combine with rural landscape features to influence nutrition of roadside plants, which could have implications for pollinator health.
2. We surveyed roadsides across Minnesota, USA and measured foliar levels of dietary macronutrients (nitrogen, phosphorous and potassium), a micronutrient (sodium) and metals (iron, zinc, copper, chromium, nickel, lead, aluminium and cadmium) in six abundant roadside forb species used by insect pollinators: *Asclepias syriaca*, *Dalea purpurea*, *Monarda fistulosa*, *Ratibida pinnata*, *Solidago* spp. and *Trifolium pratense*. We aimed to determine (1) how road variables (traffic volume and distance from road) combine with adjacent land use (railroad and agriculture) to influence element content of roadside forbs and (2) whether some forb species show consistent differences in their accumulation of potentially toxic heavy metals, which could inform selection of species to plant along roadsides.
3. We found that foliar concentrations of nine elements increased with greater traffic volume (nitrogen, phosphorous, iron, zinc, copper, chromium, nickel, lead and aluminium), and concentrations of six elements declined with distance from the road (nitrogen, phosphorous, potassium, iron, zinc and copper). Leaves collected adjacent to railroad had less phosphorous, potassium, iron, nickel and aluminium than leaves collected from sites not adjacent to railroad. Additionally, leaves collected from sites adjacent to agriculture had lower copper levels than leaves from sites without adjacent agriculture. We found no evidence that particular ford species along roadsides consistently rank higher than other species in their accumulation of heavy metals.

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4. Our results show that traffic alters more elements in roadside plants than does adjacent landscape context, alleviating concerns that landscape features exacerbate pollutant levels in roadside pollinator habitat. However, nutrient contamination of most roadside plants is unlikely to reach toxic levels for insect pollinators. This work is consistent with the positive conservation potential of low to moderate traffic roadsides for pollinators.

KEYWORDS
forb, heavy metals, herbivory, macronutrients, micronutrients, pollinator, right-of-way, roadside

1 | INTRODUCTION

Road networks dominate modern landscapes and have a major influence on ecological processes (Coffin, 2007; Spellerberg, 1998). In the United States alone, there are over 6.55 million kilometres of roadways (U.S. Department of Transportation, 2012). Roads influence the distribution and movement of many elements and have major impacts on nutrient cycles. For instance, atmospheric nitrogen deposition from vehicle exhaust can account for up to 15 kg/N/ha/year along roadsides (Cape et al., 2004; Spencer et al., 1988), with significant effects on plant uptake and nitrogen cycling, especially in urban areas (Fenn et al., 2018). Elevated nitrogen in roadside plants influences growth of insects feeding on these plants (Spencer et al., 1988). Additionally, sodium from road salt as well as essential metals (e.g. zinc, copper and iron) and non-essential metals (e.g. lead and cadmium) from vehicle wear-and-tear can accumulate in roadside soils, plants and animals (Lagerwerff & Specht, 1970; Lancaster & Beutel, 2011; Mitchell et al., 2020). For example, winter road salting increases the sodium content of both roadside milkweed and monarch caterpillar consumers (Mitchell et al., 2020).

Despite known effects of roads on ecological chemistry (Werkenthin et al., 2014), we lack a broader perspective on the extent to which roads combine with other anthropogenic landscape features (e.g. agriculture) to influence chemical movement and accumulation by plants. Chemical inputs from adjacent land uses may exacerbate effects of roads on both roadside plants and their consumers. For instance, agriculture may increase nitrogen or heavy metal supply through the use of sewage sludge as fertilizer (Alloway & Jackson, 1991; Smith, 2009) or metal-containing agrochemicals (Wolz et al., 2003). Many roadways also run parallel to railroads, which can be additional sources of heavy metal input (Chen et al., 2014; Liu et al., 2009). It is possible that landscape context, particularly in rural areas, could explain variation in plant element content more strongly than roads themselves (Frati et al., 2006); however, the extent to which roads in differing landscape contexts affect plant content of macronutrients, micronutrients and heavy metals is poorly characterized.

Given increasing attention to roadsides as habitat for native pollinators (including both herbivorous Lepidoptera larvae and nectivorous adult pollinators), understanding how roads and associated landscape features combine to influence the chemistry of the plants they consume is critical for conservation success (McCleery et al., 2015; Ries et al., 2001), especially for butterflies and moths (Ries et al., 2001; Saarinen et al., 2005; Valtonen et al., 2007). For instance, elevated supply of critical nutrients for herbivores, such as nitrogen and sodium, can attract animals to roadsides (Kaspari et al., 2010; Port & Thompson, 1980; Snell-Rood et al., 2014; Spencer et al., 1988), and elevated nitrogen and sodium might be particularly attractive to insects when available in combination (Borer et al., 2019). However, when present at high concentrations in plants, these elements can be toxic for consumers. For example, host plants in agricultural areas can accumulate nitrogen at levels high enough to reduce butterfly survival (Kurze et al., 2018). Sodium concentrations in roadside milkweed occasionally reach levels that are toxic for monarch butterflies (Mitchell et al., 2020), but monarchs do not avoid laying eggs on plants with toxic sodium levels (Mitchell et al., 2019). Additionally, many potentially toxic heavy metals are elevated in roadside soil, plants and animals (Ho & Tai, 1988; Lagerwerff and Specht, 1970). For example, lead levels in grasses adjacent to high traffic roads (>25,000 vehicles/day) can reach >400 ppm (Ho & Tai, 1988; Werkenthin et al., 2014), well above levels that are toxic to larval moths (Coleman et al., 2005).

Here, we take a field approach to assess foliar element content of six forb species that serve as food sources in roadside habitats for leaf-feeding insect pollinators (e.g. larval butterflies and moths). We surveyed roadside sites across Minnesota, USA and collected leaf tissue samples from six forb species: common milkweed (*Asclepias syriaca*), purple prairie clover (*Dalea purpurea*), wild bergamot (*Monarda fistulosa*), yellow coneflower (*Ratibida pinnata*), goldenrod (*Solidago* spp.) and red clover (*Trifolium pratense*). We chose these plants as they are common plants in roadside restorations in Minnesota that are also important nectar plants for native bees (including the Rusty-patched Bumblebee, *Bombus affinis*) and host plants for native butterflies (including the declining monarch [*Danaus plexippus*] and Northern Blue [*Lycaeides idas*], and other native butterflies common along roadsides, such as *Chlosyne nycteis*, *Phyciodes tharos* and *Cupido comyntas*). We quantified leaf element content of macronutrients (nitrogen, phosphorous and potassium), a micronutrient (sodium) and a range of potentially toxic heavy metals (iron, zinc, copper, chromium, nickel, cadmium, lead and aluminium). These elements were chosen because

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previous evidence has shown that they can be elevated near roadsides (Cape et al., 2004), railroads (Chen et al., 2014) or agricultural areas (Alloway & Jackson, 1991). Most research assessing element content of roadside plants has focused on lichens and mosses (Frati et al., 2006; Watmough et al., 2017), grasses (Ho & Tai, 1988), trees (Voegborlo & Chirgawi, 2008) or plant samples pooled across species. However, herbaceous forbs are essential food plants for many leaf-feeding butterfly and moth larvae. Understanding how roads affect chemical content of leaf tissue across forb species is crucial for conservation and management of roadsides as pollinator habitat. Additionally, plants vary significantly with respect to heavy metal accumulation (Watanabe et al., 2007), which occurs either by physiological uptake through roots (Krämer, 2010; Verbruggen et al., 2009) or accumulation of dust (Gajbhiye et al., 2016; Thompson et al., 1984). Therefore, to gain a complete understanding of the diet experienced by consumers, we conducted all analyses on unwashed leaf tissue to capture both uptake and dust accumulation.

We focused on the question of how roads combine with adjacent railroad and agriculture to influence foliar nutritional quality of roadside plants for leaf-feeding insect pollinators. While the quality of roadside foliage could of course be affected by other types of contaminants (e.g. agricultural pesticides), our study uses an elemental approach to focus on nutrient and metal contaminants from traffic, railroads and agriculture. For instance, roads, railroads and agriculture are well-documented sources of heavy metal pollution (Fergusson et al., 1980; Wolz et al., 2003). Roads and agriculture are known for elevated macronutrient supply (Cape et al., 2004, Spencer et al., 1988). Salts are directly applied to roads in regions with winter snow and ice (Novotny et al., 2009), and previous research indicates that larger salt quantities are applied to roads that are used more frequently (Sander et al., 2007). Therefore, we tested two hypotheses. First, we hypothesized that all foliar macronutrients, micronutrients and heavy metals considered would increase with daily traffic volume and proximity to a road edge. Second, we hypothesized that heavy metal content would be elevated in leaf tissue sampled from roadside sites adjacent to both railroad and agriculture but that macronutrients would be elevated in tissue samples collected from sites adjacent to agriculture but not railroad, as fertilizers are not applied to railroads. Understanding how roads combine with adjacent landscape features to affect roadside plant nutrition would help managers decide which sites to prioritize for restoration when funds are limited. To test the generality of these hypotheses, we considered six roadside forb species (five native species) that are common in roadside restorations in the upper Midwest.

2 | MATERIALS AND METHODS

2.1 | Sampling sites

We sampled 55 roadside sites in Minnesota, USA. We focused on a broad geographic area (~48,200 km^2) but sought replication of each factor of concern within geographic regions (e.g. areas surrounding Alexandria, Marshall, Rochester, Minneapolis/St. Paul and Wilmar, MN). To increase the likelihood of finding our target forb species, we focused some of our site search within areas of quality native vegetation and past roadside native reseeding, based on discussions with the Minnesota Department of Transportation and the Minnesota Department of Natural Resources. In each case, agency information was used to identify a focal area, then roadsides representing each focal category were identified within the area. We excluded sampling from forested biomes of north-eastern Minnesota, as our target forbs were most common in the deciduous and prairie biomes of Minnesota. We then identified roadside areas within each region in a fully factorial manner based on traffic volume (low or high), adjacent railroad (present or absent) and adjacent agriculture (present or absent). We excluded all sites adjacent to commercial or residential areas. We chose sites to ensure that all combinations of factors were replicated within an area and that sites were separated by at least a mile. Given these criteria, we were most limited in identifying sites with adjacent railroad and high traffic, whereas sites with low traffic and adjacent agriculture were common in this region. Out of all locations that met these criteria, we randomly selected sites from which to sample. We sampled sites across categories to ensure replicate sampling across all possible combinations of traffic volume and adjacent land use. However, we analysed roadside variables using exact (continuous) measures (see Section 2.4). For each site, we sampled 1- to 10-km sections of target roadside; the length varied depending on the search for our target species (i.e. sampling stopped at 1 km if we had found enough replicates of all species). We held a Minnesota Department of Transportation permit for 'Miscellaneous work on trunk highway right of way' to conduct this sampling (Permit number: 3B US 2017 76667).

Low traffic volume sites were defined as <2000 vehicles/day, and high traffic volume sites were defined as >6000 vehicles/day. We sampled sites using traffic categories to ensure balanced sampling across the factors of interest and to ensure sampling of the most common roads in the state (<2000 vehicles/day) and those of most conservation concern (e.g. along higher traffic highways with larger right of ways). Sites in low (annual average of 1328 vehicles/day) and high (14,250 vehicles/day) traffic volume categories differed by an order of magnitude, but on our final analyses, traffic was treated as a continuous variable. Traffic volume of each site was determined using online mapping data from the Minnesota Department of Transportation (2020). Presence of adjacent railroad and agriculture at each site was determined using GIS and then confirmed in person, and we estimated adjacent rail corridors to be, on average, 15–20 m from the edge of the sampling site (hence, 30–40 m from the road edge). All sites were adjacent to paved (rather than gravel) roads and provided safe and legal access. We focused our sampling along roads with <40,000 cars each day for several reasons. First, to construct sets of roughly matched sites that varied in adjacent railroad and agriculture, we were primarily limited to more rural areas. Second, we sought to avoid roadsides with unsafe access and residential management. Finally, the majority (>75%) of roadsides in Minnesota and the United States are rural roads, and thus the targets of roadside restoration are often rural highways (National Research Council, 2005).

Sampling occurred from mid-June to late August 2018 and was performed each week in 1- to 4-day periods. At the end of a sampling period, plant samples were returned to the laboratory. We sampled

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from each site only once. However, we sampled from sites within each of the five broader geographical regions during both early summer (mid-June to mid-July) and late summer (mid-July to late August). Sites were not sampled during rain and only two (of 55) sites were sampled within 24 h of rain. A map of all sites is included in Supporting Information (Figure S1).

2.2 | Sampling protocol

At each site, we targeted six prairie plant species that are common along Minnesota roadsides and are commonly used by pollinators: common milkweed (*Asclepias syriaca*), purple prairie clover (*Dalea purpurea*), wild bergamot (*Monarda fistulosa*), yellow coneflower (*Ratibida pinnata*), goldenrod (*Solidago* spp.) and red clover (*Trifolium pratense*). We focused on native plants, as most roadside restoration efforts stress the importance of native communities. However, we included one non-native species (red clover) that is common along roadsides and serves as both a nectar (adult pollinator) and foliar (larval pollinator) resource. For goldenrod sampling, we targeted species in the Canada Goldenrod Complex, which was most abundant along roadsides. This complex consists of three morphologically similar species that can hybridize: Canada Goldenrod (*S. canadensis*), Tall Goldenrod (*S. altissima*) and Giant Goldenrod (*S. gigantea*).

Upon arrival at each site (c. 1-10 km), we drove along the section of roadside that fit the designated characteristics (traffic volume, rail, agriculture) to search for each of the six species and marked areas where each species was observed. After this initial search period, we returned to marked areas to collect plant samples. On average, 2.4 species were observed at each site (65%, 44%, 25%, 20%, 42% and 38% of the sites contained milkweed, purple prairie clover, bergamot, yellow coneflower, goldenrod and red clover, respectively). We sampled plants that appeared healthy (i.e. free of fungus, rust or insect infestation) and were large enough to provide sufficient leaf tissue for chemical analyses (e.g. at least four pairs of leaves for milkweed). At each site, we sampled one plant of each species from each of three bands in a roadside easement: 0–6 m from the road edge, 6–12 m and 12–18 m. We chose these bands because metal contamination has been observed to drop off with distance to the source origin (Werkenthin et al., 2014), and because most rights-of-way we were sampling were no more than 18–20 m in width, and we wished to sample evenly across the area. For wider than average roads, we sampled into a fourth band (up to 24 m); 24 m was our maximum sampling width as wider roadsides likely encompass private property given the general right-of-way width of 75′ from the centre of the road (MnDOT, 2018). We measured the exact distance of each plant from the road to ensure that distance from road could be included as a continuous variable in our analysis, but used the band approach to ensure we sampled across the gradient. We also recorded whether each collected plant sample was blooming. There were enough milkweed plants that we restricted leaf tissue collections to non-blooming milkweed plants to avoid 'blooming' as an additional variable in analyses. For the other five forb species, plants were not abundant enough to sample only non-blooming plants.

We harvested above-ground biomass of each plant and stored each sample individually in plant drying presses until delivery to the laboratory at the end of each collection week. In the lab, leaf material from each plant was separated from stems and flower and dried thoroughly in paper bags at 70°C for at least 24 h. Leaf material for each individual was then transferred to coin envelopes and stored at room temperature before leaf chemistry analysis. At each site, we took one representative soil sample (in the middle of the site by width) using an AMS 401.04 7/8′ X 21″ soil probe (chrome molybdenum steel) to take the top 10 cm of soil. Soil analysis was not the primary focus of this study (but see Mitchell et al., 2020), so we limited collection to one area (the middle of the site) that would be affected by both the road runoff and adjacent land use. Soil was dried in paper bags for 3 weeks on open racks.

2.3 | Plant and soil chemistry analysis

ICP-AES and CN elemental analysis were used to determine plant leaf chemistry on samples from 185 plants ($n = 47$ milkweed, $n = 33$ purple prairie clover, $n = 19$ bergamot, $n = 18$ yellow coneflower, $n = 39$ goldenrod, $n = 29$ red clover). We performed CN elemental analysis to quantify leaf carbon and nitrogen content using a Costech CN Element Analyzer. Acetanilide was used as a standard with six standard replicates ranging from 0.5 to 3.0 mg. Two technical replicates were used per plant sample (each sample ranged from 20 to 30 mg). Samples were weighed on a microbalance to the nearest 0.0001 mg. Leaf concentrations of all other elements were determined by ICP-AES at the University of Minnesota Research Analytical Laboratory.

While our analyses focused on leaf chemistry, we ran analyses on soil chemistry for 16 sites to test two post hoc questions around adjacent railroad land use. For these analyses, we chose sites with non-agriculture adjacent land use, and either no adjacent rail ($N = 8$) or adjacent rail ($N = 8$). To quantify soil calcium and metal levels, the University of Minnesota Research Analytical Lab performed inductively coupled plasma optical emission spectroscopy (ICP-OES; Dahlquist & Knoll, 1978; Fassel & Kniseley, 1974). Soil samples were air dried, then sifted to remove roots and homogenize soil. Soil samples were microwave digested using concentrated HNO_3. The technical replicates of a certified standard of known concentration were an average of 1.54 *SD* from the mean, and the coefficient of variation for technical replicates was Na = 18.8%, Zn = 8.6%, Ni = 9.8%, Cu = 12.1%, Pb = 14.3%, Cd = 26.5%, and P = 11.5%.

2.4 | Statistical analysis

To determine the effects of traffic and adjacent landscape features on the chemical content of roadside plants, we used a linear modelling approach in R Studio version 3.5.1 (R Studio Team, 2018). We built separate models for each response variable of interest: leaf content of N, P, K, Na, Fe, Zn, Cu, Cr, Ni, Pb, and Al. First, we visually inspected response and predictor variables for normality, and we log-transformed each

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response variable and one predictor (traffic volume) to improve normality. Then, we *z*-score transformed all response variables to allow direct comparisons of effect sizes (Schielzeth, 2010). The full model for each analysis included log traffic volume, distance from road, presence of adjacent railroad, presence of adjacent agriculture and species identity as fixed effects. While we used categories of traffic volume and distance from road to ensure even sampling effort, in our analyses, we used continuous measures for these factors (total daily traffic volume and distance from road). In contrast, we focused landscape measures on categories of adjacent land use (rather than a continuous measure from google earth) because this category is more relevant for patterns of water movement that could affect element accumulation in the roadside site (e.g. land use across the street may have differed from that of a focal site, but is irrelevant for runoff given drainage patterns for the road). Species identity was included as a fixed effect in each model because we were specifically interested in understanding variation across forb species with respect to leaf heavy metal content. We excluded Cd from our analysis because nearly 50% of our plant samples contained Cd levels that were below the detectable concentration threshold for ICP-AES (limit of detection was <0.001 mg/L). Given that our sample sites occurred over a broad spatial area, we also tested for spatial autocorrelation for each model using Moran's *I* test in the DHARMa package. We detected no evidence of significant spatial autocorrelation for any of the 11 elements considered, so we did not incorporate spatial modelling into our analyses. All data are accessible via Mendeley (Shephard et al., 2022).

3 | RESULTS

3.1 | Effects of traffic features on plant element content

Busier roads had higher leaf element content for nine of the 11 elements considered (Table 1; Figure 1): N, P, Fe, Zn, Cu, Cr, Ni, Pb and Al. Traffic volume had the strongest effects on leaf content of P, Fe, Cu, Cr and Al ($ß > 0.30$). Distance from road also affected leaf content of many elements. In general, effects of distance from road on leaf element content were less pronounced than effects of traffic volume (Table 1). For six of the 11 elements considered (N, P, K, Fe, Zn, Cu), plants collected further from the road edge had lower leaf element content than plants collected closer to the road edge (Figure 2). Effects of distance from road were most pronounced for leaf content of P, Fe and Cu ($ß < -0.03$; Table 1).

3.2 | Effects of landscape features on plant element content

Effects of landscape context, specifically adjacent railroad and adjacent agriculture, were far less pronounced than effects of traffic volume or distance from a roadside. Plants from sites adjacent to agriculture had lower Cu levels than plants from sites not adjacent to agriculture (Table 1). Roadside foliage adjacent to agriculture did not contain higher levels of N and P compared to roadside foliage not adjacent to agriculture. There were significant effects of adjacent railroad presence on leaf element content for only five of the 11 elements considered (P, K, Fe, Ni, Al). In each case, plants next to railroads had lower element content than plants from non-railroad sites (Figure 3). To test whether these patterns may have been driven by erosion of limestone track ballast altering soil chemistry, we tested the element content of 16 soil samples collected from sites without adjacent agriculture that varied in railroad presence. Soil collected from roadsides with adjacent rail had lower iron, nickel and aluminium, but not calcium, phosphorus or potassium (Table 4).

3.3 | Variation in plant species responses to road features

The foliage of forb species differed in all 11 elements considered (Table 1). However, despite these differences, there was no clear evidence that some forb species consistently ranked higher than other species in terms of foliar heavy metal content (Table 2). For example, *R. pinnata* leaves contained the highest zinc concentrations of all species, but the lowest nickel concentrations (Table 2).

4 | DISCUSSION

Roadsides provide crucial habitat for insect pollinators such as bees and butterflies, but roadways are also major sources of macronutrient, micronutrient and heavy metal pollution that can be detrimental to pollinator health (Phillips et al., 2020). The primary aim of this study was to test how traffic variables and associated landscape features (i.e. railroad and agriculture presence) combine to influence the element content of a range of native forb species that are abundant along roadsides and are widely consumed by insect pollinators. To test the generality of these findings for roadside plantings for pollinators, we included six forb species in the study that are common in roadside restorations in the Upper Midwest. We found that the volume of traffic and the presence of railroad and agriculture all affected leaf chemistry of roadside forbs, but traffic volume altered more elements in roadside forbs than adjacent railroad or agriculture (Table 1). Additionally, we found no evidence that some forb species consistently accumulate greater levels of potentially toxic heavy metals than other species along roadsides (Table 2).

Vehicle traffic clearly affects plant chemistry with macronutrients and metals decreasing with distance from road edge, and sodium and metals increasing with traffic volume. Previous studies have documented similarly elevated levels of N (Cape et al., 2004) and P (Power & Collins, 2010) in roadside plants. Vehicle traffic and agriculture are well-known sources of particulate matter rich in N and P (Khalid et al., 2018; Lohse et al., 2008). Our results support the idea that roadside vegetation may act as a catchment of macronutrients, which are limiting for herbivores and may attract insects to roadsides

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TABLE 1 Summary of linear models testing for effects of traffic volume, distance from road, presence of adjacent railroad, presence of adjacent agriculture and forb species on leaf content of eleven roadside chemical pollutants

	Traffic volume	Distance from road	Railroad	Agriculture	Species
Nitrogen	$\mathbf{F_{1,171} = 6.24}$	$\mathbf{F_{1,171} = 4.47}$	$F_{1,171} = 0.91$	$F_{1,171} = 1.77$	$\mathbf{F_{5,171} = 46.58}$
	$\boldsymbol{\beta = 0.18}$	$\boldsymbol{\beta = -0.022}$	NR > RR	NA > A	$\boldsymbol{p < 0.0001}$
	$\boldsymbol{p = 0.013}$	$\boldsymbol{p = 0.036}$	$p = 0.34$	$p = 0.18$	
Phosphorous	$\mathbf{F_{1,175} = 36.97}$	$\mathbf{F_{1,175} = 8.50}$	$\mathbf{F_{1,175} = 35.03}$	$F_{1,175} = 1.90$	$\mathbf{F_{5,175} = 35.32}$
	$\boldsymbol{\beta = 0.44}$	$\boldsymbol{\beta = -0.030}$	**NR > RR**	NA > A	$\boldsymbol{p < 0.0001}$
	$\boldsymbol{p < 0.0001}$	$\boldsymbol{p = 0.001}$	$\boldsymbol{p < 0.0001}$	$p = 0.17$	
Potassium	$F_{1,175} = 1.38$	$\mathbf{F_{1,175} = 4.35}$	$\mathbf{F_{1,175} = 8.79}$	$F_{1,175} = 0.85$	$\mathbf{F_{5,175} = 31.60}$
	$\beta = 0.095$	$\boldsymbol{\beta = -0.024}$	**NR > RR**	NA > A	$\boldsymbol{p < 0.0001}$
	$p = 0.24$	$\boldsymbol{p = 0.038}$	$\boldsymbol{p = 0.0034}$	$p = 0.36$	
Sodium	$F_{1,175} = 3.44$	$F_{1,175} = 2.73$	$F_{1,175} = 2.49$	$F_{1,175} = 0.0058$	$\mathbf{F_{5,175} = 12.39}$
	$\beta = 0.18$	$\beta = -0.023$	NR > RR	NA > A	$\boldsymbol{p < 0.0001}$
	$p = 0.065$	$p = 0.10$	$p = 0.12$	$p = 0.94$	
Iron	$\mathbf{F_{1,175} = 73.43}$	$\mathbf{F_{1,175} = 8.76}$	$\mathbf{F_{1,175} = 18.96}$	$F_{1,175} = 1.88$	$\mathbf{F_{5,175} = 4.82}$
	$\boldsymbol{\beta = 0.75}$	$\boldsymbol{\beta = -0.038}$	**NR > RR**	A > NA	$\boldsymbol{p = 0.0004}$
	$\boldsymbol{p < 0.0001}$	$\boldsymbol{p = 0.0035}$	$\boldsymbol{p < 0.0001}$	$p = 0.17$	
Zinc	$\mathbf{F_{1,175} = 6.51}$	$\mathbf{F_{1,175} = 5.98}$	$F_{1,175} = 01.18$	$F_{1,175} = 0.72$	$\mathbf{F_{5,175} = 33.12}$
	$\boldsymbol{\beta = 0.20}$	$\boldsymbol{\beta = -0.028}$	NR > RR	NA > A	$\boldsymbol{p < 0.0001}$
	$\boldsymbol{p = 0.011}$	$\boldsymbol{p = 0.015}$	$p = 0.28$	$p = 0.39$	
Copper	$\mathbf{F_{1,175} = 11.77}$	$\mathbf{F_{1,175} = 10.10}$	$F_{1,175} = 2.14$	$\mathbf{F_{1,175} = 4.16}$	$\mathbf{F_{5,175} = 18.39}$
	$\boldsymbol{\beta = 0.30}$	$\boldsymbol{\beta = -0.040}$	NR > RR	**NA > A**	$\boldsymbol{p < 0.0001}$
	$\boldsymbol{p = 0.0007}$	$\boldsymbol{p = 0.0017}$	$p = 0.14$	$\boldsymbol{p = 0.043}$	
Chromium	$\mathbf{F_{1,175} = 19.12}$	$F_{1,175} = 2.07$	$F_{1,175} = 1.61$	$F_{1,175} = 0.025$	$\mathbf{F_{5,175} = 14.45}$
	$\boldsymbol{\beta = 0.40}$	$\beta = -0.019$	NR > RR	NA > A	$\boldsymbol{p < 0.0001}$
	$\boldsymbol{p < 0.0001}$	$p = 0.15$	$p = 0.20$	$p = 0.87$	
Nickel	$\mathbf{F_{1,175} = 6.78}$	$F_{1,175} = 0.20$	$\mathbf{F_{1,175} = 10.90}$	$F_{1,175} = 2.94$	$\mathbf{F_{5,175} = 9.61}$
	$\boldsymbol{\beta = 0.25}$	$\beta = 0.0063$	**NR > RR**	A > NA	$\boldsymbol{p < 0.0001}$
	$\boldsymbol{p = 0.010}$	$p = 0.65$	$\boldsymbol{p = 0.0012}$	$p = 0.088$	
Lead	$\mathbf{F_{1,175} = 12.58}$	$F_{1,175} = 0.12$	$F_{1,175} = 2.49$	$F_{1,175} = 0.40$	$\mathbf{F_{5,175} = 55.78}$
	$\boldsymbol{\beta = 0.25}$	$\beta = 0.003$	NR > RR	A > NA	$\boldsymbol{p < 0.0001}$
	$\boldsymbol{p = 0.0005}$	$p = 0.72$	$p = 0.12$	$p = 0.52$	
Aluminium	$\mathbf{F_{1,175} = 24.71}$	$F_{1,175} = 0.62$	$\mathbf{F_{1,175} = 4.03}$	$F_{1,175} = 2.43$	$\mathbf{F_{5,175} = 13.22}$
	$\boldsymbol{\beta = 0.45}$	$\beta = -0.010$	**NR > RR**	A > NA	$\boldsymbol{p < 0.0001}$
	$\boldsymbol{p < 0.0001}$	$p = 0.43$	$\boldsymbol{p = 0.046}$	$p = 0.12$	

Note: Each response variable is log-transformed and *z*-score standardized. Traffic volume is also log-transformed. Bold values indicate significant results. Abbreviations: A, adjacent agriculture; NA, no adjacent agriculture; NR, no adjacent railroad; RR, adjacent railroad.

(Mattson, 1980). In contrast to significant signatures of traffic on foliar macronutrient content, we found that there was a tendency for traffic volume to be positively related to leaf Na content but this was not significant (Table 1). Traffic is expected to influence roadside Na levels in northern climates like Minnesota, given that roads receive massive salt inputs during winter for de-icing purposes. For instance, ~317,000 metric tons of salt are applied annually in the Minneapolis–St. Paul metropolitan area alone (Novotny et al., 2009). While a previous study of roadside sites throughout Minnesota detected significant effects of traffic on roadside leaf Na content (Mitchell et al., 2020), we note that sampling for this study took place at different sites during a different year and focused exclusively on milkweed. Although we found that milkweed had the highest average Na concentration of all the plant species sampled (Table 3), our study suggests that environmental effects on sodium content may be relatively noisy.

The significant effects of traffic on leaf heavy metal content are consistent with previous studies showing elevated levels of heavy metals in roadside plants (Fergusson et al., 1980; Khalid et al., 2019; Phillips

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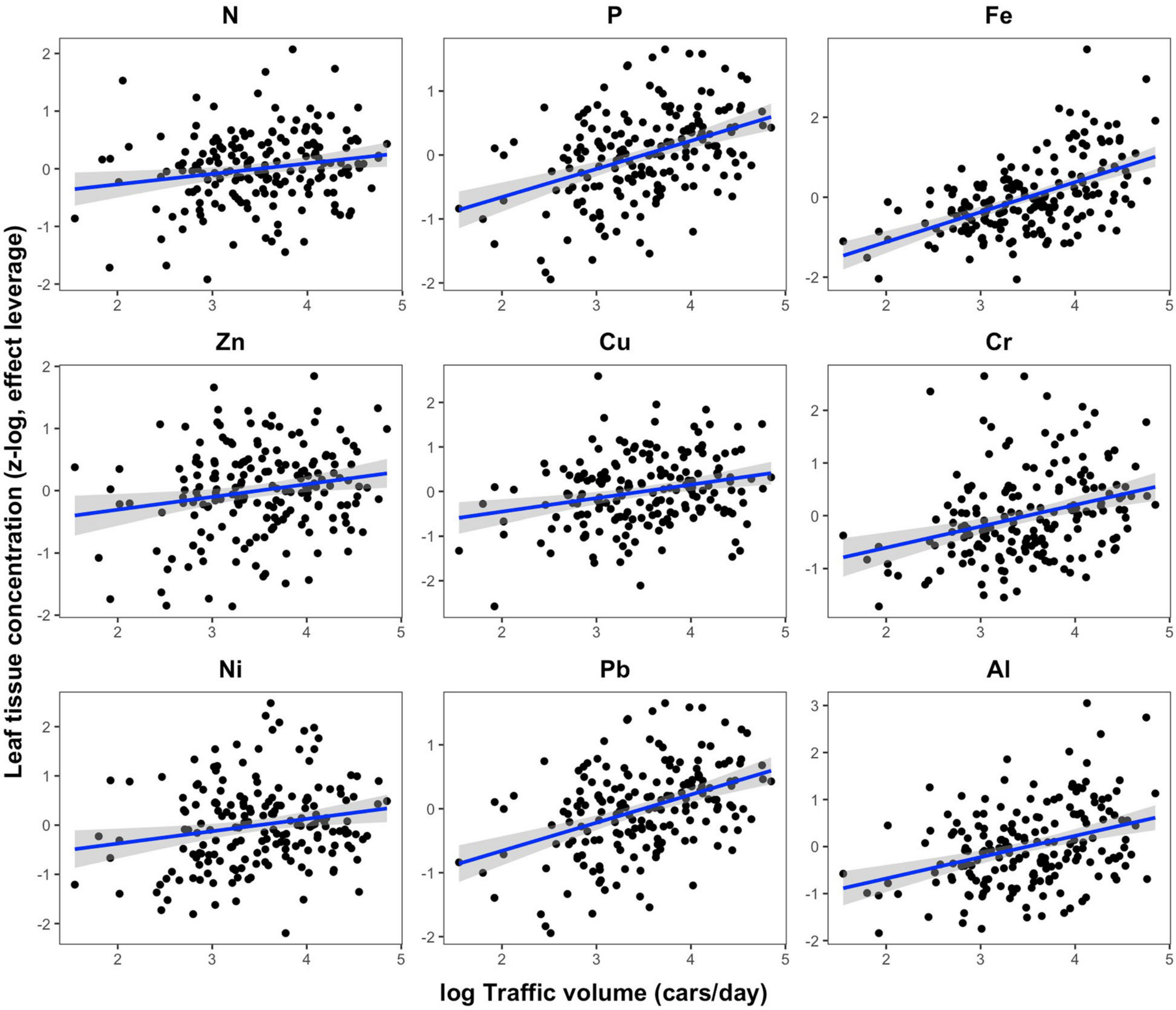

FIGURE 1 Effects of traffic volume (log-transformed) on leaf content of roadside chemical pollutants. Shown are leverage plots from models controlling for distance from road, presence of adjacent railroad, presence of adjacent agriculture and plant species. Response variables are log-transformed and *z*-score standardized. Summary statistics of raw data for each relationship can be found in Table S1.

et al., 2020). Many heavy metals, particularly zinc, copper and iron, are released from wear-and-tear of tires and brake pads (Councell et al., 2004). Our results suggest that inputs of these metals scale with traffic volume but these elements do not move far from the road edge. Lead can be emitted from brake and tire erosion and also likely remains present in roadside soils from the gasoline additive tetraethyllead, which began to decline in use in the United States by the mid-1970s (Nriagu, 1990). Our results demonstrate that the lead signature in foliar chemistry is long-lasting, but even over decades, it has not spread through the environment; it remains most concentrated close to the roadside. Although previous work has found that urban heavy metals can negatively affect the performance of insect pollinators such as bees (Meindl & Ashman, 2013; Phillips et al., 2021; Rothman et al., 2020; Sivakoff et al., 2020), our data suggest that none of the roadside forb species considered in our study are accumulating metals to levels known to be toxic to larval butterflies and moths, at least in terms of cadmium, lead, copper, nickel and zinc (Cheruiyot et al., 2013; Coleman et al., 2005; Davis et al., 2001; Gintenreiter et al., 1993; Jin et al., 2020; Martens & Boyd, 1994; Shephard et al., 2020; Table 3). For instance, across all forb species considered, mean and maximum lead concentrations ranged from 0.166 to 1.06 and 0.332 to 1.65 ppm, respectively (Table 3), concentrations far below those shown to induce mortality in moths (e.g. above 100 ppm in *Lymantria dispar* [Gintenreiter et al., 1993] and 15 ppm in *Plutella xylostella* [Coleman et al., 2005]). Additionally, mean and maximum zinc concentrations across all forb species considered ranged from 14.9 to 41.4 and 35.4 to 70.7 ppm, respectively, also far below levels shown to induce mortality in moths (e.g. above 450 ppm in *Spodoptera litura* [Jin et al., 2020] and 275 ppm in *Plutella xylostella* [Coleman et al., 2005]). However, published data on heavy metal toxicity in Lepidoptera are strongly biased towards disturbance-adapted agricultural pest species, and we know relatively little about metal toxicity thresholds in insect pollinators of conservation concern (Shephard et al., 2020). In addition, while our current measurements and lab studies with artificial diet (e.g. Shephard et al., 2020) often

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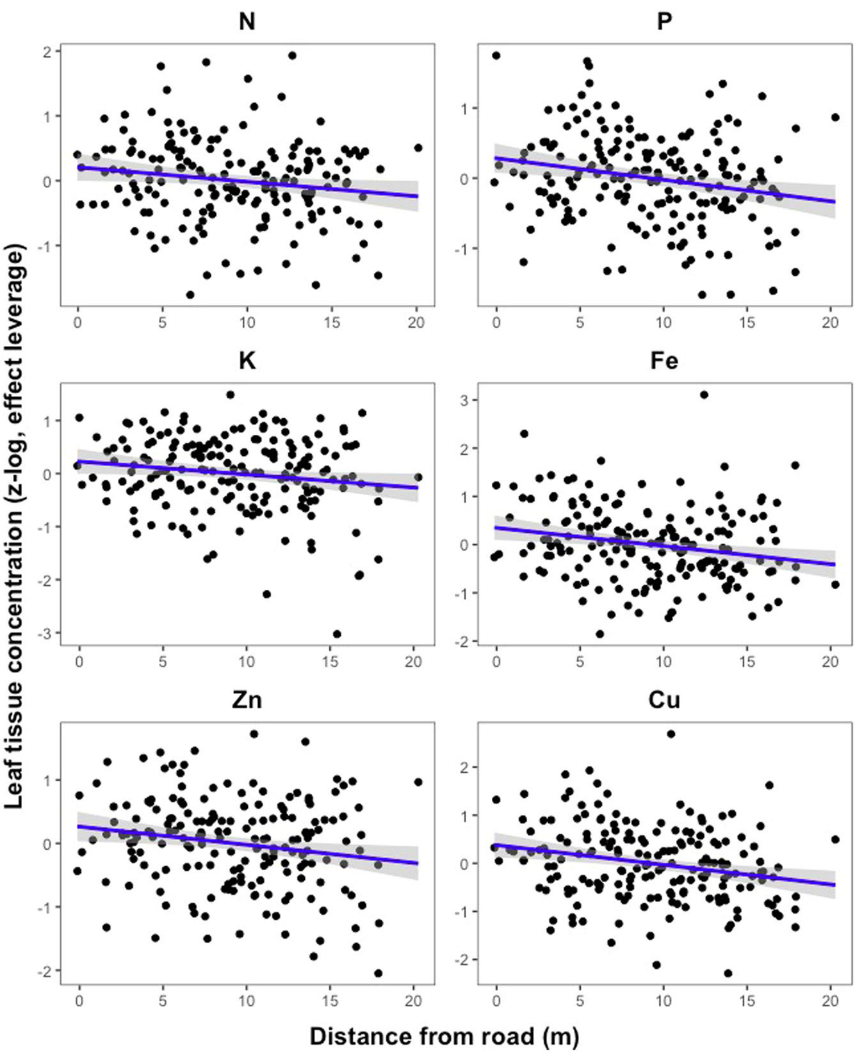

FIGURE 2 Effects of distance from road on leaf content of roadside chemical pollutants. Shown are leverage plots from models controlling for traffic volume (log-transformed), presence of adjacent railroad, presence of adjacent agriculture and plant species. Response variables are log-transformed and *z*-score standardized. Summary statistics of raw data for each relationship can be found in Table S1.

focus on measures of metals per dry mass of diet, wild herbivores will be experiencing more dilute levels of metals given the water content of their diet, which could potentially alter the toxicity of wild plants. Thus, future research assessing heavy metal tolerance in species of conservation concern is required to make stronger inferences about toxicity of roadside plants for insect pollinators. It is also possible high levels of metal pollution are currently only a concern for pollinators in urban areas, which has implications for roadside restoration given that >75% of roads in the United States are rural (National Research Council, 2005). Our results additionally suggest that roadsides in areas of rapidly increasing vehicle use have the greatest potential to become increasingly toxic (e.g. roads in many suburban and ex-urban areas) as traffic densities and urban commuting distances increase.

Relative to traffic effects, element content of roadside forbs was far less affected by landscape context (presence of adjacent railroad or agriculture; Table 1). Significant effects of adjacent railroad were only observed for some macronutrients (P, K) and metals (Fe, Ni and Al). However, contrary to our initial predictions, plants sampled from roadside sites adjacent to railroad had *lower* levels of these elements in their leaves relative to leaves sampled from sites without adjacent railroad (Figure 3). This observation contrasts with previous studies documenting increased metal content in plants and soils associated with railroads (Chen et al., 2014; Liu et al., 2009). While the reason for this contrasting pattern is uncertain, we note that previous work assessing environmental effects of railroads has often sampled directly on railroad tracks rather than in roadside verges adjacent to railroad tracks. Thus, our sampling scheme may not have included the area with increased elemental content. Alternatively, previous work has shown that significant levels of heavy metal pollution from railroads come from leaked cargo (Chen et al., 2014); thus, it is possible that we did not find signatures of metal pollution in railroad-adjacent sites because most trains moving through our site areas are not transporting cargo containing metal ores. Another possible explanation is that limestone track ballast (e.g. Giannakos & Loizos, 2008) could change adjacent soil chemistry, making metals less bioavailable to the plants growing there (Lee et al., 2011; Pierzynski & Schwab, 1993; Rehman et al., 2017). However, this is not supported by our data. Our results demonstrate that sites with adjacent railroad also had relatively lower metal content (for iron, nickel and aluminium; Table 4). Additionally, there is no elevation of soil calcium (Table 4), an indicator of limestone erosion, suggesting the use of

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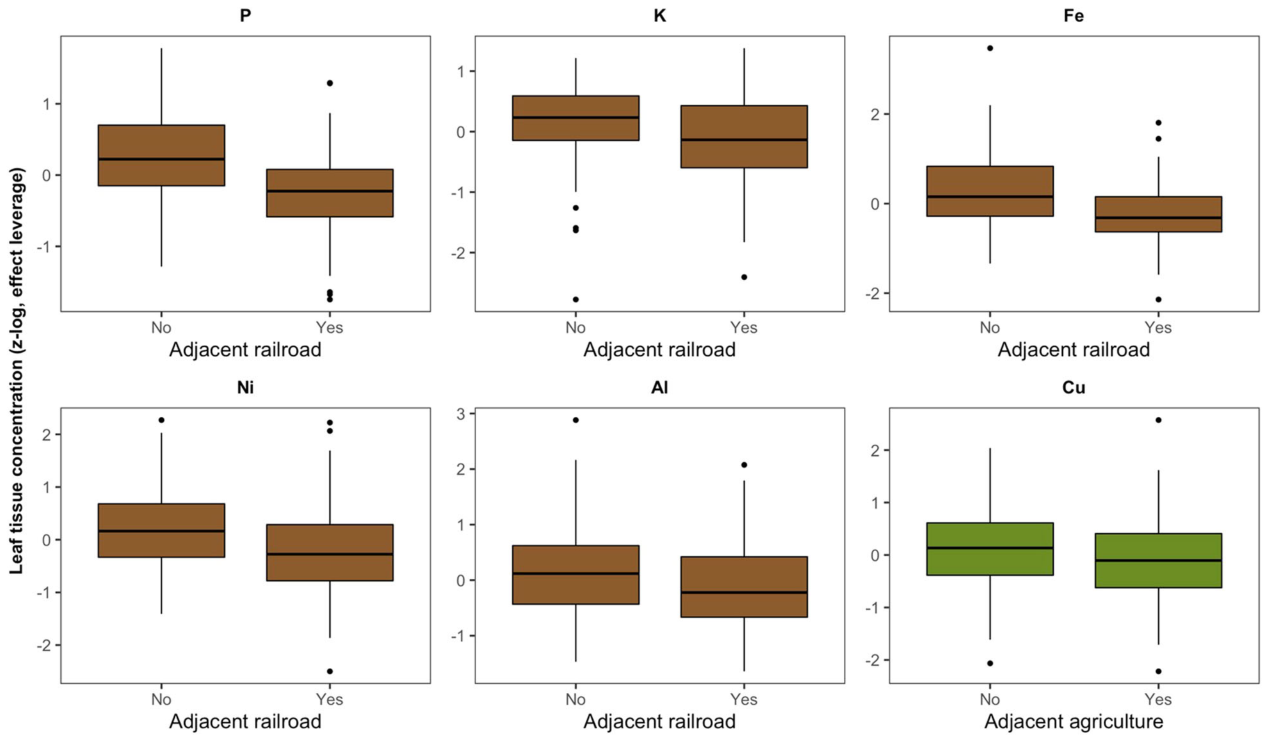

FIGURE 3 Effects of adjacent railroad (brown) or adjacent agriculture (green) on leaf content of roadside chemical pollutants. Shown are leverage plots from models controlling for traffic volume (log-transformed), distance from road, presence of adjacent agriculture (for railroad models), presence of adjacent railroad (for agriculture model) and plant species. Response variables are log-transformed and *z*-score standardized. Summary statistics of raw data for each relationship can be found in Table S1.

other ballast types (e.g. granite) or higher rates of leaching (Gunn, 1981; Trudgill, 1976).

Although agriculture can be a source of macronutrient and heavy metal pollution (Alloway & Jackson, 1991), we found a significant effect of adjacent agriculture on leaf element content of only Cu (lower in agriculture-adjacent plants; Table 1; Figure 3); yet there was a tendency for agriculture-adjacent plants to have higher levels of Ni (Table 1), possibly due to fertilizers, livestock manures and sewage irrigation that contain metals such as Ni (Alloway & Jackson, 1991; Luo et al., 2009). Although it is less clear why we did not detect an effect of agriculture on plant macronutrient content, a potential explanation could be that all sites sampled in our study were within the broader agricultural matrix of Minnesota and could therefore be similarly affected by agricultural output. While it is unclear what an appropriate agricultural control would be in this case, one way to address this issue could be to compare sites adjacent to active cropland with those adjacent to old fields or embedded in the general matrix of human activity. We avoided sampling from sites with high levels of human activity (e.g. urban, residential or commercial areas), and our agricultural control sites consisted of areas adjacent to a combination of fields, grasslands, business storage areas, tree patches, marshes, swamps, ponds, rivers and wetlands. However, future studies may benefit from sampling from a more diverse range of human-impacted areas to better control for agricultural effects.

We expected to find variation in leaf element content across roadside forb species given that accumulation of nitrogen, sodium and heavy metals varies tremendously across plant taxa (Watanabe et al., 2007). Despite finding significant species-level variation in leaf content for all elements considered (Table 1), we found no evidence that some forb species consistently ranked higher than other species in foliar content of potentially toxic heavy metals (Table 2). Heavy metal contamination of plant leaf tissue in roadside habitats occurs either through uptake of chemicals by plant roots (Verbruggen et al., 2009) or through accumulation of dust on leaf surfaces (Thompson et al., 1984). Since our study aimed to understand the complete diet of pollinators in roadside habitats, we conducted all analyses on unwashed leaf tissue and are therefore unable to conclusively determine the mechanism by which leaf contamination occurred. Thus, even if there were consistent differences among forb species in the ability to accumulate metals through root systems, it is possible that we could not observe such differences if leaves contained significant levels of dust, which has been shown to account for 20%–50% of foliar metal content in roadside plants (Shakour & Nasralla, 1986; Voegborlo & Chirgawi, 2008). Future studies could address this more conclusively by measuring metal concentrations of washed leaf tissue from roadside plants or by experimentally exposing plants to controlled levels of heavy metals through soil. Regardless of the mechanism by which these forb species accumulate metals along roadsides, our results indicate that managerial decisions to prioritize the planting of certain species over others would unlikely have a major influence on exposure of insect pollinators to metal pollution. However, as noted above, our study provides no evidence that, even on high-traffic-volume

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TABLE 2 Summary of variation in leaf heavy metal content across forb species

	Species ranked by estimated leaf heavy metal concentration (highest to lowest)	Leaf heavy metal concentration (mean ppm ± *SD*)
Iron	*Monarda fistulosa* (Lamiaceae)	155 ± 87.7
	Trifolium pratense (Fabaceae)	106 ± 32.5
	Solidago (Asteraceae)	101 ± 46.5
	Asclepias syriaca (Apocynaceae)	103 ± 55.7
	Dalea purpurea (Fabaceae)	95.1 ± 66.4
	Ratibida pinnata (Asteraceae)	95.3 ± 51.8
Zinc	*Ratibida pinnata* (Asteraceae)	41.4 ± 11.8
	Trifolium pratense (Fabaceae)	40.3 ± 14.2
	Monarda fistulosa (Lamiaceae)	30.3 ± 8.38
	Asclepias syriaca (Apocynaceae)	28.2 ± 10.9
	Solidago (Asteraceae)	19.7 ± 8.01
	Dalea purpurea (Fabaceae)	14.9 ± 6.16
Copper	*Trifolium pratense* (Fabaceae)	14.4 ± 3.87
	Monarda fistulosa (Lamiaceae)	10.3 ± 2.54
	Asclepias syriaca (Apocynaceae)	11.2 ± 4.37
	Ratibida pinnata (Asteraceae)	8.30 ± 3.60
	Solidago (Asteraceae)	8.93 ± 4.66
	Dalea purpurea (Fabaceae)	6.31 ± 2.20
Chromium	*Monarda fistulosa* (Lamiaceae)	0.541 ± 0.374
	Solidago (Asteraceae)	0.269 ± 0.351
	Trifolium pratense (Fabaceae)	0.231 ± 0.314
	Asclepias syriaca (Apocynaceae)	0.207 ± 0.259
	Ratibida pinnata (Asteraceae)	0.134 ± 0.078
	Dalea purpurea (Fabaceae)	0.0816 ± 0.087
Nickel	*Trifolium pratense* (Fabaceae)	1.030 ± 0.841
	Asclepias syriaca (Apocynaceae)	0.717 ± 0.552
	Monarda fistulosa (Lamiaceae)	0.621 ± 0.621
	Dalea purpurea (Fabaceae)	0.612 ± 0.717
	Solidago (Asteraceae)	0.362 ± 0.232
	Ratibida pinnata (Asteraceae)	0.301 ± 0.161
Lead	*Ratibida pinnata* (Asteraceae)	1.06 ± 0.281
	Solidago (Asteraceae)	0.313 ± 0.079
	Dalea purpurea (Fabaceae)	0.275 ± 0.153
	Asclepias syriaca (Apocynaceae)	0.274 ± 0.132
	Monarda fistulosa (Lamiaceae)	0.258 ± 0.112
	Trifolium pratense (Fabaceae)	0.166 ± 0.067
Aluminum	*Monarda fistulosa* (Lamiaceae)	82.5 ± 40.4
	Ratibida pinnata (Asteraceae)	48.2 ± 25.6
	Dalea purpurea (Fabaceae)	50.2 ± 54.5
	Solidago (Asteraceae)	36.7 ± 17.6
	Asclepias syriaca (Apocynaceae)	39.7 ± 32.1
	Trifolium pratense (Fabaceae)	23.1 ± 14.5

Note: For each metal, species are ranked from highest to lowest in terms of leaf tissue concentration based on estimates from linear models controlling for traffic volume, distance from road, presence of adjacent railroad and presence of adjacent agriculture. Also shown are raw data for mean leaf heavy metal concentration in parts per million (ppm).

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TABLE 3 Summary statistics of mean, median, minimum and maximum content for 12 roadside chemical pollutants in each of six roadside forb species

		Mean ± *SD*	Median	Min.	Max.
Nitrogen (%)	*Asclepias syriaca*	2.81 ± 0.687	2.83	1.71	4.66
$n = 181$	*Dalea purpurea*	2.57 ± 0.414	2.56	1.70	3.62
	Monarda fistulosa	2.06 ± 0.370	1.98	1.53	3.11
	Ratibida pinnata	1.72 ± 0.176	1.63	1.32	2.89
	Solidago	1.98 ± 0.531	1.97	1.06	3.73
	Trifolium pratense	3.74 ± 0.505	3.79	2.30	4.50
Phosphorous (ppm)	*Asclepias syriaca*	4371 ± 2053	4318	1049	9347
$n = 185$	*Dalea purpurea*	1276 ± 388	1191	567	1975
	Monarda fistulosa	2579 ± 1257	2405	1265	6486
	Ratibida pinnata	1916 ± 938	1635	1096	5045
	Solidago	3480 ± 2173	2860	945	8688
	Trifolium pratense	1964 ± 498	1728	1316	3034
Potassium (ppm)	*Asclepias syriaca*	28,416 ± 9930	29,556	8371	46,929
$n = 185$	*Dalea purpurea*	10,309 ± 3241	10,262	4399	18,298
	Monarda fistulosa	19,925 ± 4935	20,175	8540	28,700
	Ratibida pinnata	18,622 ± 5427	17,896	11,488	31,851
	Solidago	21,978 ± 5478	21,446	10,443	36,116
	Trifolium pratense	18,795 ± 6820	20,052	4112	28,485
Sodium (ppm)	*Asclepias syriaca*	250 ± 358	86.4	14.8	1538
$n = 185$	*Dalea purpurea*	70.5 ± 85.0	34.3	12.3	363
	Monarda fistulosa	59.3 ± 97.6	26.2	12.3	426
	Ratibida pinnata	80.1 ± 108	48.7	12.5	456
	Solidago	27.2 ± 25.5	23.0	6.41	133
	Trifolium pratense	135 ± 111	104	15.5	411
Iron (ppm)	*Asclepias syriaca*	103 ± 55.7	81.3	58.8	289
$n = 185$	*Dalea purpurea*	95.1 ± 66.4	77.0	43.7	429
	Monarda fistulosa	155 ± 87.7	128	82.7	379
	Ratibida pinnata	95.3 ± 51.8	80.4	42.3	215
	Solidago	101 ± 46.5	88.1	38.2	219
	Trifolium pratense	106 ± 32.5	102	60.8	220
Zinc (ppm)	*Asclepias syriaca*	28.2 ± 10.9	28.6	9.01	54.9
$n = 185$	*Dalea purpurea*	14.9 ± 6.16	14.3	6.08	35.4
	Monarda fistulosa	30.3 ± 8.38	27.3	17.9	52.2
	Ratibida pinnata	41.4 ± 11.8	41.6	23.2	61.0
	Solidago	19.7 ± 8.01	18.3	6.83	44.1
	Trifolium pratense	40.3 ± 14.2	37.8	16.9	70.7
Copper (ppm)	*Asclepias syriaca*	11.2 ± 4.37	10.2	5.46	23.6
$n = 185$	*Dalea purpurea*	6.31 ± 2.20	6.07	3.23	12.3
	Monarda fistulosa	10.3 ± 2.54	9.97	5.83	15.0
	Ratibida pinnata	8.30 ± 3.60	6.84	3.95	15.5
	Solidago	8.93 ± 4.66	8.30	2.64	25.8
	Trifolium pratense	14.4 ± 3.87	14.1	7.08	28.2

(Continues)

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TABLE 3 (Continued)

		Mean ± *SD*	Median	Min.	Max.
Chromium (ppm)	*Asclepias syriaca*	0.207 ± 0.259	0.105	0.0264	1.46
n = 185	*Dalea purpurea*	0.0816 ± 0.0875	0.0599	0.0286	0.467
	Monarda fistulosa	0.541 ± 0.374	0.445	0.168	1.50
	Ratibida pinnata	0.134 ± 0.0780	0.132	0.0472	0.302
	Solidago	0.269 ± 0.351	0.158	0.0433	1.58
	Trifolium pratense	0.231 ± 0.314	0.120	0.0324	1.60
Nickel (ppm)	*Asclepias syriaca*	0.717 ± 0.552	0.567	0.121	2.89
n = 185	*Dalea purpurea*	0.612 ± 0.717	0.374	0.125	3.19
	Monarda fistulosa	0.621 ± 0.407	0.522	0.160	1.70
	Ratibida pinnata	0.301 ± 0.161	0.252	0.130	0.695
	Solidago	0.362 ± 0.232	0.307	0.101	1.02
	Trifolium pratense	1.03 ± 0.841	0.872	0.122	4.47
Lead (ppm)	*Asclepias syriaca*	0.274 ± 0.132	0.242	0.101	0.716
n = 185	*Dalea purpurea*	0.275 ± 0.153	0.216	0.128	0.818
	Monarda fistulosa	0.258 ± 0.112	0.241	0.111	0.514
	Ratibida pinnata	1.06 ± 0.281	1.06	0.524	1.65
	Solidago	0.313 ± 0.0790	0.305	0.201	0.566
	Trifolium pratense	0.166 ± 0.0672	0.148	0.0350	0.332
Aluminium (ppm)	*Asclepias syriaca*	39.7 ± 32.1	29.5	8.61	162.0
n = 185	*Dalea purpurea*	50.2 ± 54.5	28.0	14.5	294.0
	Monarda fistulosa	82.5 ± 40.4	77.3	25.1	165.0
	Ratibida pinnata	48.2 ± 25.6	45.0	16.0	102.0
	Solidago	36.7 ± 17.6	33.4	15.7	87.8
	Trifolium pratense	23.1 ± 14.5	16.5	11.6	21.3
Cadmium (ppm)	*Asclepias syriaca*	–	–	<0.001	0.0382
n = 185	*Dalea purpurea*	–	–	<0.001	0.0562
	Monarda fistulosa	–	–	<0.001	0.00237
	Ratibida pinnata	–	–	<0.001	0.367
	Solidago	–	–	<0.001	0.293
	Trifolium pratense	–	–	<0.001	0.0972

Note: Nitrogen content is expressed as percent *N* of total leaf tissue, and all other elements are expressed as concentration in leaf tissue (parts per million).

TABLE 4 Mean element concentration (ppm) of soil samples collected from roadside sites with or without adjacent railroad (RR)

Element	RR mean (*SD*)	Non-RR mean (*SD*)	*t*-test statistic
Iron	12,691 (2553)	17,187 (3478)	$t_{14} = 2.95, p = 0.01$
Nickel	11.19 (1.99)	16.69 (3.68)	$t_{14} = 3.71, p = 0.002$
Aluminium	4307.3 (1043)	5669.5 (1613)	$t_{14} = 2.01, p = 0.06$
Calcium	28,347 (24562)	34,456 (28250)	$t_{14} = 0.46, p = 0.65$
Phosphorus	485.5 (85.6)	615.4 (340.5)	$t_{14} = 1.05, p = 0.31$
Potassium	835.6 (215)	1004 (359)	$t_{14} = 1.13, p = 0.27$

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roads, forbs are accumulating heavy metals to levels that are toxic for pollinators.

In summary, we demonstrate that roads alter leaf chemistry of a range of forb species. With increasing traffic volume and road proximity, we found elevated macronutrients, micronutrients and heavy metals in plant leaf tissue. However, surrounding landscape context (railroad or agriculture) was less important in determining variation in foliar chemistry. This suggests that adjacent railroad and agriculture are not exacerbating pollutant levels in roadside habitat, so restoration effort in these areas is unlikely to increase the risk of pollutant exposure for pollinators that rely on plant foliage. Additionally, our results demonstrate that forb species do not consistently differ in heavy metal accumulation along roadsides, but, importantly, we found no evidence that any of these plant species accumulate metals to levels known to be toxic for pollinators. These results suggest that restoration managers do not need to prioritize specific native forbs in roadside habitats to alter the risk of metal contamination. Overall, our work is consistent with previous research illustrating that the risks of managing and restoring roads for insect pollinators are much smaller than the benefits associated with additional pollinator habitat (for review, see Phillips et al., 2020), and managers should continue to use lower traffic density roadsides as an important component of insect pollinator conservation. However, future work should aim to quantify levels of other contaminants that could affect roadside plants, such as pesticides from agriculture. Additionally, it will be important for future work to consider how the shift to electric vehicle use may affect the suitability of roadsides for pollinator conservation. For example, while electric vehicle use may be expected to reduce deposition of roadside nitrogen (a major component of vehicle exhaust; Cape et al., 2004), deposition of heavy metal pollution may not change as much, since metals are primarily released from wear-and-tear of brake pads and tires (Councell et al., 2004).

AUTHOR CONTRIBUTIONS

Alex Shephard led writing, data analysis and visualization. Lauren Agnew collected data and assisted with project conceptualization and manuscript editing. Annika Herdtle assisted with data collection and manuscript editing. Tim Mitchell assisted with conceptualization, analysis and manuscript editing. Elizabeth Borer led conceptualization and contributed to analysis and manuscript editing. Emilie C. Snell-Rood led grant funding and project conceptualization and contributed to writing, analysis and manuscript editing.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All raw data can be accessed via Mendeley: https://doi.org/10.17632/vmc6znh66m.2 (Shephard et al., 2022)

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SUPPORTING INFORMATION

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

Appendix 1: Supplementary Tables

Table S1: Summary statistics of mean, minimum, and maximum concentration of eleven roadside chemical pollutants in foliage of roadside forbs, grouped by traffic volume (split into upper and lower halves of the data), distance from road (split into upper and lower halves of the data), railroad (split into adjacent and non-adjacent railroad), and agriculture (split into adjacent and non-adjacent agriculture)

Appendix 2: Supplementary Figures

Figure S1: Map of the 55 roadside sites where plant samples in the analysis were collected

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