RESEARCH ARTICLE

Roads pose a significant barrier to bee movement, mediated by road size, traffic and bee identity

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Abstract

1. Roads are a major driver of environmental stress, yet we know surprisingly little about how roads impact the movement of insect pollinators, and consequent pollination.

2. We investigated the influence of roads on pollinator movement and pollination by examining patterns of pigment transfer between focal plants of two species, *Coreopsis verticillata* and *Monarda fistulosa*. We asked whether roads reduced pigment transfer, and what characteristics of roads were important in driving this reduction. We also evaluated whether pollinator assemblage differed between species, and if this mediated the effect of roads on pigment transfer.

3. Plants across a road from a pigment-added plant received significantly less pigment than plants on the same side of the road. This effect was stronger for coreopsis than for monarda. The mean body size of visitors to coreopsis was significantly smaller than that of visitors to monarda, suggesting that smaller bees are more limited by roads.

4. Road width was the best predictor of pigment transfer, with a smaller effect of traffic volume; further research is needed to fully disentangle the effects of different road characteristics. Roadside habitat had little influence on pigment transfer, and roadside plants did not receive significantly less pigment than plants in contiguous habitat.

5. *Synthesis and applications.* This study demonstrates that roads pose substantial barriers to bee movement, reducing pollen flow between plants located across roadways from one another. Road characteristics, particularly width and traffic volume, mediated this effect, as did bee size. Our results suggest that the effects of roads on pollinators and pollination can be mitigated by many of the same design strategies currently being implemented to reduce human traffic accidents, offering the opportunity for win–win scenarios.

KEYWORDS

barrier effect, bees, movement ecology, pollen movement, pollinator movement, road ecology

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Gordon Fitch and Chatura Vaidya contributed equally to this paper.

1 | INTRODUCTION

Road development is a ubiquitous driver of environmental stress (Van Der Ree et al., 2015). Currently, the road network extends to about 32 million km across the globe (IRF, 2017), and it is projected to increase by an additional 25 million km globally by 2050 (Dulac, 2013). While the bulk of studies measuring the effect of roads on ecological communities have focused on vertebrate animals (Bennett, 2017), there is increasing evidence that roads also impact invertebrates—and particularly insects—both via mortality from vehicle collisions (Baxter-Gilbert et al., 2015) and by altering movement patterns (Andersson et al., 2017; Bhattacharya et al., 2003). Yet the few studies evaluating the degree to which roads represent barriers to insect movement are largely anecdotal or poorly replicated (Bhattacharya et al., 2003; Franzén et al., 2009; Remon et al., 2018; Zurbuchen et al., 2010), save for a small number of studies on butterflies (Munguira & Thomas, 1992; Ries & Debinski, 2001). In general, we lack a rigorous quantification of the extent to which roads limit insect movement.

Further complicating our understanding of the effects of roads on insects, in landscapes otherwise dominated by agriculture, roadsides are important habitat for insects (Gardiner et al., 2018; Phillips et al., 2020). This is particularly true when roadsides are managed to resemble semi-natural meadow or prairie habitat (Hopwood, 2008; Phillips et al., 2019; Ries et al., 2001). Fully understanding the effects of roads therefore requires disentangling the effects of the roads themselves (i.e. of the bare surface and vehicle traffic) from management of roadside vegetation. Moreover, all roads are not created equal. The degree to which roads represent barriers to the movement of insect pollinators likely depends on the characteristics of the roads—particularly their width and the speed and volume of traffic. Yet, despite widespread recognition that roads pose a barrier to insect pollinator movement, little research has been done to determine how particular road attributes mediate this effect.

Understanding the effects of roads on pollinating insects is particularly crucial. Since insect pollination is essential to reproduction in many plant species, road impacts on pollinators are likely to have cascading effects on pollination and plant populations. Indeed, studies have documented reduced pollination (Cunningham, 2000; Dargas et al., 2016) and seed set (Cunningham, 2000) in insect-pollinated plants growing alongside roads (but see Grobler & Campbell, 2020). As barriers to pollinator (and therefore pollen) movement, roads may also genetically isolate plant populations (Nobarinezhad et al., 2019). While urbanization, which includes but is not limited to increasing road density, has been shown to result in high rates of local extinction and increased selfing (Cheptou & Avendaño V, 2006; Dornier & Cheptou, 2012), the role of roads per se in driving pollen limitation and population fragmentation in plants has been scarcely evaluated.

Here, we begin to fill these research gaps by reporting the results from an investigation into how roads of varying characteristics affect pollen movement in two plant species. We examined patterns of transfer of fluorescent pigment (an analogue for pollen) between focal plants of two native, insect-pollinated species, wild bergamot (*Monarda fistulosa*; Lamiaceae; hereafter 'monarda') and threadleaf coreopsis (*Coreopsis verticillata* 'Zagreb'; Asteraceae; hereafter 'coreopsis'), at 47 road- or pathside sites in Ann Arbor, Michigan, USA. Using these experimental plants, we asked (a) if patterns of pigment transfer differ depending on whether a plant is located across the road versus along the road from a pigment-added plant, and (b) if this effect is mediated by pollinator assemblage. Additionally, we asked (c) which road characteristics (lane number, traffic volume, traffic speed, roadside habitat) determine the degree to which roads serve as barriers to pollinator movement. Finally, we asked (d) whether proximity to a road or path influenced the magnitude of pigment transfer, relative to pigment transfer through contiguous habitat not adjacent to a road.

We hypothesized that plants across a road from the pigment-added plant would receive less pigment than plants alongside the road. We expected the magnitude of the barrier posed by roads to differ based on pollinator body size, which in bees is strongly correlated with flight ability (Greenleaf et al., 2007). Since we expected the pollinator assemblage of coreopsis to be comprised of smaller-bodied insects than that of monarda, we hypothesized that coreopsis would see greater declines in pollen transfer. We further hypothesized that road width, traffic volume and speed would mediate the degree to which roads impede pollinator movement. Finally, we hypothesized that roadsides would support fewer pollinators than contiguous habitats away from a road, and those pollinators present would experience greater disruption to foraging, so pigment transfer along roads would be reduced relative to contiguous sites.

2 | MATERIALS AND METHODS

2.1 | Study system

This study was conducted in Ann Arbor, Michigan, USA, a small city (population 130,000), from 6 July to 10 August 2020. We used two species of flowering plants native to the region: monarda and coreopsis. Both species are insect-pollinated; monarda is capable of selfing but seed set increases dramatically with insect pollination (Cruden et al., 1984). Coreopsis is likely self-incompatible, given what is known about the breeding system of congenerics (Banovetz & Scheiner, 1994; Smith & Deng, 2012). Differences in flower morphology between the species suggest that they are visited by distinct assemblages of pollinators (see insets in Figure 1). We purchased plants from Bluestone Perennials, Inc. and maintained them individually in 5.7-L plastic pots until flowering began.

2.2 | Data collection

We selected 47 sites adjacent to a road or path (hereafter road/path site), representing a wide spectrum of road sizes and traffic volumes and speeds (see Table S1 for site characteristics, and Figure S1 for representative images of sites). Sites were separated
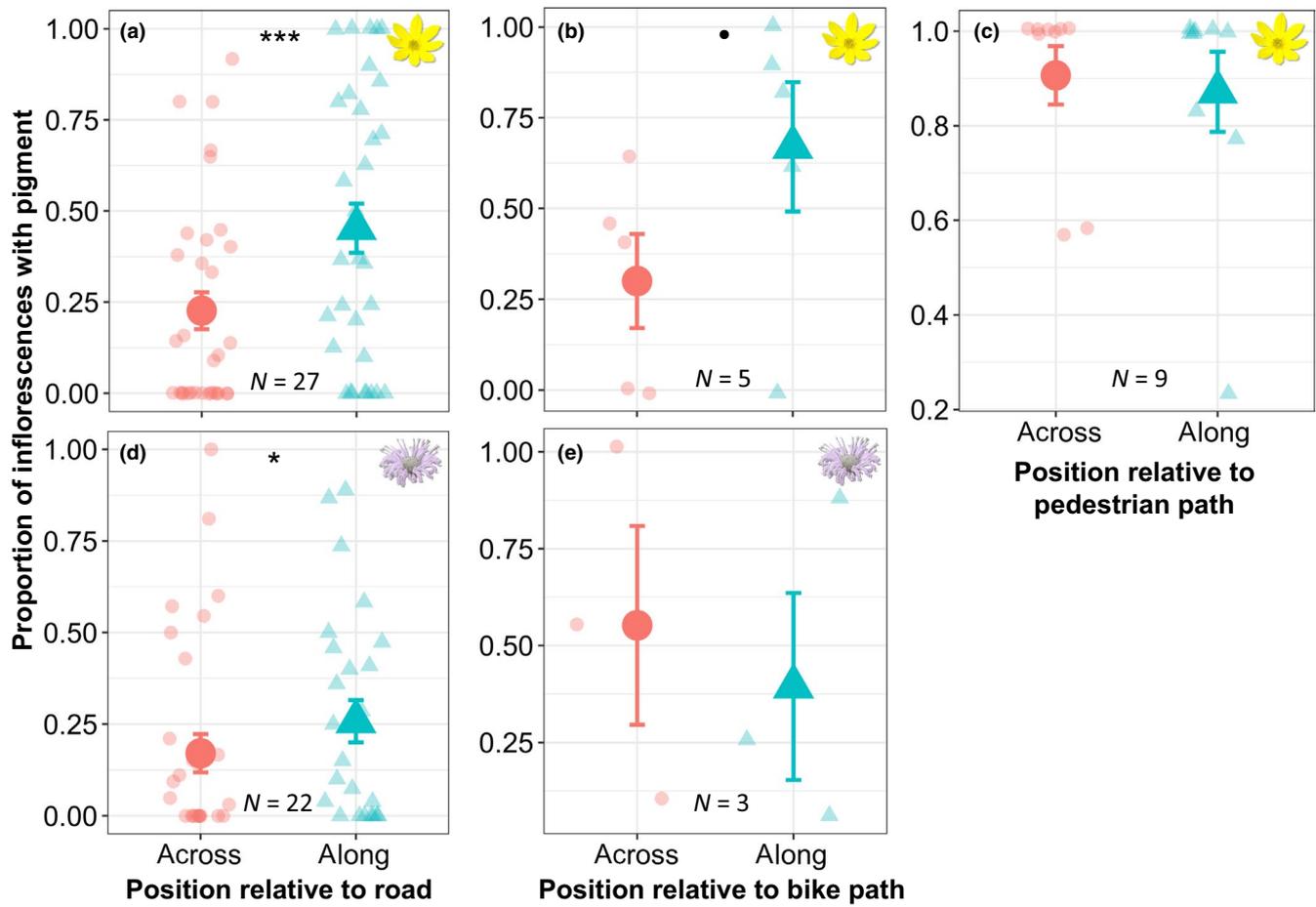
FIGURE 1 Effect of position relative to road or path on pigment deposition in coreopsis (a–c) and monarda (d, e). Large points represent means and error bars ±1 *SE*; small points represent observations from individual sites, jittered to improve legibility. Significance codes, according to paired *t*-tests: ***$p < 0.001$; *$p < 0.05$; •$p = 0.05$

from one another by at least 500 m, with the exception of paved sidewalks, which were located within 50 m of a road site (but plants were set out on a different day). Monarda and coreopsis were each present in low densities at fewer than five sites. At these sites, we situated experimental plants such that there were no intervening conspecifics.

A set of three conspecific plants (either alone or together with a set of plants from the other species) were deployed at each road/path site. We collected data from coreopsis at a total of 41 sites (27 roads, 5 bike paths, 9 pedestrian paths), and from monarda at 25 sites (22 roads, 3 bike paths). On one plant of the three, we applied luminous pigment (BioQuip, Rancho Dominguez) to all inflorescences (red for coreopsis, blue for monarda; Figure S2). This plant was placed alongside the road/path. We placed a second plant ('across' plant) across the road/path from the pigment-added plant, and measured the distance between these two plants (distance between plants ranged from 1.4 to 41.1 m). The third plant ('along' plant) was placed on the same side and at the same distance from the pigment-added plant as the 'across' plant (Figure S3 illustrates the experimental setup). The distance between experimental plants and the road or path edge varied somewhat depending

on site conditions, but was always <3.5 m. Plant setup occurred between 08:00 and 10:30 hr on warm, sunny days during the work week (Monday–Friday) and collection between 16:30 and 19:00 hr on the same day.

Upon collection, we took the 'across' and 'along' plants from each site into a dark location and used a UV flashlight to detect pigment deposited on flowers. On each plant, we counted the total number of inflorescences (and, for monarda, individual flowers) that held pigment on reproductive structures, as well as the total number of open inflorescences (and flowers for monarda). Since we observed pigment being moved by both wind and non-pollinating insects, we only counted inflorescences where the pigment was found on reproductive structures alone, that is, not on petals. To avoid potential bias, we obscured plant position (i.e. across or along) and site until after checking for pigment. After all flowers were tallied, we removed inflorescences (for coreopsis) or flowers (for monarda) that held pigment, so the plants could be used for data collection again on subsequent days. We also counted the number of open inflorescences and flowers with pigment on the pigment-added plants; these were not removed, though fresh pigment was added each sampling day. Thus pigment-added plants were always pigment-added, while

across and along plants were randomly assigned to location from one day to the next.

At each road/path site, we recorded: (a) GPS coordinates for the centre of the arranged plants, (b) the distance between plants, (c) the number of striped lanes for vehicular traffic, (d) the posted speed limit (measure of traffic speed), (e) traffic volume and (f) four binary attributes of roadside vegetation that we hypothesized might influence pigment transfer [presence of (a) unmowed weedy vegetation, (b) semi-natural meadow, (c) ornamental flower beds and (d) lawn]. We additionally combined attributes 1–3 to assess the effect of the presence of significant floral resources, since each of these habitats supported high floral densities.

For 'along' plants at road sites, we also recorded whether their orientation relative to the pigment-added plant was with or against the flow of traffic in the adjacent lane. Traffic volume was determined by recording the number of vehicles passing by on the road for 5 min, either at the time of setup or collection which corresponded to high-traffic commuting hours. For car-free roads, traffic surveys separately tallied the number of bicycles and pedestrians passing the plants. The study occurred during the COVID-19 pandemic, when traffic volume was substantially reduced.

To see whether proximity to a road or path influenced pigment transfer, we selected six sites ≥100 m from a road with contiguous, unbroken habitat; either mowed lawn (three sites) or semi-natural meadow (three sites). At each site, we set up an identical array of five plants, with a pigment-added plant at the centre, and four plants situated perpendicular to one another at distances of 5, 15, 25 and 35 m from the pigment-added plant in each cardinal direction (Figure S3). This range of distances nearly spans the range of distances at which our road/pathside plants were placed (1.4–41.1 m). Due to its shorter flowering period, monarda was included at only three of the six sites (two lawns and one meadow). Protocols for quantifying pigment transfer were identical to those used at road/path sites.

We also conducted pollinator observations at 46 sites where we observed one plant for 5 min, and recorded all floral visitors. We identified visitors to morphospecies on the wing, and recorded the number of visits by each morphospecies. Any contact with the reproductive parts of the floral unit constituted a visit. Visits by the same individual to multiple floral units were recorded separately. For coreopsis, we recorded visits to inflorescences, while for monarda we recorded visits to flowers, including multiple flowers within the same inflorescence. We also recorded the number of open floral units at the time of the observation. Pollinator observations were used to determine the composition of the pollinator assemblage for each species.

2.3 | Data analysis

We performed all analyses using R v.4.0.2 (R Core Team, 2020). All analyses were conducted separately for the two plant species.

2.3.1 | Do pollinator assemblages between the two plant species differ by body size?

To test whether the pollinator assemblages of the two plant species differed by body size, we used intertegular distance (ITD), a close correlate of body size and flight ability (Greenleaf et al., 2007; Ricketts et al., 2008), as our measure of body size. Most visits to both species were made by bees (97%), with additional visits from Coleoptera, small Diptera, a wasp species and a large butterfly species. Because they accounted for so few visits, non-bees were removed from the dataset prior to analysis. We calculated a community-weighted mean ITD per observation by multiplying the number of visits from each species by its ITD, summing these values and dividing by the total number of visits. We then performed linear regression of community-weighted mean ITD against plant species.

2.3.2 | Do roads and paths influence pigment transfer?

We calculated the proportion of inflorescences with pigment by dividing the number of inflorescences with pigment by the number with open flowers. For monarda, we additionally calculated the proportion of flowers that received pigment. Results were qualitatively similar for flowers and inflorescences. Since inflorescence data are more easily compared with data from coreopsis, we only report inflorescence-level data here (see Table S2 for flower-level results) To determine whether the proportion of inflorescences with pigment differed between 'across' and 'along' plants, we used a paired *t*-test, both with data from all sites combined and separately considering road, bike path and pedestrian path sites. We compared overall levels of pigment transfer between the two species using a *t*-test.

2.3.3 | Which road characteristics influence pigment transfer?

We evaluated the effect of four road characteristics (interplant distance, number of lanes of vehicular traffic, speed limit and traffic volume) on the proportion of flowers with pigment using binomial GLMs. We counted bike paths as 0.5 lanes, and pedestrian paths as 0 lanes. Because of the high degree of collinearity among the four road characteristics (Table S3), including more than one variable in a model resulted in variance inflation factors >4. Therefore, we constructed four separate models, one for each road characteristic. All models had the proportion of flowers with pigment as the dependent variable, and plant position ('along' or 'across') and the relevant road variable as predictors. Analysis of model residuals indicated significant heteroscedasticity in all models for coreopsis. Thus, we ran updated models with observations weighted by the reciprocal of the absolute value of the residuals from the unweighted model

(Strutz, 2016). After weighting, all models conformed to assumptions of normality and heteroscedasticity. To evaluate the relative importance of the four road characteristics in determining patterns of pigment transfer, we compared pseudo-R^2 and AICc values for the four models. To determine whether the effect of the road characteristics depended on plant position, we ran another set of models that included a plant position ×road characteristic interaction term and checked for significance of the interaction term and overall model fit.

Because the distance between plants, while related to road width, was experimentally imposed, we examined the effect of the other three road variables on pigment deposition while controlling for the effect of interplant distance. To do so, we ran linear models with the residuals from the binomial GLM for interplant distance as the response variable, and one of the remaining three road variables (number of lanes, traffic volume and speed limit) as the predictor. Because lane number and traffic volume had similar relationships with pigment deposition (see Results), we did the same procedure with these two variables (i.e. test the effect of one using the residuals from a model of the other) to identify which was a more important determinant of pigment movement patterns.

To test for the effect of road/pathside vegetation attributes, we updated the best model (as selected by the procedure outlined above) to include the habitat attributes. We compared this model to the model without habitat attributes using AICc, and conducted stepwise model simplification, removing the habitat attribute with the smallest effect on pigment transfer, until the best model was found.

To test whether traffic-induced airflow impacted pigment transfer, we only used data from 'along' plants at road sites. Using the best model for pigment transfer on this subsetted dataset, we added a binary variable indicating orientation to the pigment-added plant relative to flow of traffic ('with' or 'against' traffic), and checked for significance.

2.3.4 | Does pigment transfer differ between road/path sites and contiguous sites?

To test whether being adjacent to a road affected pigment transfer, we used the data from contiguous sites to regress the proportion of flowers with pigment against distance from the pigment-added plant, again using weighted binomial GLMs. We then compared the predicted relationship to that predicted using data drawn from the 'along' plants.

3 | RESULTS

3.1 | Do pollinator assemblages between the two plant species differ by body size?

We observed 65 insect visits to coreopsis and 356 to monarda. The overwhelming majority of visits to both species were from bees (97%). The ITD of observed bees ranged from 1.2 to 3.3 mm

(Table S4); this represents nearly the full range of body sizes for locally occurring bees (Fitch, Glaum, et al., 2019).

Visitor community-weighted mean ITD was significantly larger for monarda ($M \pm SE$: 3.1 ± 0.34 mm) than coreopsis ($M \pm SE$: 1.75 ± 0.22 mm; $R^2 = 0.34$, $F_{1,16} = 9.8$, $p = 0.006$). Coreopsis was visited mostly by sweat bees (60% of visits), while corbiculate bees dominated visitation to monarda [*Bombus* spp. (56% of visits) and *Apis mellifera* (35% of visits)].

3.2 | Do roads and paths influence pigment transfer?

Plants located across a road from a pigment-added plant received less pigment than plants located alongside the road (Figure 1a,b). The magnitude of this difference was greater for coreopsis than for monarda, with a 50% reduction in the number of inflorescences receiving pigment for coreopsis (paired *t*-test: $t = -3.89$, $df = 26$, $p < 0.001$), compared to a 34% reduction for monarda (paired *t*-test: $t = -2.22$, $df = 21$, $p = 0.04$). For coreopsis, the effect of bike paths on pigment transfer appeared similar to the effect of roads, while for monarda plant location relative to the bike path appeared to have no effect on pigment transfer, though sample size was small in both cases ($N = 5$ for coreopsis, $N = 3$ for monarda; Figure 1b,e). Position relative to pedestrian paths, whether unpaved or paved, appeared to have no effect on pigment transfer in coreopsis (Figure 1c; we did not deploy monarda at any pedestrian path sites). Across all sites, the proportion of inflorescences receiving pigment was significantly lower for monarda (0.25 ± 0.04) than for coreopsis (0.46 ± 0.04; *t*-test: $t = 3.59$, $df = 126.5$, $p < 0.001$).

3.3 | Which road characteristics influence pigment transfer?

For coreopsis, all four measured road characteristics (interplant distance, number of lanes, traffic volume, traffic speed) had a significant negative relationship with the proportion of inflorescences receiving pigment (Figures 2a–d and 3). However, once the effect of interplant distance was controlled for, traffic speed no longer had a significant effect on pigment transfer (Figure 3). Similarly, when the effect of lane number was controlled for, traffic volume no longer affected pigment transfer, while lane number still had a significant negative effect on pigment transfer even after controlling for traffic volume (Figure 3). For all models, while plant position had a significant effect, there was no effect of a plant position × road characteristic interaction (Table S2).

For monarda, only interplant distance had a significant effect on the proportion of inflorescences receiving pigment (Figures 2e–h and 3) Neither plant position nor the plant position × road characteristic interaction term significantly influenced pigment transfer in any model (Table S2). This was true when all sites were considered together and when road sites were considered separately from path sites (Table S2).
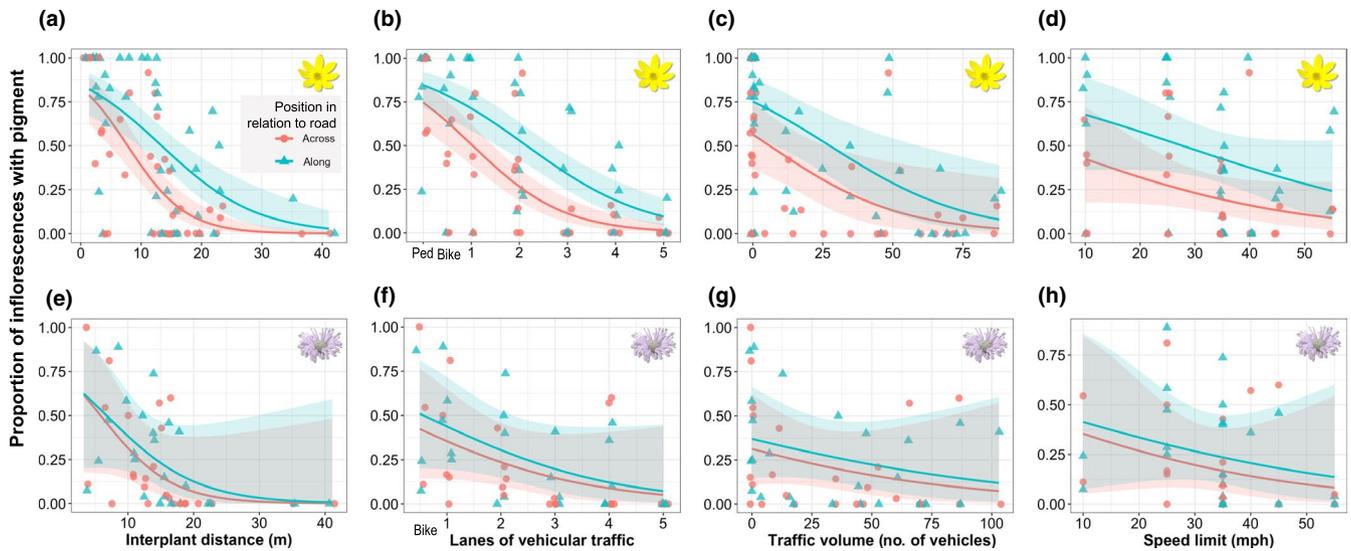
FIGURE 2 Relationship between road characteristics and pigment transfer in coreopsis (a–d) and monarda (e–h). Red circles represent data from plants located across the road/path from the pigment-laden plant, while cyan triangles represent plants alongside the road/path. Lines show best-fit regression according to binomial GLMs; shading indicates 95% confidence intervals
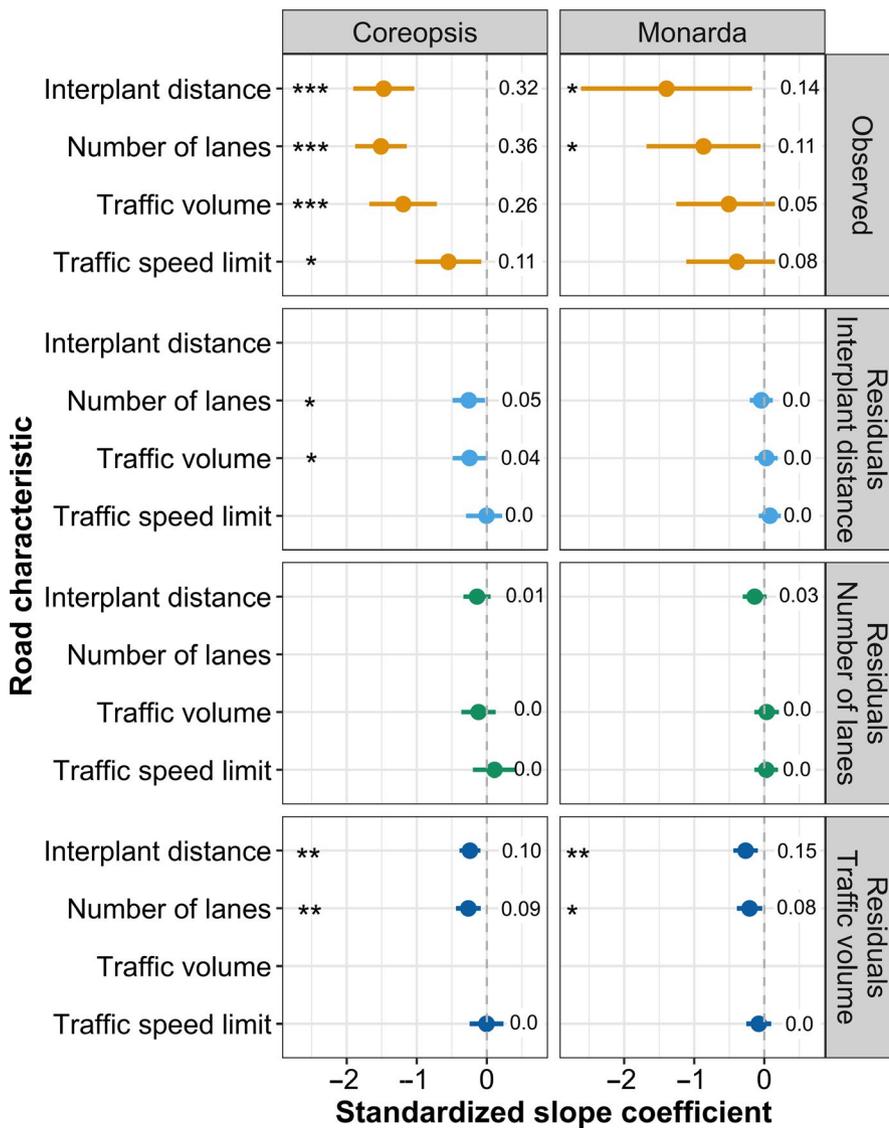

FIGURE 3 Effect of road characteristics on pigment transfer in coreopsis and monarda. Points represent β estimates and bars represent $\pm SE$ for each predictor, derived from binomial GLMs. Numbers to the right are R^2 values for that model. In the top panel, β and R^2 values are for model including plant position; all other panels show values for model using residuals from models in top panel as the response variable. Significance codes: $*p < 0.05$, $**p < 0.005$, $***p < 0.001$

While the magnitude of the difference in levels of pigment transfer between 'across' and 'along' plants was greatest for smaller roadways, 'across' plants on smaller roads nevertheless received substantial pigment in both species. On larger roads (≥3 lanes), by contrast, few 'across' plants received any pigment: for the 14 roads with ≥3 lanes, 71% of 'across' coreopsis plants received no pigment, compared to 19% of plants on the 26 roads/paths with ≤2 lanes; for monarda, the numbers were 75% and 1%, respectively.

None of the vegetation attributes of road/path verges (regular mowing, presence of semi-natural habitat, presence of significant floral resources) affected pigment transfer in coreopsis ($p > 0.2$ in all cases). For monarda, regular mowing had a marginally significant positive effect on pigment transfer ($\beta = 3.7 \pm 2.0, z = 1.81, p = 0.07$); including this habitat attribute as a predictor of pigment transfer improved model fit over the model including only interplant distance ($\Delta AICc = 5.3$).

For coreopsis, the orientation of the 'along' plant relative to the flow of traffic had a significant effect on pigment transfer, with plants oriented with the flow of traffic relative to the pigment-added plant having a higher proportion of inflorescences with pigment ($M \pm SE = 0.52 \pm 0.13, N = 9$) than those oriented against traffic (0.40 ± 0.08, $N = 18; z = 2.50, p = 0.01$). There was no equivalent effect on pigment transfer for monarda (with traffic: $0.17 \pm 0.14, N = 6$; against traffic: $0.31 \pm 0.06, N = 15; z = 0.21, p = 0.8$).

3.4 | Does pigment transfer differ between road/path sites and contiguous sites?

For coreopsis, the proportion of inflorescences with pigment was, unexpectedly, lower on average in contiguous sites than in road or path sites ($M \pm SE$, contiguous sites: 0.13 ± 0.05; road/path sites: 0.46 ± 0.04; Mann–Whitney U-test: $W = 593.5, p < 0.001$). This was driven primarily by low levels of pigment transfer to nearby plants (5 m from pigment-added plant; Figure S4). Plants in lawn contiguous sites received substantially less pigment than those in meadow contiguous sites (lawn: 0.04 ± 0.02; meadow: 0.26 ± 0.11), though due to the small sample size this difference was not significant (Mann–Whitney U-test: $W = 70, p = 0.2$). When the two contiguous site habitats were considered separately, the estimated relationship between distance and pigment transfer for meadow sites was indistinguishable from that for road/path sites, while that for lawn sites had a significantly reduced intercept (Figure S4).

For monarda, there was only a slight, non-significant difference in the proportion of inflorescences with pigment between contiguous sites and road sites (contiguous sites: 0.17 ± 0.03; road/path sites: 0.25 ± 0.04; Mann–Whitney U-test: $W = 297, p = 0.9$; Figure S4).

4 | DISCUSSION

Our study shows that roads and paths pose a significant barrier to bee movement, and therefore substantially reduce pollen transfer. Separation by a road reduced pigment transfer (a proxy for pollen transfer) between coreopsis individuals by half and between monarda individuals by one-third. Surprisingly, the negative effect on pigment transfer persisted even on narrow and quiet roads and paths, though this effect differed between plant species. For monarda, we detected an effect of roads but not of dedicated cycling paths (though the small number of path sites sampled may have obscured any effect of such structures). For coreopsis, even narrow cycling paths impeded pigment transfer, though pedestrian-only paths and sidewalks appeared not to (Figure 1).

Differences between coreopsis and monarda in the effect of roads and paths on pigment transfer may be due to differences in the assemblage of bees visiting each species. Mean body size of bees visiting coreopsis was significantly smaller than that of bees visiting monarda. In bees, foraging distance is correlated with body size (Greenleaf et al., 2007). Thus, a road that is devoid of floral resources may pose more of a barrier to smaller bees. It may also be that smaller bees are more vulnerable to vehicle collisions, since evidence suggests that they cross roads at lower heights (Munguira & Thomas, 1992; Ries et al., 2001; Saarinen et al., 2005). Additionally, smaller bees may be more vulnerable to traffic-induced air turbulence, both within and alongside roads. The fact that 'along' coreopsis plants oriented downstream from pigment-added plants (i.e. in the direction of vehicle travel) received more pigment than plants located upstream suggests that traffic-induced airflow may influence small bee movement alongside roads. Our results are consistent with findings from Franzén et al. (2009) that only 10% of marked individuals of a solitary bee, *Andrena hattorfiana*, crossed a road <10-m wide, even though it was unpaved.

We hypothesized that traffic characteristics (volume and speed) would be the road characteristic that best explained pigment transfer patterns, that is, impeding pollinator movement primarily by acting as conduits for fast-moving vehicles. Instead, we found that road width, not traffic volume or speed, was the best predictor of pigment transfer in coreopsis, and that in monarda only interplant distance was a significant predictor. This suggests that the physical presence of the road, rather than the vehicles that travel along it, is the primary impediment to bee movement. However, this result should be interpreted with caution. Traffic volume and road width were highly correlated ($R^2 = 0.56$). Moreover, we measured traffic volume over only a 5-min interval during peak traffic, which may not accurately capture traffic volume over the course of the day at all sites (e.g. our traffic survey of a site close to a hospital, with a shift schedule that differs from the typical 09:00–17:00 hr, may have underestimated total traffic volume). Similarly, our measure of traffic speed was the posted legal speed limit; the degree to which traffic obeyed these limits, and thus the accuracy of this measure, varied across sites (authors' pers. obs.). Thus, while we cannot entirely disentangle the effects of the physical presence of roads from the effects of traffic, our results suggest that both play a role. However, more controlled experiments (e.g. comparing pollinator or pigment movement between high- and low- traffic days) are needed to disentangle the relative importance of physical infrastructure and traffic.

We had expected that higher quality habitats, characterized by the presence of substantial floral resources and areas of semi-natural habitat, would support higher pollinator activity and thus promote pigment transfer. Instead, we found no effect of vegetation attributes on pigment transfer in coreopsis, and a weak but counterintuitively positive effect of the presence of lawn on pigment transfer in monarda. This study occurred in an urban area, while most other studies of the effects of roadside vegetation on pollinator communities have been conducted in rural landscapes (but see Baldock et al., 2019). Perhaps, aspects of the urban environment, such as ecological filtering (Fitch, Glaum, et al., 2019; Fitch, Wilson, et al., 2019) or impediments to dispersal (Jha & Kremen, 2013) reduce the effects of roadside management and vegetation characteristics documented by studies in rural landscapes (Hopwood, 2008; Phillips et al., 2019).

Finally, we hypothesized that plants alongside a road would experience reduced pigment transfer in comparison to plants in contiguous habitat away from a road. We did not find that to be the case for either species (Figure S4). For monarda, there was no difference in pigment transfer between contiguous and road/path sites. Surprisingly, for coreopsis pigment transfer was significantly lower at contiguous sites than at road/path sites. Our contiguous sites comprised two habitats, lawn and semi-natural meadow. Our finding of low pigment transfer at contiguous sites was largely driven by lawn sites; levels of pigment transfer at meadow sites were indistinguishable from road/path sites. It is not surprising that isolated plants within lawns—a habitat that typically has few flowers and thus attracts and supports few pollinators—would be visited less than plants in higher-quality meadow habitats. It is puzzling, however, that road/path sites, many of which also included lawns, did not show parallel habitat-based differences in pigment transfer or overall lower levels of pigment transfer. It may be that road/path verges, even those maintained as lawns, are less intensively managed than equivalent lawns in city parks, and therefore provide better habitat for pollinators than the contiguous site lawns. The idea that road verges provide good habitat for pollinators is supported by several studies showing that the density and species richness of both flowers and pollinators are generally higher in road verges as compared to agricultural (Hanley & Wilkins, 2015; Osgathorpe et al., 2012; Phillips et al., 2019) and forest and woodland habitats (Riva et al., 2018). Moreover, Baldock and colleagues found that the density and species richness of flowers and pollinators in road verges in three cities in the UK were similar to several other urban habitats (Baldock et al., 2019). In addition, bees may use road and path edges as navigational aids (Menzel et al., 2019), and, as our research suggests, traffic-induced patterns of airflow may channel bees' flight along roadsides. Such channelling would help explain increased pigment transfer to 'along' plants over plants in contiguous sites where pollinator flight direction is not constrained. This latter explanation is supported by our finding that pigment transfer to coreopsis in contiguous sites was much lower than expected for plants close to the pigment-added plant, but at greater distances from the pigment-added plant was equivalent to levels seen at road/path sites.

Taken together, the results of this study indicate that although roadsides may attract and support sizable bee populations, roads pose barriers to bee movement, and consequently pollen vectoring. While our findings suggest that even small roads and bicycle paths are barriers to bee movement, we nevertheless observed substantial pigment transfer across these roads, suggesting that this barrier does not preclude dispersal of bees and insect-vectored pollen. However, pigment transfer across roads was rare in either species for roads with three or more lanes of traffic. While we surveyed roads only up to five lanes wide, many roads often exceed this width. Moreover, our estimate of the effect of roads is likely conservative, since the study took place during the COVID-19 pandemic, when traffic was substantially reduced from pre-pandemic levels. Therefore, we suggest that medium-sized and large roads may impede the movement of bees sufficiently to impact foraging and pollination. We predict that this is particularly likely in plants that rely on insect-vectored cross-pollination for successful reproduction (particularly those pollinated primarily by small bees), and in urban areas where habitat fragments are commonly surrounded on all sides by busy roads. Further research on the genetic structure of populations of pollinating insects (particularly smaller species) and, insect-pollinated plants, with explicit reference to roads as potential barriers, is needed to evaluate this claim.

In light of our findings, we recommend the evaluation and implementation of strategies to make roads less of a barrier to pollinators. Habitat corridors have been effective in reducing the impact of roads for many vertebrate taxa (Gilbert-Norton et al., 2010), and this concept can be adapted for pollinators. With any such measure that encourages pollinators to cross the road, it will be important to evaluate whether it results in elevated mortality due to increased vehicle collisions, and if so whether this outweighs the benefits of increased population connectivity (Keilsohn et al., 2018). Importantly, these interventions have the potential to dovetail with efforts to promote alternative modes of transportation and reduce traffic accidents via so-called 'road diets', which reduce the area of a road dedicated to vehicular traffic (Ewing, 2008; Huang et al., 2002), and consequently reduce the barrier to pollinator movement. These and related efforts have the potential to reduce the environmental stress roads exert on all of us, human and non-human alike.

AUTHORS' CONTRIBUTIONS

G.F. and C.V. are both first authors and listed alphabetically; G.F. and C.V. conceived and designed the study, collected field data, carried out data processing and analysis, and wrote and revised the manuscript.

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SUPPORTING INFORMATION

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