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Forum

Roadside habitat: Boon or bane for pollinating insects?

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Abstract

Pollinators, which provide vital services to wild ecosystems and agricultural crops, are facing global declines and habitat loss. As undeveloped land becomes increasingly scarce, much focus has been directed recently to roadsides as potential target zones for providing floral resources to pollinators. Roadsides, however, are risky places for pollinators, with threats from vehicle collisions, toxic pollutants, mowing, herbicides, and more. Although these threats have been investigated, most studies have yet to quantify the costs and benefits of roadsides to pollinators and, therefore, do not address whether the costs outweigh the benefits for pollinator populations using roadside habitats. In this article, we address how, when, and under what conditions roadside habitats may benefit or harm pollinators, reviewing existing knowledge and recommending practical questions that managers and policymakers should consider when planning pollinator-focused roadside management.

Keywords: pollinators, roadside ecology, road verge management, butterflies, bees

Roads have become a ubiquitous part of terrestrial environments: The United States alone has paved enough roads to circle the equator 168 times (Brown 2001, Federal Highway Administration 2017). Although roadways themselves occupy a small percentage of land area, their ecological impacts extend far beyond their physical dimensions: Researchers estimate that roads affect about 20 times the area actually covered by pavement (Forman et al. 2002). The direct impacts of existing roads on animals include mortality from collision with vehicles, chemical effects from traffic, population fragmentation, and increased edge effects; in addition, roads alter habitat by changing hydrology, increasing erosion, and disturbing soils (Forman and Alexander 1998, Coffin 2007). Nonetheless, vegetated roadsides may also provide valuable habitat and corridors for feeding, breeding, and movement (Villemey et al. 2018).

For most vertebrates, the negative effects of roads—particularly habitat fragmentation and vehicle collisions—outweigh the potential benefits roadside habitats may offer, and the expanding global network of roads poses a serious threat to many vertebrate species (Benítez-López et al. 2010, Laurance and Balmford 2013, Ouédraogo et al. 2020). For invertebrates like pollinating insects, however, the impact of roads and road verges (the vegetated zones bordering roads) is more nuanced, because road verges can provide significant habitat for small insects. Although vehicle collisions may cause levels of mortality for mobile insects similar to—or higher than—those for vertebrates, road verges often harbor floral and vegetative resources in otherwise depauperate landscapes (Seibert and Conover 1991, Muñoz et al. 2015). As land becomes increasingly developed and homogenized for urban and agricultural uses, the narrow but extensive bands of habitat available alongside roads may provide important refuges for pollinating insects (hereafter, *pollinators*).

Pollinator populations and habitats are facing steep global declines (Zattara and Aizen 2021). This is especially alarming because three quarters of global human food crops (Klein et al. 2007) and the function of most wild plant communities depend on pollinators (Ollerton et al. 2011). With land-use change and habitat loss identified as the primary causes of global declines in bees and butterflies (Sánchez-Bayo and Wyckhuys 2019, Zattara and Aizen 2021) and over 50% of Earth's terrestrial surface now used by humans (Hooke et al. 2012), supporting and increasing pollinator populations through strategic use of the remaining undeveloped land is of paramount importance for both humans and natural systems. Many transportation departments and road managers are therefore considering measures to attract pollinators to road verges, using these undeveloped zones to benefit pollinator populations (Hopwood et al. 2015, Cariveau et al. 2019). In the United States, hundreds of millions of dollars have recently been directed to expanding and enhancing pollinator habitat in road verges (Raichel 2021), and similar investments are under consideration in other countries (Phillips et al. 2020).

Road verges have several potential advantages for pollinators. They provide diverse floral resources in otherwise homogenous landscapes (e.g., crop monocultures) and may be able to increase population connectivity by providing bands of habitat alongside roads. Road verges host forbs that can serve as nectar and host plants for endangered butterflies (Smallidge et al. 1996, Cariveau et al. 2019) and other pollinators. They receive additional moisture from runoff in arid landscapes, resulting in enhanced plant growth and resources for pollinators (Holzapfel and Schmidt 1990, Wojcik and Buchmann 2012). However, road verges also come with potential risks; for example, runoff may contain pollutants that result in contaminated roadside plants (Van Bohemen and Van de Laak 2003, Mitchell et al. 2020), and pollinators using road verges may collide with traffic or be killed by the mowing and spraying of roadside vegetation (Martin et al. 2018, Phillips et al. 2019, Steidle et al. 2022). Some researchers express concern that road verges may be ecological traps for pollinators, luring them into risky and harmful environments (Berenbaum 2015,

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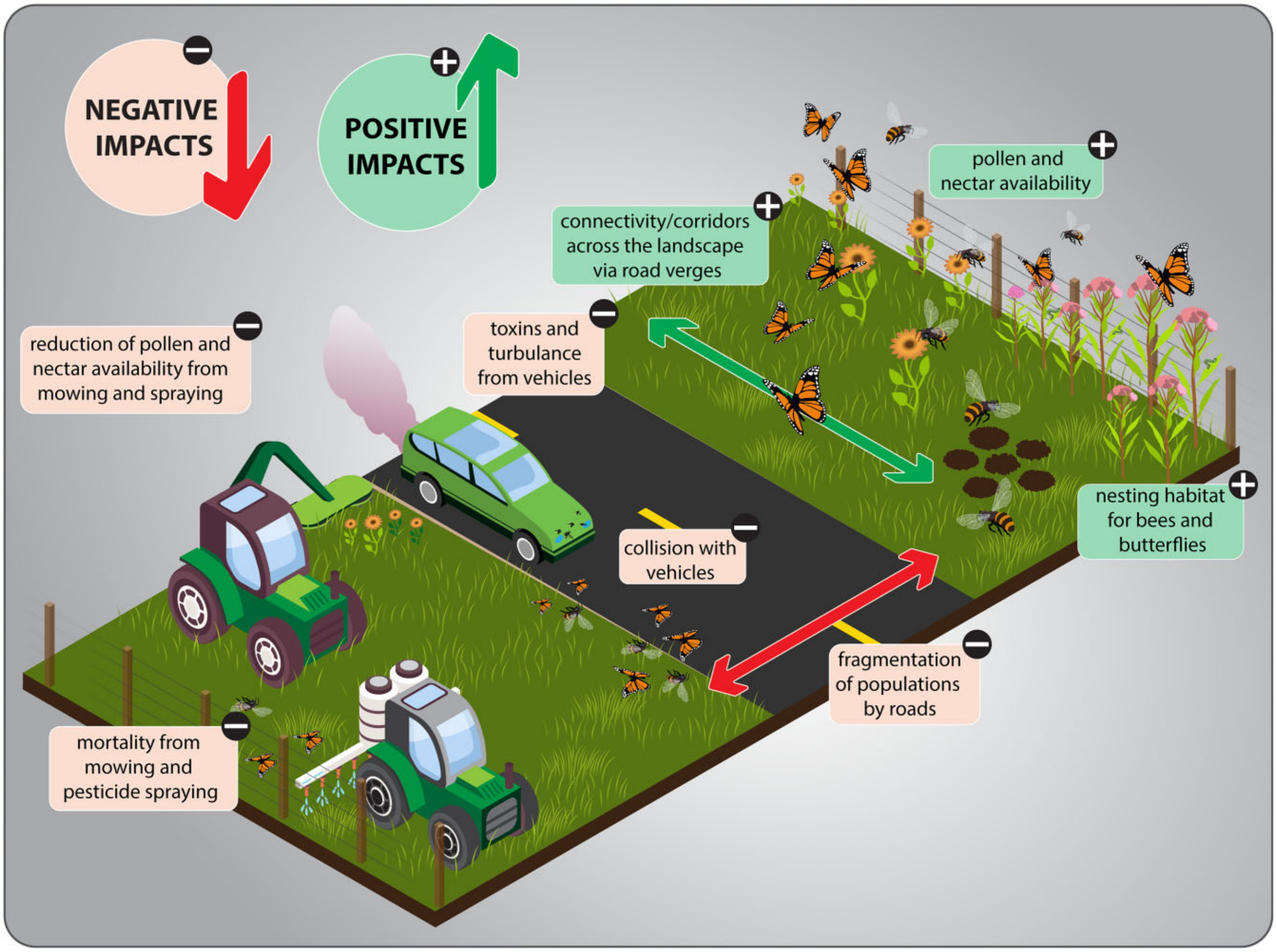

Figure 1. Roads and roadsides provide both benefits and hazards to pollinators, and road verge management practices can help shift the balance of positive (+) and negative (–) impacts on pollinator populations. Vehicles emit toxins, create turbulence in the air adjacent to roadsides, and can cause direct mortality through collisions. Roads can fragment populations of organisms existing on either side of the road. Although practices such as mowing and spraying can harm pollinators directly or indirectly (e.g., by reducing food availability), well-placed and well-timed management activities can also help reduce pollinator collision mortality and toxin exposure. Farther from the roadway, beneficial roadside plantings can provide food, larval host plants, and nest sites and can potentially enhance pollinator habitat connectivity.

Teixeira et al. 2017, Keilsohn et al. 2018), whereas others conclude that planting flowers along road verges is an important way to enhance pollinator populations (Raemakers et al. 2001, Ries et al. 2001, Hanley and Wilkins 2015).

Such conflicts among researchers highlight the need to thoroughly review the costs and benefits of road verge use for pollinators and to ask whether—and under what conditions—road verge restoration for pollinators is a good conservation choice. Are there data to show that roadside plantings actually benefit pollinator populations, or could they instead be attractive sinks, enticing dispersing insects into more dangerous and less productive habitats? Although reviews of road impacts on insects exist (Muñoz et al. 2015, Villemey et al. 2018, Phillips et al. 2020), they leave this vital question unanswered or conflate abundance with benefit; habitat *used* by pollinators is not necessarily habitat that *benefits* pollinator populations (Van Horne 1983). Given the range of novel anthropogenic threats in roadsides (e.g., traffic, pollutants, mowing, herbicides), dispersing pollinators may incorrectly assess vegetated roadsides as good habitat, but the rates of survival and reproduction may, in fact, be lower there than in other habitats, resulting in a negative effect on pollinator populations (Delibes et al. 2001). As funding pours in to support pollinators in road verges, it is critical that we summarize what is known—and highlight what is still unknown—about how roadside habitats and their management affect pollinator populations, thereby guiding funds toward actions that will best serve declining pollinators. In this review, we discuss the factors that affect roadside pollinators and synthesize current knowledge and data gaps, providing recommendations for future research, policy, and management.

Roadside attraction: Life and death for pollinators

Assessing roadsides' impacts on pollinator populations requires weighing opposing positive and negative impacts (figure 1). For example, road verges provide habitat where pollinators can breed, but traffic kills a portion of the pollinators that breed there (Phillips et al. 2019). Keilsohn and colleagues (2018) framed the question well: "How extensive does a [roadside] restoration planting have to be before it produces more insects than it kills?" The answer to that question depends on many factors, including the density and type of nectar and pollen resources and nest sites in the planting, the proportion of pollinators killed by vehicles, and the relative fidelity and survivorship of pollinators on roadsides compared with other available habitats. All those factors likely vary among roadsides and among pollinator species, making the answer difficult to determine.

Even if they can be measured, the most direct population effects of roads—birth and death—can be challenging to compare, because pollinators that breed in road verges might have alternatively bred successfully elsewhere, and individuals killed by roads may be transient and not breeding in the roadside habitat. Nonetheless, a few studies in the farmlands and grasslands of southern Poland have shown that the community profile of road-killed pollinators more closely matched the community using roadside habitats than habitats away from roads, suggesting that roadside breeders likely represent a high proportion of road-killed pollinators (Skórka et al. 2013, 2018).

Insect population sizes and birth rates are very difficult to estimate, and data on reproductive output along roadsides are lacking. A few studies document that butterflies and bees do reproduce and nest in roadside habitats, but their reproduction rates are not quantified (Munguira and Thomas 1992, Heneberg et al. 2017). Comparison studies suggest that insects breeding in road verges may have a lower chance of survival and exhibit higher physiological stress levels (e.g., elevated heart rates) than those breeding away from roads (Snell-Rood et al. 2014, Davis et al. 2018). For example, monarchs developing on roadsides have lower survivorship as larvae, even before potentially colliding with traffic as adults (Snell-Rood et al. 2014). Given that pollinators using roadside habitat are more likely killed by traffic (Skórka et al. 2013) or poisoned by pollutants (De Silva et al. 2021), the breeding habitat along roadsides might not produce a net benefit for pollinator populations. However, without studies quantifying pollinator reproductive output along roadsides (and comparing this with the output from nonroadside habitat in the same type of landscape), we cannot conclude whether roadside birth rates exceed mortality rates.

Collision mortality—insects colliding with moving vehicles—is estimated to kill billions of insects annually (Baxter-Gilbert et al. 2015). However, studies investigating its relative impact suggest that traffic kills a small proportion of the insects using roadside habitat. The estimates of butterfly mortality by vehicle collision in three studies were 0.6% to 7% of adults surveyed in roadside habitat, which the researchers suggested is a much lower proportion than the mortality caused by natural factors (Munguira and Thomas 1992, Skórka et al. 2013, 2018). Road-crossing frequency and collision mortality varies by species. Studies have shown greater mortality for butterfly species that are smaller (Skórka et al. 2013), that fly below 2 meters (Rao and Girish 2007), and that are more mobile (de la Puente Ranea et al. 2008, Remon et al. 2018). Flight style and speed vary greatly among taxa and likely affect an insect's susceptibility to vehicle collisions (Cant et al. 2005). Most studies estimating insect collision mortality focus on butterflies, dragonflies, or carabid beetles; data on bees and pollinating flies are rare (Muñoz et al. 2015, Phillips et al. 2020). Some bees exhibit high site fidelity and may therefore be less likely to cross roads and be killed (Bhattacharya et al. 2002, Hopwood et al. 2010). However, a study in Ontario, Canada, showed higher collision mortality in bees (26.8 per kilometer [km] per day) and flies (202.3 per km per day) than in butterflies (10.1 per km per day; Baxter-Gilbert et al. 2015). This matches a correlation between smaller size and higher collision mortality (Skórka et al. 2013). Smaller species may take more time to cross roads, may be less able to avoid traffic, or may simply be more common. In addition, the small size and relative density of bees and flies mean that they are more likely to remain stuck to vehicles and to be overlooked and undercounted in roadside roadkill surveys (Rao and Girish 2007).

Overall, data on the relative or absolute cost of collision mortality to pollinator populations are limited. Studies suggest higher traffic and medium-high-speed roads may be especially detrimental (McKenna et al. 2001). Roads appear to kill less than 10% of adult butterflies using roadsides habitats; the data are lacking for other taxa, but the percentages may be higher (Munguira and Thomas 1992, Skórka et al. 2013, Baxter-Gilbert et al. 2015, 2018). Holometabolous insects (those that undergo complete metamorphosis, including most pollinators) exhibit very high mortality as eggs and first-instar larvae and again as pupae; therefore, prebreeding collision mortality of the relatively small proportion of individuals that reach adulthood could have an outsized impact on pollinator populations (Ito 1959). Also, collision mortality may compound other roadside-related causes of death, such as herbicide application, mowing, and toxin exposure (Peterson et al. 2009).

Although available evidence suggests that roads kill less than 1 in 10 butterflies using roadside habitats (Skórka et al. 2013), the long-term impact of collision mortality on pollinator populations is unknown, and its potential impacts are often understated (Teixeira et al. 2020). Further research is required, and many questions remain. Besides population reduction, collision mortality may also influence morphology by selecting for certain attributes. For example, roadside-nesting cliff swallows demonstrate selection for shorter wings and more maneuverability to avoid traffic (Brown and Brown 2013), and in three European bumblebee species, there is a positive correlation between body size and road density (Theodorou et al. 2021). In addition to affecting population dynamics, the ubiquity of roads could be altering pollinator morphology or behavior (Taylor and Merriam 1995, Fahrig 2007) or selecting for a novel community of pollinators with particular morphologies and behaviors (Rebrina et al. 2022).

Road impacts: Habitat fragmentation or habitat corridor?

In addition to affecting vital rates, roadsides alter pollinator dispersal. Roadsides may connect pollinator metapopulations by providing habitat corridors parallel to roads (Dániel-Ferreira et al. 2022). Alternatively, roads can fragment pollinator populations by limiting dispersal between habitats across roads (Andersson et al. 2017). How do these opposing effects on dispersal balance out, and what influences that balance? Advances in fine-scale remote sensing—particularly, harmonic radar—and the application of fluorescent powered dyes may help address this question by enabling researchers to follow the paths of many individual insects over time (Osborne et al. 2002, Dániel-Ferreira et al. 2022, Rhodes et al. 2022). Comparing the extent to which pollinators travel alongside and across roads with their movements in the broader landscape can illuminate the influence of roads on pollinator dispersal and population connectivity.

As of yet, however, there is very little definitive evidence that roadsides serve as a habitat corridor for insects. Insect dispersal is difficult to study, and effective studies must compare dispersal rates of roadside insects with those away from roadsides (Villemey et al. 2018). A recent study showed that, indeed, pollinators tended to move along vegetated roadsides more frequently than into adjacent seminatural pastures and meadows, suggesting a corridor effect (Dániel-Ferreira et al. 2022). A modeling study showed similar movement patterns in monarch butterflies, presumably because of the high density of their host plants in road verges (Grant et al. 2018). Roads, like other linear landscape features, can also be used as navigation aids by insects, influencing pollinator movements (Cranmer et al. 2012, Menzel et al. 2019). Improving roadside floral resources and habitat quality may reduce the frequency that butterflies leave the roadside and cross the road; therefore, high-quality roadside habitat might promote corridor-like movement parallel to roads and reduce the proportion of pollinators killed by crossing roads (Ries et al. 2001, van Rossum et al. 2011, Skórka et al. 2013). However, more studies are needed to adequately assess the effect of roadside habitat quality on collision mortality and patterns of pollinator movement.

Ample evidence exists that roads can fragment species' populations, resulting in reduced gene flow, potential genetic bottlenecks, and threatened population viability for many imperiled species, including some invertebrates (Keller et al. 2004, Shepard et al. 2008, Diffendorfer et al. 2020). Even mobile insect species that could easily cross roads may avoid doing so, resulting in an effective loss of gene flow (Holderegger and Di Giulio 2010). For example, researchers found that bumblebees avoided crossing roads even when adequate or superior floral resources were present across the road, and, when their favored plants were removed, bumblebees moved to other patches of plants on the same side of the road rather than across it (Bhattacharya et al. 2002). Despite this, bumblebees that were captured and moved to flower patches across the road readily crossed it to return to their original patch, suggesting that tendencies toward site fidelity may work in concert with roads to fragment populations (Bhattacharya et al. 2002, Hopwood et al. 2010). This result is corroborated by a study that showed substantially different bee and wasp communities on opposite sides of a large highway, indicating again that bees and wasps were not dispersing across the road despite their physical capacity to cross it (Andersson et al. 2017). Butterflies, by contrast, show limited or variable barrier effects; mark–recapture studies suggest that roads partially restrict the movement of some butterfly species but not others (Munguira and Thomas 1992, Fry and Robson 1994, Askling and Bergman 2004). This likely reflects that butterfly species vary from highly local habitat specialists to long-distance migrants. However, the increasing prevalence of roads could alter these movement patterns too; a landscape-scale study of the bog fritillary butterfly, for example, showed that individuals were more reluctant to cross habitat patch boundaries as fragmentation increased (Schtickzelle et al. 2006).

Fragmentation by roads may reduce insect genetic diversity, especially for species with limited dispersal capacity (Tepedino 2016). Metapopulation research shows that limiting dispersal can threaten population viability even without removing habitat (Levins 1969, Templeton et al. 2011); roads can do both. Roads can negatively affect genetic diversity in compounding ways by reducing (although typically not eliminating) gene flow and by reducing population size through collision mortality (Jackson and Fahrig 2011).

Similar to collision mortality and roadside reproduction, far more evidence exists of roads' potential negative role in reducing dispersal than their positive role in facilitating it. To what extent this matches the actual balance of dispersal impacts is an important question. To address this, studies are needed that compare insect dispersal rates along roadsides with those in the same type of landcover away from roads. In the meantime, limited available data suggest that native roadside plantings that connect with habitat on adjacent lands are the most likely type of roadside plantings to benefit pollinators, potentially reducing road collision mortality and fragmentation effects (Ries et al. 2001, Hopwood 2008, Hopwood et al. 2015).

Chemical costs of roadside life

Although roadsides provide floral resources, nest and oviposition sites, and host plants for pollinators, they also harbor high levels of toxins from vehicle emissions, exhaust fumes, tire and road wear, herbicide applications, and road salts. These toxins provoke concern that roadside vegetation might harm or poison the pollinators that use it (Mitchell et al. 2020). Vehicle emissions, tire and road wear, and exhaust all release toxic heavy metals into the local environment. As would be expected, these toxins show a declining concentration gradient away from roads, with the highest concentrations in the 0–50 meters closest to the road (Van Bohemen and Van De Laak 2003). Most research on the impacts of vehicular toxins on insects occurred in the 1970s through the 1990s, before leaded gasoline was phased out in many countries—although in some countries, its legal use continued as late as 2021 (Ritchie 2022). This research has shown that some insect families, including butterflies, had fewer individuals in areas of higher exhaust closer to roads, whereas others, such as hemipterans, increased in population size in proximity to roads, possibly because of lower predator density (Przybylski 1979, Muskett and Jones 1980). Higher concentrations of lead and other toxic heavy metals were found in the tissues of butterfly larvae, beetles, true bugs, and bees closer to roads (Price et al. 1974, Beyer and Moore 1980, Udevitz et al. 1980). One study showed that lead in insects and other invertebrates decreased by 64% from 2 to 150 meters from the road (Wade et al. 1980).

Decades after leaded gas was banned in most countries, lead concentrations in roadside plants and animals still exceed the limits recommended by the World Health Organization, whereas new, potentially toxic elements have been recently introduced in vehicle emissions, including antimony from brake linings, platinum group elements from abraded catalytic converters, and manganese, which replaced lead as an antiknock additive in gasoline (World Health Organization 2019, De Silva et al. 2021). The impacts of pollutants on invertebrates depend largely on their bioavailability, and the bioavailability of most of these newer pollutants is unknown (De Silva et al. 2021). However, manganese contamination is now common in roadside soils and plants, often exceeding levels known to cause toxicity in rodents and humans (Lytle et al. 1995) and to negatively affect honeybee foraging behavior by altering brain chemistry (Søvik et al. 2015). Pollinators, including honeybees and bumblebees, may also respond to heavy metals by reducing foraging time at contaminated flowers (Xun et al. 2018, Phillips et al. 2021). Perhaps because of these avoidance behaviors or because of toxin-induced mortality, researchers have found a strong negative correlation between heavy metal concentrations in the environment (measured in pollen) and solitary bee diversity and abundance (Moroń et al. 2012).

Sodium poses an additional threat to roadside pollinators. In cold regions, salt is applied to reduce ice on roads, often in significant amounts (e.g., 300,000 tons per winter in the Minneapolis–St. Paul metropolitan area; Sander et al. 2007). Running off into roadsides, road salt increases the sodium concentration in soils and roadside plants, affecting pollinators (Mitchell et al. 2020). Road salt accumulates most in poorly drained clay soils and can result in high mortality of milkweeds and other nectar-providing forbs in those habitats (Haan et al. 2012, Malcolm 2018, Hintz and Relyea 2019). Monarch larvae that develop on roadside milkweed plants contain significantly higher sodium concentrations than do monarchs that developed on milkweed away from roads (Mitchell et al. 2020). Given that sodium is an essential insect micronutrient, this increased concentration can (up to a point) benefit monarchs, causing increased muscle mass in males and larger eyes in females (Snell-Rood et al. 2014). As with other pollutants, sodium concentrations are highest in the plants closest to the road, and milkweed sodium may reach toxic levels for monarchs in less than 10% of plants (Mitchell et al. 2020). Experimental manipulations show that egg-laying monarchs do not avoid plants with toxic levels of sodium (Mitchell et al. 2019). Road salt therefore exemplifies another risky trade-off of roadside use. Although sodium might have potential fitness benefits for monarchs, monarch larval survivorship was lower on sodium-rich roadside milkweed than on milkweed grown away from roads, suggesting that road salt, as with other pollutants, likely does more harm than good for monarchs (Snell-Rood et al. 2014, Mitchell et al. 2020).

In addition to sodium, heavy metals, and other contaminants, roadside pollinators also face chemical exposure from herbicides, which are commonly applied to road verges to maintain visibility, discourage woody growth, and control noxious weeds (i.e., invasive alien plants). Herbicide use can result in weed reduction, which may benefit pollinators by favoring native floral diversity (Ries et al. 2001, Valtonen et al. 2006); however, herbicides are often applied broadly and sometimes misapplied, resulting in the deaths of insect host plants at critical developmental periods, the loss of floral resources, and the direct death of pollinators (Pleasants and Oberhauser 2013, Hopwood et al. 2015). Herbicide use has been identified as a key threat to roadside monarch and milkweed populations in the western United States (Waterbury et al. 2019). Although some studies have shown that the benefits of reducing weeds through targeted herbicide use may outweigh the negative impacts of herbicides on butterflies (Yahner 2004), most studies have shown that broad-spectrum herbicides increase pollinator mortality and can cause sublethal negative effects on foraging ability and disease resistance and that they should therefore be used sparingly (Larsen 2010, Prosser et al. 2016, Cullen et al. 2019). Both active and inert ingredients (e.g., adjuvants or surfactants) in common herbicides harm bees by damaging their gut microbiomes (Motta et al. 2018), impairing their navigation (Hahn et al. 2015) and adult learning capabilities (Ciarlo et al. 2012), and reducing sperm counts and survival rates (Belsky and Joshi 2020).

Whether herbicide application benefits pollinators (by reducing unpreferred weeds) or harms them (directly or by killing host plants and nectar-providing forbs) depends on when, where, and how the herbicide is applied. Blanket herbicide application and herbicide application in peak flowering season, both common practices in roadside management, are likely to adversely affect pollinators and tip roadside habitats toward becoming an ecological trap. In many regions, especially in the developing world, roadsides are used for growing crops (e.g., Igwegbe et al. 1992) and may therefore be sprayed with a variety of pesticides. Where roadsides are not cultivated for crops, they may receive far less herbicide, fungicide, and insecticide input than the surrounding agricultural land, making them a relatively safe option for pollinators in many areas. In parts of the United States, roadside managers even place "No-spray zone" signs in roadways to protect pollinator habitat, and a study showed that bumblebees preferred road margins over similar crop-facing margins by a factor of two (Hanley and Wilkins 2015). In some cases, agrochemical inputs may be more detrimental to pollinators than roadside herbicides and vehicle pollutants (Hanley and Wilkins 2015).

Plastics present another chemical threat to roadside insects and an important area for future study. Microplastics from tire wear could affect foraging and especially ground-nesting bees, potentially affecting bee health and cognition (Balzani et al. 2022). Plastic trash thrown from vehicles may affect plant growth, soil moisture, and insects that live underground for a portion of their lifetime, which includes most bee species (Chae and An 2018). Microplastics are an emerging threat to ecosystem functioning and biota and could affect plant function, soil physicochemical characteristics, soil-dwelling microbes, and fauna (Khalid et al. 2020). Studies suggest that microplastics can negatively affect insect survival, development, reproduction, and gut microbiota, especially at higher doses (Khalid et al. 2020). However, the effects of plastics on pollinators are still poorly understood, and further research is needed in this area.

Roadsides in a changing climate

Climate change has a variety of effects on roadside habitats, which vary geographically and seasonally. With increasing drought and aridification in many regions, the slightly higher roadside moisture availability caused by pavement runoff may make roadsides increasingly important for plants (and their pollinators) that require more moisture (Wojcik and Buchmann 2012). On the other hand, warming conditions will also heat the pavement adjacent to roadsides and warm roadside soils, potentially killing plants, overheating nesting bees, and releasing toxins from asphalt that could affect roadside pollinators (Khare et al. 2020). This is another area of roadside ecology in need of future research.

Less lawn, longer pastures for pollinators

As with herbicides, mowing road verges poses a major threat to roadside pollinators but may also provide them with benefits. Many ground-nesting bees require very short grass or bare ground in which to nest. For these species, a matrix of long and short grass areas is likely optimal. Mowing may also stimulate regrowth and extend the bloom period of certain plants. First-instar monarch survival more than doubled on milkweed stems that regenerated after mowing compared with undisturbed controls, for example, even though mowing reduced floral resource abundance for adult pollinators for 3–5 weeks (Haan and Landis 2020). Although mowing can promote beneficial regrowth in certain plants, it temporarily reduces floral resource availability and can change roadside vegetation composition, typically benefiting disturbance-prone exotics over native forbs (Prevéy et al. 2014, Phillips et al. 2019). Most critically, mowing road verges destroys pollinator habitat and larval host plants, and the blades can kill nesting adult pollinators, eggs, and larvae, presenting a significant—and understudied—mortality risk to roadside pollinators. Mowing may also compound other negative effects; for example, one study showed mowing verges increased butterfly collision mortality, likely by prompting dispersal across the road (Skórka et al. 2013).

The timing and extent of mowing is critical: Mowing when roadside vegetation is in flower and mowing entire road verges (fence line to fence line) heighten negative impacts on pollinators (Hopwood et al. 2015, Phillips et al. 2019). However, as was discussed previously, vegetation immediately bordering well-trafficked roads may be toxic to pollinators because of accumulated pollutants and salts. Therefore, regularly mowing a close-cropped clear zone of about 2 meters next to the road pavement is generally recommended for the safety of both drivers and pollinators, whereas the rest of the road verge should be mown as infrequently as possible—at most, once or twice a year, very early and late in the growing season (Hopwood et al. 2015). When mowing occurs, the use of arthropod-friendly mowing heads (such as

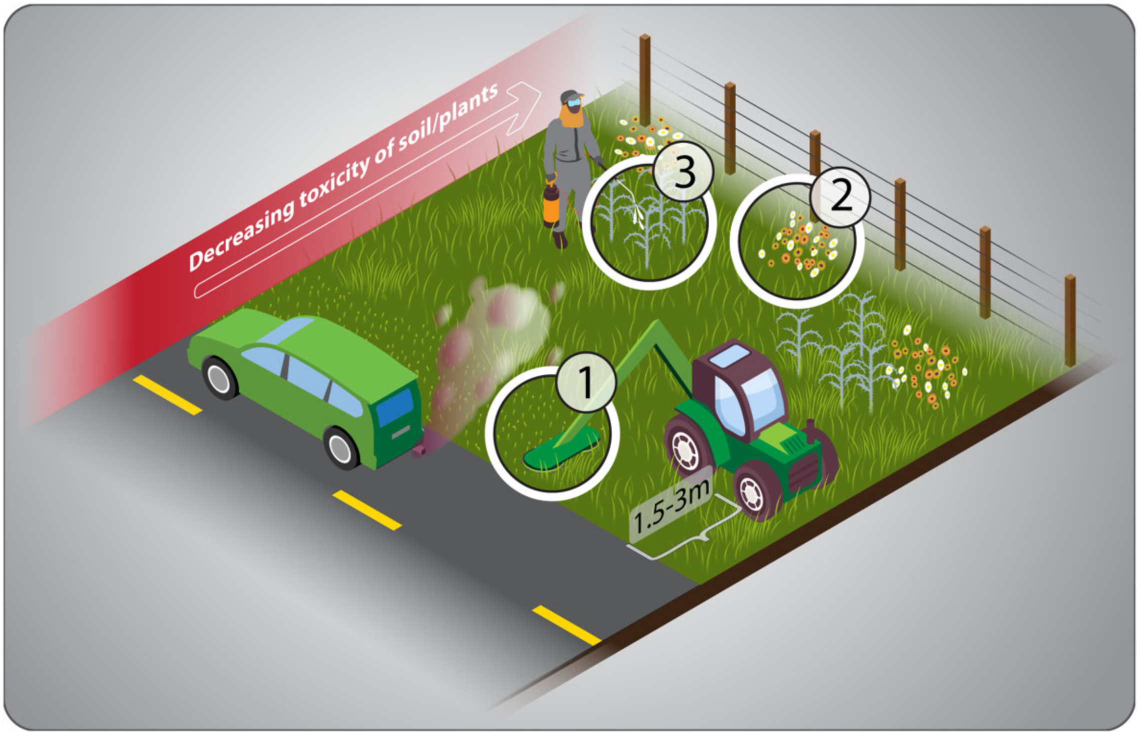

Figure 2. Best practices in road verge management can help support pollinators. (1) For roads with considerable traffic, mow a close-cropped clear zone of 1.5 to 3 meters bordering the pavement (narrower on lower-traffic roads), reducing pollinator exposure to roadway toxins. (2) Plant diverse native wildflowers in areas farthest from the road, away from the zone of toxicity. These areas should not typically be mown in the growing season. (3) Spot treat noxious weeds with herbicides before they flower rather than blanket treating road verges.

the MULAG Eco 1200 mowing head) and flushing bars is recommended and can substantially reduce the mortality of some insect groups, including butterflies (Humbert et al. 2010, Steidle et al. 2022).

From roadside ecology to management and policy

As pollinator populations decline and undeveloped lands become scarcer, understanding the potential impacts of road verge habitat on pollinators is increasingly important. Roads and roadsides present many risks to pollinating insects, and whether their potential benefits outweigh their harms likely depends on many factors, including herbicide use, mowing regime, traffic levels, and habitat quality. Judicious management of road verges increases their potential to benefit pollinators (figure 2), and substantial benefit can come from reductions in mowing frequency and herbicide use—actions that have the added benefit of saving funds.

There are reasons for optimism about the potential of roadside pollinator habitat. Better roadside habitat might decrease per-capita collision mortality by encouraging insects to stay on one side of the road rather than cross it (Ries et al. 2001), and limited data suggest that roadsides could serve as corridors to connect habitat fragments (Grant et al. 2018, Dániel-Ferreira et al. 2022). Locally, the numbers of butterflies observed in roadside habitats appear to substantially exceed (by 10 to 30 times) the numbers of butterflies killed by vehicles (Munguira and Thomas 1992, McKenna et al. 2001, Skórka et al. 2013). In some areas, the increasing scarcity of quality pollinator habitat in agricultural and developed landscapes may necessitate pollinators' reliance on roadsides as a last stronghold of local wild plant diversity.

However, the concerns of roadsides as an ecological trap and a population sink for pollinating insects remain. Lost in the buzz of attention around roadside pollinators is the fact that no studies have successfully addressed whether *any* roadsides are a source or a sink for *any* pollinators. This stands in stark dissonance with the millions currently being spent on roadside pollinator habitat initiatives (Raichel 2021), raising important concerns that well-intentioned projects might be doing a disservice to pollinator populations by attracting more pollinators into environments where traffic, toxicity, and road verge management reduce their survival and reproduction rates below the replacement rate (Delibes et al. 2001). Evaluating whether habitats are a source or a sink is very difficult, especially given the cryptic or inaccessible reproductive phases of most pollinating insects and the challenge of tracking individuals (Lewis et al. 2021). Nonetheless, we urge that future studies focus on measuring pollinator reproduction in roadside habitats, investigating the rates of immigration to and emigration from roadsides and, especially, assessing how roadside habitat restoration (e.g., planting flowers) affects the rates of collision mortality on roads.

Even without data on whether roadsides are a source or a sink for pollinators, managers and policymakers can still prioritize actions that will benefit roadside pollinators—particularly, by reducing the causes of their mortality, including summer mowing (Phillips et al. 2019), near-traffic vegetation and vegetated medians (Keilsohn et al. 2018), and roadside herbicide and insecticide use (Prosser et al. 2016, Cullen et al. 2019). We predict that mitigating these dangers, especially those that would be difficult to anticipate for pollinators selecting habitat (Delibes et al. 2001), will make roadsides less of a potential attractive sink for pollinators,

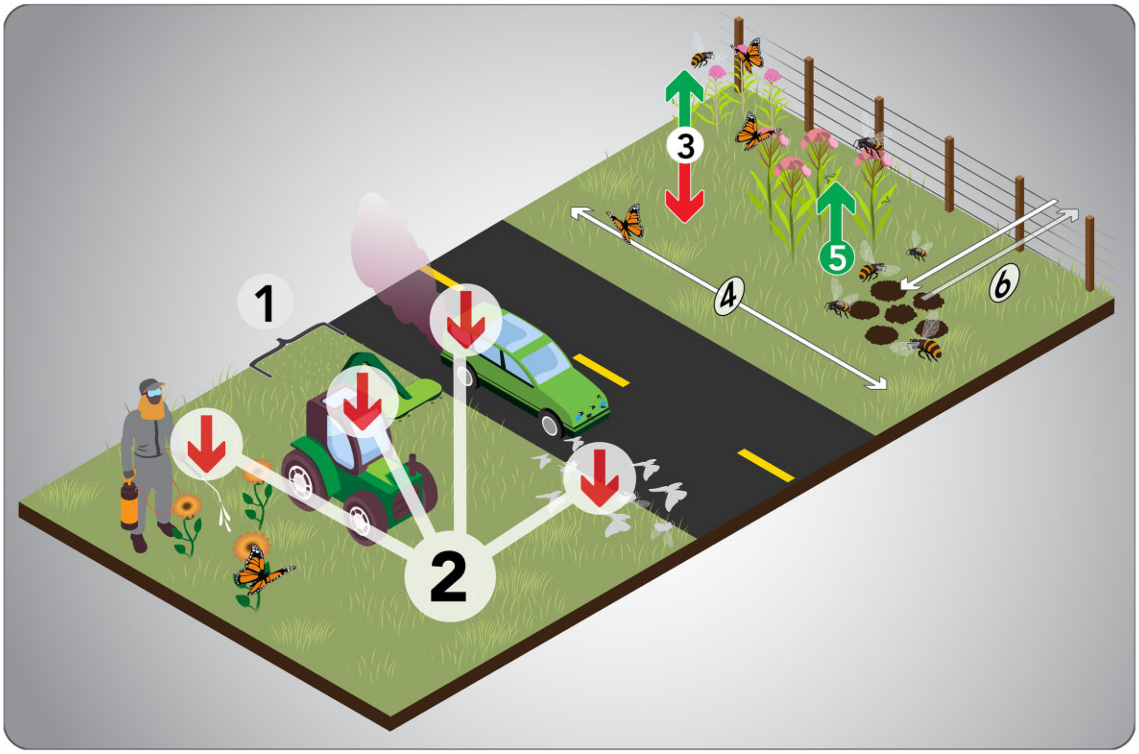

Figure 3. Important—and challenging—research opportunities and data gaps remain in assessing the impacts of roads and roadside habitats on pollinator populations. Among them are (1) identifying the ideal clear zone width for pollinator health on the basis of collision risk and contamination of vegetation near the roadway; (2) quantifying pollinator mortality rates in roadsides from multiple causes; (3) understanding the effects of pollinator-friendly roadside plantings on pollinator populations and their rates of reproduction and mortality; (4) evaluating the extent of connectivity and corridor-like pollinator movement occurring within road verges; (5) quantifying pollinator birth rates in roadsides; and (6) investigating pollinator immigration and emigration rates into and from roadside habitats.

raising survival rates without necessarily increasing immigration rates. Planting roadside flowers, on the other hand, will likely increase immigration rates, improving habitat quality but drawing more pollinators into risky habitats and potentially magnifying the sink effect. To return to Keilsohn and colleagues' (2018) question, we don't know how extensive a roadside restoration planting must be to produce more insects than it kills, but we *do* know how to reduce the killing of roadside insects. With this in mind, we stress the importance of several changes to roadside management and policy.

Most risks of roadside habitat are associated with the roads themselves (e.g., collision with vehicles, pollutants) and therefore decrease from higher to lower risk as organisms move farther from the road. Therefore, managers should prioritize leaving pollinator habitat in wider road verges and in parts of road verges farthest from the road (Keilsohn et al. 2018). The regionally popular practice of cultivating pollinator habitat in highway medians (wildflower medians) should be suspended; vegetated medians have been shown to significantly increase the level of insect collision mortality (Keilsohn et al. 2018) and may be toxic. For most highways, a clear zone—an unobstructed area of close-cropped vegetation bordering the edge of a roadway—is recommended of 1.5–3 meters, because plants growing this close to the road are likely to be toxic for pollinators (Moroń et al. 2012, Hintz and Relyea 2019, De Silva et al. 2021). Clear zones are especially important—and should be slightly wider—on roads with higher traffic and those that are deiced in winter, because traffic increases deposition of toxins and deicing salt can result in toxic sodium concentrations in roadside plants (Lytle et al. 1995, Mitchell et al. 2020). Although further studies are needed, providing diverse floral resources in the edges of road verges farthest from the road may draw pollinators away from the road, toward less toxic plants (Xun et al. 2018, Phillips et al. 2021), potentially benefiting pollinator health and reducing collision mortality.

Mowing and herbicides are frequently employed to control weeds, maintain visibility, and prevent woody growth in road verges. Although mowing can create short-grass or bare zones preferred by some ground-nesting bees, mowing typically reduces floral resource availability, may disturb or kill nesting and developing pollinators, and can benefit disturbance-prone species (often invasive species, but also native plants such as milkweed; Phillips et al. 2019). Outside of clear zones immediately adjacent to roadways, which should be kept short, road verges should generally be mown as little as possible—at most, once or twice a year, early and late in the growing season, when mowing is less likely to affect flowers or developing pollinators. Even when no flowers are present, mowing can destroy overwintering pollinator eggs and larvae, so leaving grass and forbs standing—and when mowing is necessary, using flushing bars and mowing heads designed to reduce arthropod mortality—is recommended (Humbert et al. 2010, Steidle et al. 2022). In specific cases, well-timed mowing (typically in mid-July) may benefit milkweed, monarchs, or other target species, but timing mowing effectively requires location-specific and species-specific knowledge of phenology (Phillips et al. 2020). Herbicide use, on the other hand, is almost always detrimental to pollinators, except when it is applied very selectively to control invasive species and foster higher native plant diversity (Hopwood et al. 2015). Noxious weeds should therefore be spot treated (specifically targeted) early or very late in the growing season on nonwindy days to minimize detrimental impacts on pollinators and native forbs (Hopwood et al. 2015). Insecticide use should be avoided in roadside management.

Even under the best management practices, road verges vary considerably in their safety and potential benefit for pollinators. On the basis of available evidence, habitat is most likely to benefit pollinators when it occurs along roads with less traffic, less intensive management regimes (mowing, grading, and herbicides), wider road verges, and adjacency with native habitat (McKenna et al. 2001, Skórka et al. 2013, Villemey et al. 2018). Further research is required (figure 3) to identify the thresholds of traffic, pollutants, and disturbance from management activities that create overall negative effects for pollinator populations, and these responses are likely to be species specific and based on insect morphology, life history, and dispersal behavior. Studies that compare pollinator birth and development rates in roadside habitat with mortality rates are critically needed to answer the question of whether roadsides are net producers (sources) of specific insect species or whether they are population sinks, with mortality exceeding reproduction. In addition, mark–recapture studies comparing pollinator dispersal along road verges with dispersal across nonroadside land of the same habitat type are required to test the common but weakly supported notion that roadsides serve as pollinator habitat corridors. Although roadside pollinator ecology has rapidly expanded in recent years, critical questions remain unanswered, and new studies must attempt to assess both roadside pollinator reproduction and mortality if they are to successfully evaluate the impacts of roadside restoration on pollinators.

Although roadsides have garnered much attention for their pollinator habitat potential, it is important to consider alternatives—lands where the threats of collisions, pollutants, salts, mowing, and herbicide use are lower or absent. In addition to protected sites such as parks, refuges, and reserves, powerline and pipeline right-of-way corridors, railway embankments, undeveloped lots, and buffer strips along waterways and streams represent good alternatives for cultivating pollinator habitat that often have fewer risks to pollinators (Wojcik and Buchmann 2012, Villemey et al. 2018). Where non-roadside land is available that is not subject to more severe disturbance or pesticides, roadsides may be better targets for reductions in mowing and herbicide use than for pollinator plantings.

So, is roadside habitat a boon or a bane for pollinating insects? The answer, of course, likely lies in the details—the intensity of traffic, the distance of plants from the roadway, the frequency of mowing and spraying, and the local availability of alternative habitats. Pollinator-conscious management practices can help roadsides become more of a boon and less of a bane. However, we lack the data needed to understand road verges' overall impact on pollinator populations and should therefore be cautious about relying on these areas. Roadside habitats are far from a panacea for pollinator declines, and although roadside managers can and should promote pollinator-friendly practices, restoration funding for pollinator plantings should be prioritized in safer areas when available.

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