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Review

Enhancing road verges to aid pollinator conservation: A review

Benjamin B. Phillips[a,*], Claire Wallace[b], Bethany R. Roberts[a], Andrew T. Whitehouse[c], Kevin J. Gaston[a], James M. Bullock[d], Lynn V. Dicks[b,e], Juliet L. Osborne[a]

[a] *Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE, United Kingdom*
[b] *School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom*
[c] *Buglife, The Lindens, 86 Lincoln Road, Peterborough, PE1 2SN, United Kingdom*
[d] *UK Centre for Ecology and Hydrology, Maclean Building, Wallingford, Oxfordshire OX10 8BB, United Kingdom*
[e] *Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, United Kingdom*

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ABSTRACT

Road verges provide habitats that have considerable potential as a tool for pollinator conservation, especially given the significant area of land that they collectively cover. Growing societal interest in managing road verges for pollinators suggests an immediate need for evidence-based management guidance.

We used a formal, global literature review to assess evidence for the benefits of road verges for pollinators (as habitats and corridors), the potential negative impacts of roads on pollinators (vehicle-pollinator collisions, pollution, barriers to movement) and how to enhance road verges for pollinators through management.

We identified, reviewed and synthesised 140 relevant studies. Overall, the literature review demonstrated that: (i) road verges are often hotspots of flowers and pollinators (*well established*), (ii) traffic and road pollution can cause mortality and other negative impacts on pollinators (*well established*), but available evidence suggests that the benefits of road verges to pollinators far outweigh the costs (*established but incomplete*), and (iii) road verges can be enhanced for pollinators through strategic management (*well established*). Future research should address the lack of holistic and large-scale understanding of the net effects of road verges on pollinators.

We provide management recommendations for enhancing both individual road verges for pollinators (e.g. optimised mowing regimes) and entire road networks (e.g. prioritising enhancement of verges with the greatest capacity to benefit pollinators), and highlight three of the most strongly supported recommendations: (i) creating high quality habitats on new and existing road verges, (ii) reducing mowing frequency to 0–2 cuts/year and (iii) reducing impacts of street lighting.

1. Introduction

Animal pollinators are essential for the production of many crops (Klein et al., 2007) and for the reproduction of many wild plants (Ollerton et al., 2011), yet declines of some pollinator species have been recorded in several regions worldwide (Potts et al., 2016). A central cause of declines is the loss and degradation of suitable habitats due to urban and agricultural expansion and intensification (Potts et al., 2016). Pollinators require habitats for feeding (e.g. nectar and pollen, larval hostplants), reproduction, nesting and overwintering. Adequate provision of suitable habitats is therefore crucial to pollinator conservation.

Roads are a ubiquitous feature of human civilisation that extend 36 million km across the world (Central Intelligence Agency, 2017). Whilst they cause a wide range of negative ecological impacts (Forman et al., 2003; Muñoz et al., 2015), the habitats alongside roads, henceforth "road verges", can support many species (Gardiner et al., 2018). Road verges are vegetated strips, generally consisting of grassland, shrubland, woodland or forest, which often form distinctly managed borders that separate roads from adjacent land. They may serve a number of practical purposes, for example accommodating road infrastructure, improving visibility for road users and providing refuge for pedestrians, but can simultaneously be managed to benefit wildlife (Gardiner et al., 2018). Given the extent of the road network, road verges cover very large areas of land: an estimated 2400 km^2 (1% of land) in Great Britain (Plantlife, 2013), 50,000 km^2 (0.5% of land) in the USA (Forman et al., 2003) and 270,000 km^2 globally (Phillips et al., 2020). As such, verges provide a significant opportunity to benefit wildlife, especially pollinators because many such taxa are highly mobile and so able to use small, isolated habitat patches across landscapes.

* Corresponding author.
E-mail address: B.B.Phillips@exeter.ac.uk (B.B. Phillips).

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In light of concerns about pollinator declines, there is growing societal interest in managing road verges for pollinators. In the UK, a campaign by the charity Plantlife is proposing road verge management guidelines that benefit plants, pollinators and other wildlife (developed in partnership with highways agencies, highways managers and conservation organisations), which have been adopted by regional governments in a number of areas (Plantlife, 2020). Several other UK organisations have projects involving managing road verges for pollinators, including Highways England (Highways England, 2019), Butterfly Conservation (Butterfly Conservation, 2020) and Buglife (Buglife, 2020). There are similar projects in other countries, including in the USA by the Monarch Joint Venture to support the monarch butterfly *Danaus plexippus* (Monarch Joint Venture, 2020) and by the Xerces Society to support pollinators generally (Xerces Society, 2020).

In light of growing societal interest in managing road verges for pollinators, practitioners have an immediate need for an evidence synthesis to inform guidelines. Whilst existing reviews have considered the use and management of road verges for nature conservation in general (Gardiner et al., 2018; Jakobsson et al., 2018; Villemey et al., 2018), they identify relatively few studies on pollinators and highlight that many of the related issues are taxon specific. Similarly, the recent IPBES pollinator assessment identified the potential of road verges as habitats and corridors for pollinators, but provides only a brief overview, highlights uncertainty about possible negative impacts of traffic and pollution and provides little advice on how to manage them effectively (IPBES, 2019). This review provides a detailed consideration of each of the issues around using road verges for the conservation of pollinators - a specific focal group that is of major scientific and societal interest. Specifically, the benefits that road verges provide to pollinators must be weighed against the potential negative impacts of roads: road verges may provide beneficial habitats for feeding, reproduction, nesting and overwintering that are scarce in the surrounding landscape, and act as corridors or navigational features; but the pollinators drawn to road verges may be negatively affected by pollution, vehicle-pollinator collisions and poor management, possibly resulting in net harm to these species at the landscape scale (i.e. ecological traps; Hale and Swearer, 2016). In most cases, road verges are already present alongside existing roads and will be constructed along new roads regardless, but they could be enhanced to benefit pollinators. In this study, we used a formal, comprehensive literature review of global scope to address the following questions (Fig. 1):

- Q1) What pollinator communities and associated resources are found in road verges, and how do they compare to those in other habitats in the surrounding landscape?
- Q2) How do roads and road verges affect pollinator movement and dispersal?
- Q3) How much do vehicle-pollinator collisions affect pollinators?
- Q4) How much does road pollution affect pollinators?
- Q5) How does road verge management affect pollinators?
- Q6) How do road verge, road and landscape characteristics affect pollinators in road verges?

In each case, we consider impacts on pollinator individuals, populations and communities.

2. Materials & methods

We carried out a search using Web of Science Core Collection databases (in English language only) for scientific publications addressing the outlined research questions (Fig. 1) – relating to both pollinators and road verges, or to impacts of roads on pollinators. Following much of the literature and conservation strategy documents, we use the term 'pollinators' for all flower visitors that are likely to have the potential to transfer pollen. We aimed for a formal, representative and comprehensive review, and so used detailed search criteria, which were refined by testing against a set of fifteen papers known to be relevant (Appendix A). All studies up to 1st November 2019 were considered. The search criteria resulted in 629 studies. Studies were split between two reviewers, who assessed them (using the title and abstract, or full text where necessary) against the inclusion criteria in Appendix A. Relevant studies were recorded in a spreadsheet, allocated to the relevant research question from Fig. 1 and relevant information was extracted. To ensure consistency in studies that were considered to be relevant, the first reviewer verified the relevance of each of the second reviewer's allocated studies. Verification did not result in any excluded studies being included, though several included studies were excluded. Extracted information was used to write a narrative synthesis of the combined results.

We used meta-analysis to assess how the density and species richness of flowers and pollinators in road verges compared to in other habitats (Q1). For each study that compared flower or pollinator density or species richness, we extracted the mean, standard deviation and sample size from the text, tables, graphs (using WebPlotDigitizer 4.2; Rohatgi, 2015), appendices, or raw data provided by the authors. Studies were split into individual cases of a single habitat comparison for a single pollinator taxon, i.e. each study could provide many individual cases. When data were provided for multiple time points (e.g. multiple surveys across the same year, presented separately), we used the comparisons from the middle time point. Where comparisons were provided for multiple taxonomic levels of pollinators, we used the lowest taxonomic level provided (excluding species, which would have resulted in two studies on Lepidoptera providing the majority of cases). When the mean and standard deviation were not provided, we calculated the standard deviation from the standard error or confidence intervals, or estimated the mean and standard deviation from the median and quartiles using the method of Wan et al. (2014). Of 41 studies initially identified, 14 provided sufficient information (details in Appendices A–B). Meta-analyses were conducted in R 3.6.1 (R Core Team, 2019) using the 'metafor' package (Viechtbauer, 2010). We used Hedge's *d* standardised mean difference as a measure of the effect size and compared the mean effect size for each pollinator taxa and habitat comparison. Studies were weighted by the inverse of the variance. We tested the significance of the main effects using mixed models with restricted maximum-likelihood estimator, with taxa and habitat comparison as moderator effects, and study cases nested within studies as a random effect. It was not possible to use meta-analysis to address the other research questions due to a lack of studies providing similar comparisons or quantitative outcomes.

3. Results & discussion

We identified 140 relevant studies (Appendix A). All but one study had been published since 1990 and 61% had been published since 2015, demonstrating that this is a rapidly growing research area. Studies covered a diverse range of road types; of studies that provided information, most included at least 10 road verges and focused on paved roads (including large, busy, high-speed roads, quiet rural roads in agricultural landscapes, urban roads and forest roads – often a mixture of these), though at least 15 studies focused on (or included) unpaved roads (Appendix A). However, studies were limited in terms of (i) geographic location, (ii) pollinator taxa and (iii) methodology. Geographically, most studies were from Europe (72 studies, 51%) and North America (45 studies, 32%). Taxonomically, only 11 studies considered entire pollinator communities, whilst 46 studies (33%) focused on a single species (including 15 studies on monarch butterflies *Danaus plexippus* and 13 studies on honeybees *Apis mellifera*) and 49 studies (35%) focused on a single pollinator order. Overall, 64 studies (52%) focused on Lepidoptera and 32 studies (26%) on Hymenoptera, whilst only 6 studies focused on other pollinator taxa such as Diptera or Coleoptera (Appendix A). Methodologically, most studies were purely observational (104 studies, 74%), whilst 27 studies (19%) were

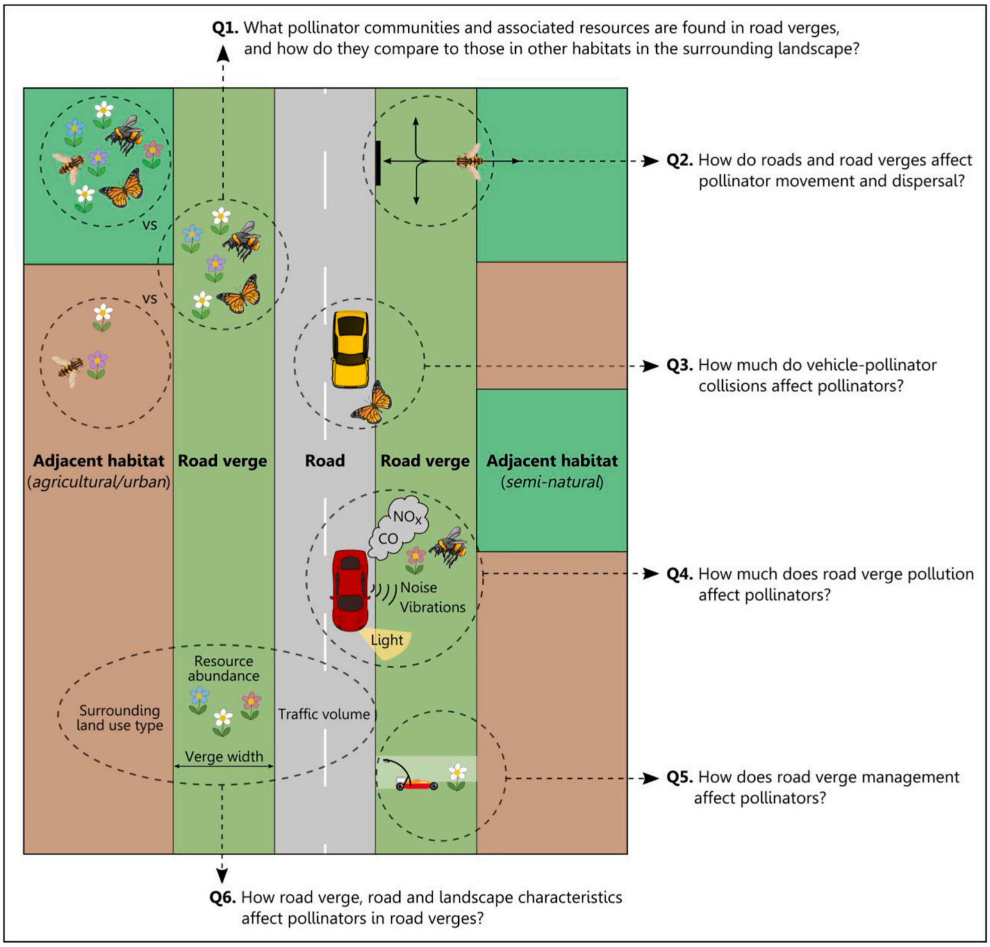

Fig. 1. The research questions about the positive and negative aspects of roads and road verges for pollinators, which are addressed in this review.

experimental, 2 used modelling and 7 were reviews. These limitations mirror those of other systematic reviews (e.g. Villemey et al., 2018), and may introduce bias into the conclusions drawn and limit generalisability because: (i) Road verges might be relatively more important for pollinators in Europe and North America where there is less remaining natural and semi-natural habitat, (ii) The behaviours and responses of hymenopteran and lepidopteran pollinators are not necessarily representative of other pollinator taxa, and (iii) The low number of experimental studies makes it difficult to disentangle drivers of effects of roads, road verges and their management on pollinators. Studies were also apparently dominated by those of grassland road verges, with few considering other common verge habitats (e.g. shrubland) or habitats that are important for pollinator lifecycles but which may be lacking on road verges (e.g. areas of wetland as larval habitats for dipteran pollinators and areas of bare ground as nesting habitats for hymenopteran pollinators). Future studies should focus on other continents, consider entire pollinator communities and non-grassland road verge habitats, and where possible carry out experimental studies. Nevertheless, we found at least 17 relevant studies addressing each research question. We take the research questions in turn. Then we provide an overall assessment, an agenda for future research and management recommendations. Additional information and interpretation of the reviewed studies are provided in Appendix A.

3.1. Q1) What pollinator communities and associated resources are found in road verges, and how do they compare to those in other habitats in the surrounding landscape?

Many studies provide information about the pollinator communities and associated resources that are found in road verges (Appendix A), so we provide a summary and some key examples. Road verges are often important early or mid-successional habitats providing feeding and reproductive opportunities for pollinators including diverse floral resources (e.g. Halbritter et al., 2015; Noordijk et al., 2009; Phillips et al., 2019) and larval hostplants (e.g. Munguira and Thomas, 1992; Valtonen et al., 2006b). Notably, road verges in North America are an important source of milkweeds (*Asclepias* spp.) – the larval hostplant of monarch butterflies (e.g. Daniels et al., 2018; Kasten et al., 2016). Unsurprisingly then, road verges can contain diverse pollinator communities (Hopwood, 2008; Munguira and Thomas, 1992; Phillips et al., 2019; Valtonen et al., 2006b), including rare species. For example, Heneberg et al. (2017) recorded 32 threatened (including four critically endangered) bee and wasp species from 14 verges along a single highway in the Czech Republic, and Helldin et al. (2015) found that road verges in Sweden contained >20% of observations for 13 red-listed pollinator species (5 bee, 6 moth and 2 butterfly species) despite only covering 1.5% of land. Beyond feeding, there is evidence that road verges are used by hymenopteran pollinators for nesting (Heneberg et al., 2017; Hopwood, 2008; Oleksa et al., 2013; Wuellner, 1999), by lepidopteran pollinators for reproduction (e.g. Goodwin et al., 2017; Munguira and Thomas, 1992) and by various pollinator taxa for overwintering (both as adults and as immature stages, further evidencing reproduction in road verges; Schaffers et al., 2012), though these aspects of pollinator lifecycles have been far less studied.

3.1.1. How do road verges compare to other nearby habitats?

We found 41 studies comparing pollinators and their associated resources in road verges to other habitats (Appendix A), including 14

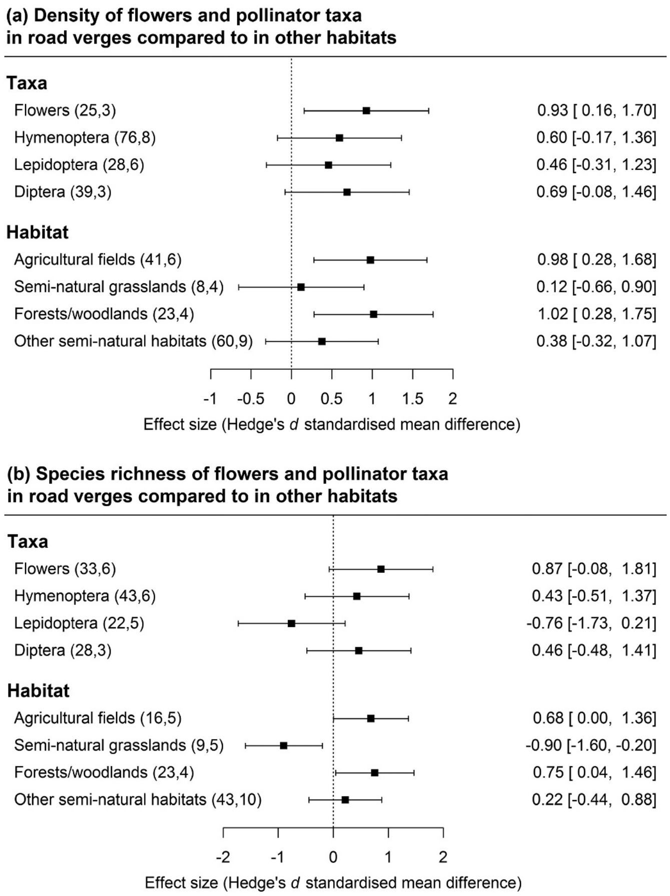

Fig. 2. The mean effect sizes (Hedge's *d*; mean ± 95% confidence intervals) for studies comparing the (a) density and (b) species richness of flowers and pollinators in road verges to those in agricultural fields, semi-natural grasslands, forests/woodlands, and other semi-natural habitats (e.g. hedges). Studies (n = 14) were identified from the literature review (Appendix A) and were split into individual cases (n = 300) of a single habitat comparison for a single pollinator taxon, i.e. each study could provide many individual cases (cases per study: median = 5, range = 1–88). Mean effect sizes are only presented for groups where there was more than one study. Numbers in round brackets are the number of study cases and the number of studies for each category. The full list of studies, cases and effect sizes are provided in Appendix B.

studies comparing the density or species richness of flowers or pollinators (Appendix B). Most studies refer to measures of abundance, but in fact measure density, namely counts per total area of a transect survey, so we use the term density throughout for clarity.

Overall, meta-analysis revealed that the density and species richness of flowers and pollinators in road verges are generally similar or greater than in other habitats in the surrounding landscape (Fig. 2). However, patterns differ depending on the habitat comparison: flower and pollinator density and species richness are greater in road verges than in agricultural fields or forests and woodlands, and similar to those in other semi-natural habitats (Fig. 2), but the species richness of flowers and pollinators is lower in road verges than in semi-natural grasslands (Fig. 2b). Studies in UK agricultural landscapes find that pollinator communities in road verges are similar to in other semi-natural habitats and far richer than in agricultural fields (Hanley and Wilkins, 2015; Osgathorpe et al., 2012; Phillips et al., 2019), with the most extensive study finding generally at least 3–4 times greater densities and 1.5 times greater species richness of bumblebees, butterflies and hoverflies than in field interiors and most semi-natural habitats (Cole et al., 2017). Hall et al. (2019) found more mixed results for wild bees in an agricultural landscape in Australia, compared to open farmland and other linear semi-natural habitats. Studies in forested landscapes in Canada and Sweden suggest that road verges provide important open habitats; allowing light infiltration that results in a more favourable microclimate for pollinators and their hostplants (Hanula et al., 2016), resulting in greater density and species richness of butterflies (Berg et al., 2011; Riva et al., 2018) and bumblebees (Hill and Bartomeus, 2016). The role of road verges in providing favourable microclimates and conditions (e.g. south-facing slopes) in non-forested landscapes has been little studied. Furthermore, just a single study has compared flowers and pollinators in urban road verges to other urban habitats: Baldock et al. (2019) found that urban road verges in three UK cities supported similar densities and species richness of flowers, bees, hoverflies and other flies to most other urban habitats and land-use types, though generally much lower than in gardens and allotments. Beyond feeding, only five studies (limited to monarch butterflies) have compared the availability and use of resources for other aspects of pollinator lifecycles in road verges to other habitats. They show that road verges have similar or greater densities of milkweeds (larval hostplants) compared to arable fields and restored prairie, but lower densities than remnant prairie (Hartzler and Buhler, 2000; Kaul and Wilsey, 2019) and an average of roughly 25–50% fewer monarch eggs and larvae per milkweed plant than in various non-roadsite habitats (Kasten et al., 2016; Pitman et al., 2018). Future research should compare pollinator nesting, reproduction and overwintering in road verges to in other habitats.

3.2. Q2) How do roads and road verges affect pollinator movement and dispersal?

Roads might be a partial or complete barrier to movement for pollinators, though might also act as navigational aids, and road verges might act as parallel corridors along which pollinators move and disperse, so improving habitat connectivity at a landscape scale. We found 23 relevant studies, with 15 focusing on butterflies.

3.2.1. Do pollinators cross roads?

Roads might present a barrier to pollinator movement if pollinators are not physically able to cross, or if they are deterred from doing so by some aspect of the road. This will largely depend on pollinator flight range and flight height, which are affected by taxon and whether the pollinator is foraging, dispersing or migrating. Roads are unlikely to be a barrier to larger-scale movements by pollinators (e.g. migration), which are generally direct, cover large distances, are at altitudes of up to hundreds of metres, and use environmental cues that are unlikely to be affected by roads (Chapman et al., 2011). For example, bumblebees *Bombus* spp. can fly distances of several kilometres (Greenleaf et al., 2007), and migrating monarch butterflies readily cross roads, mostly at heights of >6 m (Mora Alvarez et al., 2019). However, most studies that we found focus on local-scale movement of pollinators, where pollinators with shorter flight ranges might be physically unable to cross roads, or otherwise where pollinators are more likely to be deterred from crossing roads because they are responding to local cues (e.g. from floral resources or the road).

Evidence from four mark-recapture studies shows that butterflies are able to cross roads, but that sedentary species are less likely to do so than expected by chance. This was found to be the case for three busy main roads (Munguira and Thomas, 1992; Remon et al., 2018) and similarly for a relatively quiet road (approximately 1500 vehicles/day; Polic et al., 2014), though Valtonen and Saarinen (2005) found that a third fewer butterflies crossed a main highway than nearby smaller roads. Similarly, three studies on bees and wasps provide preliminary evidence that roads are a partial barrier to movement, especially for smaller species, which typically have shorter flight ranges (Greenleaf et al., 2007). First, a mark-recapture study in Boston, USA found that bumblebees displaced to a foraging site on the opposite side of a road

(4-lane, 14 m wide) soon crossed the road to return to their original site, but rarely crossed the road naturally (without artificial displacement) due to high foraging site fidelity (Bhattacharya et al., 2003). Second, studies of bees and wasps near Stockholm, Sweden found a significantly different community composition between the two sides of a large highway (90,000 vehicles/day) despite similar vegetation, especially for smaller species (Andersson et al., 2017), and that the density and species richness at 23 urban locations were best explained using cost-weighted distance based on landscape friction, with large roads, other paved ground and built-up land acting as barriers (Johansson et al., 2018). Similarly, studies along small, often unpaved rural roads reaffirm that they are a minor barrier to movement for butterflies (Ries et al., 2001; Ries and Debinski, 2001; Severns, 2008), but two studies suggest they can be a major barrier for smaller species. First, a study on the hoverfly *Melanostoma fasciatum* found that dispersal was equally reduced by different types of bare ground (a road, dirt track or ploughed field) (Lövei et al., 1998). Second, mark-recapture of a rare, specialised solitary bee *Andrena hattorfiana* found that unpaved roads were a barrier, even when <10 m wide (Franzén et al., 2009). Overall, evidence suggests that roads are a relatively minor barrier to local-scale movement for larger and more mobile species such as butterflies and bumblebees, but can be a major barrier for some smaller and less mobile pollinator taxa.

3.2.2. Are roads and their verges used by pollinators as corridors for movement and dispersal?

Road verges that provide the habitat requirements for pollinator species may facilitate their movement and dispersal across landscapes. We found six relevant studies, with five on Lepidoptera. Brunzel et al. (2004) found that the probability of colonization by the moth *Tyria jacobaea* was greater when the site was linked to the nearest population by a road, probably due to provision of their larval hostplant in road verges. Similarly, a study modelling monarch butterfly movement and egg-laying suggested that they preferentially moved along road verges due to high hostplant density (Grant et al., 2018). Gene flow of *Maniola jurtina* butterflies was positively related to the proportion of road, perhaps because road verges were facilitating dispersal (Villemey et al., 2016). A mark-recapture study of a rare butterfly *Phengaris nausithous* found lower dispersal rates in road verges than in meadows (Jansen et al., 2012). A study of four butterfly species observed almost twice as many individuals moving along experimental grass strips (simulating road verges) compared to a control (22% versus 12%), but only the two habitat specialist species moved along the grass strips more than expected by chance, and only when the strips provided food or shelter (Söderström and Hedblom, 2007). Finally, radar tracking revealed that honeybees used gravel roads (and other linear features) for navigation (Menzel et al., 2019). Overall, evidence suggests that road verges can be used as corridors and roads as navigational aids by some larger pollinator taxa, but research is too limited in scope to draw general conclusions.

3.3. Q3) How much do vehicle-pollinator collisions affect pollinators?

Pollinators that attempt to cross roads at low heights may be killed by collision with vehicles. Few studies provide information on road crossing height, though Mora Alvarez et al. (2019) observed that most migrating monarch butterflies crossed highways at heights of >6 m, whilst other butterfly species have been observed exhibiting resource-searching behaviour along roads (zig-zagging low to the ground) (Severns, 2008; Skórka et al., 2013), which puts them at high risk of being hit by road traffic. Most studies estimate mortality from vehicle-pollinator collisions using counts of dead insects along roads, which are likely to underestimate (e.g. sampling is unlikely to find all individuals, especially those that become attached to vehicles, disintegrate, are eaten by scavengers, or are ricocheted or washed off the road) and may be subject to bias (e.g. detectability varies with road and verge surface and with the size of insect) (Munguira and Thomas, 1992; Skórka, 2016). Five studies broadly assess insect or animal roadkill, and include information on pollinator taxa, whilst 12 studies focus on butterflies (Table 1).

Overall, studies show that many pollinators are killed by collisions with vehicles across a wide range of road types and traffic volumes (Table 1). Average roadkill rates range from 0.45 to 10.1 roadkills/km/day for Lepidoptera along diverse paved road types (Baxter-Gilbert et al., 2015; Keilsohn et al., 2018; Rao and Girish, 2007; Skórka et al., 2015) and 21.31 to 26.8 roadkills/km/day for Hymenoptera, but have only been measured along paved highways (Baxter-Gilbert et al., 2015; Keilsohn et al., 2018) (Table 1). However, the impact of roadkill at the population level is unclear. Relative (rather than absolute) roadkills, i.e. roadkills as a proportion of pollinators observed in the road verge, provides a better measure of the net impact of road verges on pollinators. Estimates of relative roadkill range from 0.6 to 7% of butterflies in road verges (Table 1) – which is an order of magnitude lower than the proportion of butterflies killed by predators and parasitoids, so probably having little impact on butterfly populations (Munguira and Thomas, 1992), but no estimates exist for other pollinator taxa. Ultimately, impacts of roadkill on pollinator populations are difficult to assess in the field, but could be estimated using population modelling.

Pollinator roadkill is often concentrated in spatial or temporal hotspots. For example, Skórka et al. (2015) found that 49% of butterfly roadkill was concentrated in hotspots that covered just 4% of total road length, and Baxter-Gilbert et al. (2015) recorded a bloom of bibionid flies in May (spring) of one study year, which resulted in 100 times more roadkill (1463 dipteran roadkills/km/day). Keilsohn et al. (2018) found that average insect roadkill was three to four times greater for roads adjacent to meadows and lawns than wooded areas, and more than double when there was a median strip (central vegetated strip separating the opposing lanes of traffic) (Table 1). Studies on the monarch butterfly also show that roadkill is concentrated in hotspots (Tracy et al., 2019), for example >200,000 monarchs were killed each year at two paved, rural highways (14,330/8862 vehicles/day) in Mexico that are known monarch roadkill hotspots due to their importance as migratory crossing locations (Mora Alvarez et al., 2019) (Table 1). Along the entire migratory route, monarch roadkill can be considerable – killing an estimated 2.1 million monarchs – equivalent to 3% of the overwintering population (Kantola et al., 2019). Overall, studies on butterflies have found that butterfly roadkill is greater for more mobile taxa and increases with traffic volumes and road width (Halbritter et al., 2015; Munguira and Thomas, 1992; Skórka et al., 2013, 2015) (Table 1).

3.4. Q4) How much does road pollution affect pollinators?

Pollinators in road verges are exposed to diverse forms of pollution from roads and road traffic, including light, noise, exhaust fumes and heavy metals. The risk of road pollution to pollinators depends both on their exposure and on the hazard that field-realistic levels pose. Whilst pollinators that feed in road verges might be exposed to road pollution for short durations, pollinators using road verges for nesting, as larval stages or that have low mobility, will be exposed over much longer durations. We found 28 studies that assess the exposure of pollinators and/or the associated hazard for specific forms of road pollution: light, noise, turbulence, exhaust fumes and metals (Table 2). Specifically, studies show that streetlights attract nocturnal pollinators from multiple taxa (Coleoptera, Diptera, Hymenoptera and Lepidoptera), diminish nearby moth communities and inhibit moth predator evasion behaviour (Table 2). Research for other forms of pollution is limited: noise and turbulence have been addressed in only one study each, heavy metal studies have only reported observed concentrations (exposure) but not the impact on pollinators (hazard), and four studies of air pollution show that vehicle exhaust fumes can degrade floral odours and subsequent detection and learning by honeybees but have not

Table 1
Studies providing measures of vehicle-pollinator collisions and roadkill, from the literature review (Appendix A).

Pollinator taxa	Study	Location	Number of roads	Road type(s)	Pollinator roadkill measure	Pollinator roadkill information
All	Baxter-Gilbert et al. (2015)	Canada	1	Rural highway (9700 vehicles/day) in an otherwise natural landscape	Absolute roadkill (roadside counts)	Roadkills/km/day of 10.1 for Lepidoptera, 26.8 for Hymenoptera and 10.4 for Diptera, though one month in one of the two years experienced a bloom of bibionid flies (excluded above), which resulted in 1463.2 Diptera roadkills/km/day. These values scale up to millions of pollinator roadkills per year along this 388 km stretch of road, and potentially billions of pollinator roadkills per year across North America.
	Ciolan et al. (2017)	Romania	1	Paved woodland road (1-lane; 3–6 vehicles/h)	Absolute roadkill (roadside counts)	Frequently found killed bees and butterflies, but in low numbers compared to ground-dwelling invertebrates. There were seasonal differences in the amount of insect roadkill.
	Keilsohn et al. (2018)	USA	30	Busy, high-speed urban/suburban roads (38,650 ± 32,144 *SD* vehicles/day)	Absolute roadkill (roadside counts)	27% of insect roadkill were Hymenoptera (13% *Bombus* spp.) and 8% were Lepidoptera (mean ± SD roadkill/km/weekly survey was 7.79 ± 6.62 for butterflies, 21.31 ± 32.26 for bees and 132.73 ± 260.71 for all insects), but roadkill was much higher along roads adjacent to meadows and lawns than wooded areas (mean ± SD roadkill/km/survey in meadow 156.56 ± 168.31, lawn 196.44 ± 403.27, wooded 45.19 ± 25.78) and was more than double when there was a median strip (mean ± SD roadkill/km/survey: median strip 194.13 ± 348.48, no median strip 71.33 ± 83.45).
	Martin et al. (2018)	Canada	20	Paved rural roads (10 medium traffic: 367 ± 224 *SD* vehicles/h, 10 low traffic: 41 ± 19 *SD* vehicles/h)	Absolute roadkill (sticky traps on a vehicle)	Most collected insects were flies (77% Diptera, 9% Hymenoptera, 2% Coleoptera, 0 Lepidoptera) that were small-sized (96.8% < 5 mm long, 2.7% 5–10 mm, 0.4% > 10 mm), though perhaps biased towards taxa and sizes that more easily adhere to sticky traps.
	Rao and Girish (2007)	India	3	2 roads in a National Park (50–125 vehicles/h), 1 peri-urban highway (125–150 vehicles/h)	Absolute roadkill (roadside counts)	Butterfly roadkills (0.45–3.11 roadkills/km/day) were greater along two roads in a National Park than along a highway, despite less traffic, but few roadkills of other pollinator taxa.
Butterflies	Halbritter et al. (2015)	USA	3	Highways (4-lanes, average 11,000 vehicles/day)	Relative roadkill (roadside counts)	Relative roadkill of 42% but acknowledged that densities of live butterflies in road verges were considerably underestimated compared to densities of roadkill. Significantly greater relative roadkills (proportion of butterflies observed in the adjacent road verge) of large butterflies (0.689) compared to small butterflies (0.055), and of migratory species (0.596) compared to non-migratory species (0.224), probably because they cross roads more frequently.
	Munguira and Thomas (1992)	UK	1	Peri-urban highway (9 m wide, 1080 vehicles/h)	Relative roadkill (roadside counts)	Relative roadkill of 0.6–1.9% for sedentary species and 7% for mobile species.
	Ries et al. (2001)	USA	3	Small paved and gravel roads	Relative roadkill (visual observation)	2.8% of butterflies observed crossing roads were killed.
	Skórka et al. (2013)	Poland	60	Paved rural roads (mean 155.4 ± 12.8 *SE* vehicles/h)	Relative roadkill (roadside counts)	Relative butterfly roadkill of 6.8%. Roadkill was positively related to traffic volume, road width and number of butterflies in the adjacent verge, but no effect of species mobility, though small-bodied species were over-represented so might be more affected by vehicle-pollinator collisions.
	Skórka et al. (2015)	Poland	All roads in 3 landscapes	Mixed	Absolute roadkill (roadside counts)	Mean roadkills of 1.37 ± 0.12 *SE* butterflies/km. Roadkill hotspots covered just 4% of total road length but contained 49% of butterfly roadkill.
	Skórka et al. (2018)	Poland	20	10 paved roads (50–100 vehicles/h) and 10 unpaved roads (<1 vehicles/day)	Relative roadkill (roadside counts)	Relative butterfly roadkills of 2.2% along paved roads, but no roadkills along unpaved roads.

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Table 1 (*continued*)

Pollinator taxa	Study	Location	Number of roads	Road type(s)	Pollinator roadkill measure	Pollinator roadkill information
Butterflies - *Danaus plexippus*	Kantola et al. (2019)	USA	16.1 km of roads	Mixed	Absolute roadkill (roadside counts)	Average roadkill of 0.34 monarchs/km/survey, but up to 6.6 monarchs/km/survey in one area, resulting in an estimated 2.1 ± 0.5 SD million road-killed monarchs across the Central Funnel migratory route, which is about 3% of the overwintering population.
	Mora Alvarez et al. (2019)	Mexico	2	Paved rural highways (2-/4- lane, 14,330/8862 vehicles/day)	Absolute roadkill (roadside counts)	Estimated that at least 200,000 monarchs were killed each year at the two study highways in Mexico, which are important crossing locations during autumn migration.
	Tracy et al. (2019)	North America	Continent-scale modelling	Mixed	Absolute roadkill (roadside counts), Modelling	Roadkill of 5.2–57.5 monarchs/km/survey.
Butterflies - *Icaricia icarioides fenderi*	Severns (2008)	USA	1	Paved, rural road (2-lane, 30–60 vehicles/day)	Absolute roadkill, relative roadkill (roadside counts, visual observation)	No vehicle-butterfly collisions or roadkills were observed, though vehicles were rarely present when butterflies were crossing the road, and butterflies moved out of the road in response to approaching cars (moving relatively slowly at 40 km/h).
Butterflies - *Speyeria zerene hippolyta*	Zielin et al. (2016)	USA	1	Rural highway (2100 vehicles/day)	Absolute roadkill, relative roadkill (visual observation)	One observed vehicle-butterfly collision and nine potential collisions (1–10.5% of road crossings).

considered other pollinator taxa. Additionally, experimental studies have only assessed these forms of road pollution individually, most studies are limited to a single pollinator species and are often performed under laboratory conditions (Table 2), and several other forms of road pollution remain completely unstudied (e.g. vibration, particulate matter and nitrogen enrichment from vehicle emissions) (Table 2).

At a population and community level, road pollution might: (i) deter pollinators from road verges, especially highly mobile species and (ii) deplete local pollinator populations, especially less mobile species, due to direct (impacting pollinators) or indirect (e.g. impacting flowers) lethal or sublethal effects. Some observational studies have reported fewer pollinators closer to roads (Corcos et al., 2019; Phillips et al., 2019) and along roads with greater traffic densities (Martin et al., 2018; Phillips et al., 2019), where pollution is likely to be greater. Five studies on butterflies (Flick et al., 2012; Munguira and Thomas, 1992; Skórka et al., 2013, 2018; Valtonen et al., 2006b) and one on bees (Hopwood, 2008) found no such trends (Flick et al., 2012; Hopwood, 2008; Munguira and Thomas, 1992; Skórka et al., 2013, 2018) though most studies only measure and assess traffic volume as a covariate. Specifically, Martin et al. (2018) recorded an average of 23.5% fewer insects along medium-traffic (367 ± 224 *SD* vehicles/h) compared to low-traffic (41 ± 19 *SD* vehicles/h) roads. Phillips et al. (2019) recorded an average of 61% fewer pollinators along high-traffic roads (1200–1400 vehicles/h) compared to low-traffic roads (0–200 vehicles/h) and (compared to 10 m from the road edge) 70% fewer pollinators 1 m from the road and 59% fewer pollinators 5 m from the road edge. Corcos et al. (2019) observed that tachinid fly density and species richness decreased with road proximity in urban areas. The potential drivers of these patterns are difficult to disentangle and could be due to pollinators being repelled by pollution, pollinator population being depleted by pollution, or confounding factors such as pollinator populations being depleted by vehicle-pollinator collisions or resource quality being lower closer to roads. Studies on honeybees have also found that hives closer to roads contained bees with greater wing shape asymmetry, perhaps due to air pollution because CO_2 levels have been shown to affect wing asymmetry in a bumblebee species (Leonard et al., 2018), and that hives in a polluted area next to a busy trunk road had honeybees with activity of body surface enzymes that are important for combating disease and infection, whilst hives in a control area did not (Strachecka et al., 2012). Further research is needed to determine the singular and combined impacts of different forms of road pollution on pollinators, using field-realistic conditions and pollution levels.

3.5. Q5) How does road verge management affect pollinators?

In the first instance, road verge management can benefit pollinators by creating high-quality habitats in new verges and restoring and maintaining high-quality habitats in existing verges. Second, road verge management (e.g. mowing regime) can affect the capacity of road verge habitats to support pollinators. Whilst studies about grassland management were beyond the scope of the review, they are likely to be broadly relevant to road verge management, so we also signpost to some key studies.

3.5.1. Habitat creation and restoration

Studies about road verge habitat creation and restoration are limited in number, but studies in Iowa and Kansas, USA show that prairie-vegetation road verges are much better than weedy (dominated by non-native vegetation) road verges for bees (2 times greater density and 1.5 times greater species richness of bees, despite little difference in floral density) (Hopwood, 2008) and better than weedy or grassy (low forb cover) verges for habitat-sensitive butterflies (5 times greater density, 2 times greater species richness) (Ries et al., 2001). Similarly, Valtonen et al. (2006a) found that road verges in Finland dominated by an invasive plant *Lupinus polyphyllus* had significantly fewer butterflies. More generally, a recent systematic review by Villemey et al. (2018)

Table 2
Studies assessing how road pollution affects pollinators, from the literature review (Appendix A), including whether they assessed the hazard or exposure (which collectively determine the risk) of road pollution to pollinators.

Road pollution	Pollinator taxa	Impact on pollinators	Assessed hazard or exposure?	Reference
Light	All	Artificial light at night (e.g. street lighting) has various negative effects on insect (including pollinator) behaviour and communities.	Hazard, Exposure	Grubisic et al. (2018) (review)
		Street lighting attracts insects (including pollinators) from diverse taxa (e.g. Coleoptera, Diptera, Hymenoptera and Lepidoptera).	Hazard, Exposure	Holzhauer et al. (2015) and references below
		The type of street lighting affects the impacts on pollinators, and responses can differ between pollinator taxa:	Hazard, Exposure	
		• On average LEDs captured 48% more insects than high-pressure sodium lights. There was no evidence that the colour temperature of white LEDs affected capture of insects.		Pawson and Bader (2014)
		• The number of insects caught depended on the light source. Mercury vapour lights captured significantly more insects than the five other lighting types, whilst LED lights captured significantly less insects than the five other lighting types. The response to different lighting type differed between taxa.		van Grunsven et al. (2014)
		• More than five times as many insects were attracted to white metal halide streetlights than to white LED or orange high-pressure sodium streetlights.		Wakefield et al. (2018)
		• Mercury vapour streetlights attracted approximately twice as many beetles compared to high-pressure sodium streetlights. High-pressure sodium streetlights with a UV filter attached captured substantially fewer beetles.		de Medeiros et al. (2017)
		• For high-pressure sodium lights, shorter wavelength lights (white) attracted significantly more moths and species of moths than longer wavelength lights (yellow). Shorter wavelength lights attracted significantly more Noctuidae moths, whereas both wavelengths were equally attractive to Geometridae moths.		Somers-Yeates et al. (2013)
	Moths	Street lighting has been found to affect various aspects of moth behaviour and moth communities:	Hazard, Exposure	
		• Lepidoptera biomass in light traps was greater at forest edges with streetlighting than dark forest edges or interiors, but the number of individuals did not differ, suggesting that larger Lepidoptera were dominant in lit areas.		Haddock et al. (2019)
		• On average, sites lit by street lighting had 50% lower density at ground level, >25% lower species richness, and 70% greater flight activity.		Macgregor et al. (2017)
		• Street lighting reduced moth evasive behaviour, putting them at greater risk of predation.		Acharya and Brock Fenton (1999)
		• Less than half as many moths performed evasive manoeuvres in response to bat calls under an LED light than in the dark.		Wakefield et al. (2015)
		• Arrangement of street lighting in an array revealed that street lighting limited moth dispersal because moths were much less often caught at streetlights in the middle or edges of the array, than at streetlights at the corners of the array.		Degen et al. (2016)
		• Plants of a lepidopteran larval hostplant were tougher under streetlights than control sites, which (combined with the direct effect of street light exposure) resulted in lower larval body mass, though did not affect survival.		Grenis and Murphy (2019)
Noise	Butterflies *Danaus plexippus*	Monarch butterfly larvae that were exposed to recorded traffic noise (12,000 vehicles/day) in laboratory conditions had 16–17% increased heart rate after 2 h exposure, but long-term exposure (7 or 12 days) resulted in habituation or desensitisation, which may reduce survival by impairing reactions to real-world stressors.	Hazard	Davis et al. (2018)
Turbulence	Bees, butterflies	Traffic velocity (along a single stretch of Amazonian highway where vehicles were slowing down to a new speed limit, split into three sections: mean km/h ± SD: low 51 ± 13.5, medium 67 ± 12.2, high 76 ± 10.1) was negatively related to pollinator (bee and butterfly) visit duration. Visit duration was roughly one third lower in the medium velocity section and two thirds lower in the high velocity section. This was because 84% of pollinators stopped foraging when a vehicle passed. This is probably due to turbulence, but other possibilities cannot be excluded.	Hazard, Exposure	Dargas et al. (2016)

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Table 2 (*continued*)

Road pollution	Pollinator taxa	Impact on pollinators	Assessed hazard or exposure?	Reference
Air	All	Air pollution from traffic can affect pollinator behaviour and perception of plant odours.	Hazard	Reviewed in Jürgens and Bischoff (2017)
	Honeybees *Apis mellifera*	Four laboratory studies found that exhaust fumes can affect floral volatiles and the subsequent ability of honeybees to recognise previously learnt floral odours (using proboscis extension reflex). The first three studies used high concentrations of diesel exhaust fumes, e.g. 17.5 ppm NO_2 (175 times EU ambient air quality standards), whilst the fourth study used concentrations that were magnitudes lower (mean concentrations 246 ppm CO, 21 ppb NO, 21 ppb NO_2; reported as being realistic for urban areas and roadsides).	Hazard	
		• Diesel exhaust fumes degraded three of eight common floral volatiles; the absence of two of these significantly reduced detectability by honeybees by approximately half.		Girling et al. (2013)
		• Four of eight floral volatiles from a flowering crop were rapidly degraded (two made undetectable) by exposure to diesel exhaust fumes (primarily due to NOx); of the two compounds made undetectable, removal of one resulted in only about 25% of honeybees recognising the floral odour, but removal of the other had little effect. However, for lower levels of NOx (2 ppm, 0.2 ppm), there was only a small effect for one of eight floral volatiles.		Lusebrink et al. (2015)
		• Diesel exposure reduced honeybees' ability to recall an odour after 72 h by 44%, but didn't affect survival, though did reduce honeybees' ability to survive a second subsequent stressor (43 °C heat stress) by 57%.		Reitmayer et al. (2019)
		• Honeybees could distinguish between polluted floral volatile blends (exposed to petrol exhaust fumes) from non-polluted blends, took approximately 10–50% longer to learn polluted blends (depending on the blend), and forgot polluted blends faster (approximate recognition after 48 h: polluted 25–45%, unpolluted 60–90%).		Leonard et al. (2019)
Metal	All	Six studies assessed how concentrations of metals in insects are related to roads (four using honeybees as bioindicators of heavy metal pollution), but did not assess the impacts of these elevated metal concentrations on pollinators:	Exposure	
		• For insects (including pollinators) collected in arable fields, coverage and length of paved roads (but not dirt roads) within 100 m radius was positively correlated with Na, Ca and Mn concentrations in most insects, and with As concentrations in Coleoptera (increasing from approximately 0.5 to 1.0 ppm), but not with K, Mg, Cu, Zn Fe, Cd, Co or Pb concentrations.		Orłowski et al. (2019)
	Honeybees *Apis mellifera*	• Higher levels of Pb, Cd and Cr were found in honeybees in a city centre than in four reference sites.		Conti and Botré (2001)
		• High traffic levels contributed to greater levels of Cd, Co, Mn, Cu, Ba, Fe, Ni, and Sr in honeybees.		Zarić et al. (2016, 2018)
		• Concentrations of Pb in honeybees, wax and honey were extremely similar to current or historical levels in the environment.		Zhou et al. (2018)
	Paper wasps *Polistes dominulus*	• Traffic density was directly correlated with Pb concentrations in larval faecal masses.		Urbini et al. (2006)
	Butterflies *Danaus plexippus*, *Pieris rapae*	Two studies assessed the impact of Na from road de-icing salt on monarch and cabbage white butterflies:		
		• Significantly higher levels of Na were found in two of four larval hostplants in roadside ditches (< 5 m from road) than in control sites (> 100 m from road): one was slightly higher (50.9 vs 35.8 ppm Na), the other (milkweed *Asclepias syriaca*) was substantially higher (2065 vs 62 ppm Na). Monarchs reared on roadside milkweeds (764 ppm Na; control: 47.5 ppm Na) had six times more Na in their abdomens (636.6 vs 129.7 ppm Na) and significantly lower survival (40.5% vs 58.2%), and cabbage whites fed on an artificial diet that varied in Na (~400, 3000, and 6000 ppm Na) had significantly lower survival on the high-Na diet (high: 10.9%; medium: 34.3%; low: 41.7%).	Hazard	Snell-Rood et al. (2014)
		• No preference for butterflies laying eggs on Na-enriched plants (Na ppm in plant tissues: control 83, low 2277, medium 4857, high 4861), though monarch caterpillars somewhat avoided the plants highest in Na, but this is unlikely to compensate for the failure of ovipositing females to avoid toxic high-Na plants.	Exposure	Mitchell et al. (2019)

Table 3
A summary of current knowledge about pollinators and road verges, from the literature review (Appendix A). Confidence was based on the quantity, quality and consensus of evidence using a four-box model for the qualitative communication of certainty (IPBES, 2019). The definitions for categories are: (i) well established: comprehensive meta-analysis or other synthesis, or multiple independent studies that agree, (ii) established but incomplete: general agreement although only a limited number of studies exist but no comprehensive synthesis, and/or the studies that exist imprecisely address the question, (iii) unresolved: multiple independent studies exist but conclusions do not agree, and (iv) inconclusive: existing as or based on a suggestion or speculation, no or limited evidence (IPBES, 2019). A copy of the table is provided in Appendix D with references to the evidence for each statement.

Topic	Conclusion	Confidence	Limitation(s)
Pollinator communities & resources in road verges	Road verges are used by pollinators for…		
	…feeding	Well established	
	…reproduction	Established but incomplete	Studies limited to Lepidoptera
	…nesting	Established but incomplete	Four studies
	…overwintering	Inconclusive	A single study of a single site
	Road verges contain a similar or greater density and species richness of pollinators and flowers to…		
	…agricultural fields	Well established	
	…urban habitats	Unresolved	A single study
	…natural/semi-natural habitats	Well established	
	Road verges are used by pollinators for reproduction, nesting and overwinter to a similar or greater extent than…		
	…agricultural fields	Inconclusive	Three studies, limited to monarch butterflies
	…urban habitats	Inconclusive	No studies
	…natural/semi-natural habitats	Inconclusive	Five studies, mostly on monarch butterflies
Pollinator movement & dispersal	Roads are a…		
	…minor, impermeable barrier to movement for larger pollinator taxa	Established but incomplete	Studies mostly limited to Lepidoptera
	…major barrier to movement for smaller pollinator taxa	Established but incomplete	Four studies
	Road verges are corridors for movement and dispersal for some pollinator taxa	Inconclusive	Five studies, but limited contexts
	Roads/road verges are navigational aids for some pollinator taxa	Inconclusive	A single study on honeybees
Vehicle-pollinator collisions	Vehicle-pollinator collisions kill pollinators	Well established	
	The benefits of road verges for pollinators outweigh the negative impacts of roadkills	Established but incomplete	Studies limited to Lepidoptera
Road pollution	Road pollution negatively affects pollinators in road verges	Well established	
	Pollinators in road verges are negatively affected by…		
	…light pollution	Well established	
	…noise pollution	Inconclusive	A single study
	…vibrations	Inconclusive	No studies
	…turbulence	Inconclusive	A single study
	…air pollution	Established but incomplete	Studies limited to honeybees
	…metal pollution	Established but incomplete	Studies limited to sodium and Lepidoptera
	The benefits of road verges for pollinators outweigh the negative impacts of pollution	Inconclusive	Inferred, but no studies
Road verge, road & landscape characteristics	Road verges with higher quality habitat (e.g. greater plant species richness, density and species richness of flowers)…		
	…contain a greater density and species richness of pollinators	Well established	
	…have fewer pollinator road crossings and roadkills	Established but incomplete	Studies mostly on Lepidoptera
	Wider road verges contain a greater density and species richness of pollinators	Established but incomplete	Studies mostly on Lepidoptera
	Roads with greater traffic volumes have…		
	…lower pollinator density in road verges	Unresolved	Five studies (four on Lepidoptera) find no effect
	…more pollinator roadkills	Established but incomplete	Three studies, limited to Lepidoptera
	The composition of the surrounding landscape affect pollinator communities and their associated resources in road verges, and pollinator roadkill	Well established	Various effects

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Table 3 (*continued*)

Topic	Conclusion	Confidence	Limitation(s)
Road verge management	Road verges can be enhanced for pollinators through strategic management	Well established	
	Road verge mowing directly kills pollinators, eggs and larvae	Inconclusive	No studies
	Road verge mowing regime affects…		
	…flower density and species richness	Well established	
	…the availability and suitability of larval hostplants	Established but incomplete	Studies limited to monarch butterflies
	…pollinator density and species richness	Well established	
	…use of road verges for pollinator movement and dispersal	Inconclusive	No studies
	…pollinator road crossing	Inconclusive	Inferred, but no studies
	…pollinator roadkill	Established but incomplete	Inferred, but two studies on Lepidoptera
	Pollinator communities in road verges benefit from…		
	…creating high quality habitats on new road verges	Well established	
	…controlling/removing invasive, non-native plant species	Established but incomplete	Three studies, but limited contexts
	…reducing mowing frequency to 0–2 cuts/year	Established but incomplete	Inferred, but a single study
	…avoiding mowing during summer	Unresolved	Disagreement between studies
	…removing cuttings	Inconclusive	A single study
	…leaving some areas unmown	Established, but incomplete	Inferred, but a single study
	…using mosaic mowing/management	Inconclusive	Inferred, but a single study
	…creating habitat diversity across the road network	Inconclusive	Inferred, but no studies
	…identifying pollinator roadkill hotspots and applying reduction measures	Inconclusive	Inferred, but no studies
	…reducing impacts of street lighting	Well established	
	…prioritising enhancement of road verges with the greatest capacity to benefit pollinators	Inconclusive	Inferred, but no studies
	Monarch butterflies benefit from mowing road verges around mid-July	Well established	
Overall	The benefits of road verges as habitats and corridors for pollinators outweigh the costs of vehicle-pollinator collisions and pollution.	Established but incomplete	Large-scale modelling studies are needed to collectively assess the benefits and costs

concluded that management of verges aimed at restoring natural or semi-natural vegetation types had positive to neutral effects on insect biodiversity.

3.5.2. Mowing regimes

Recommendations for mowing frequency vary from 0 to 2 cuts per year, though optimum management differs among pollinator taxa. Most studies focus on butterflies, though two studies consider entire pollinator communities. An observational study of 19 road verges in the UK found that mown verges (cut once between May and August, cuttings not removed) had on average 67% fewer flowers and 61% fewer pollinators across the summer than unmown verges (Phillips et al., 2019). Noordijk et al. (2009) experimentally manipulated mowing frequency (cuts/year: 0, 1 (early autumn) or 2 (early summer and early autumn)) and removal of cuttings (left in the verge or removed) in a single road verge (with a species-rich plant community) in the Netherlands. Increasing the number of cuts from 0 to 1 cut resulted in 3.5 times greater flower density and 2 times greater flower species richness, but no significant effect on pollinator density, though increasing from 1 to 2 cuts/year resulted in 3.5 times greater pollinator density. Two cuts per year combined with removal of cuttings resulted in the greatest flower density, flower species richness and pollinator density, though removal of cuttings by itself generally did not result in significant increases. More generally, systematic reviews have found a greater plant species richness (which is likely to benefit pollinators) in road verges mowed once or twice per year with removal of cuttings than in unmown verges (Jakobsson et al., 2018) and in European meadows where mowing was delayed from spring to summer (whilst delaying from spring to fall or from early summer to later in the season had a negative effect; Humbert et al., 2012), though another review for European semi-natural grasslands found relatively little effect of mowing frequency on biodiversity (Tälle et al., 2018). However, none of these studies account for the direct mortality of pollinators, eggs and larvae during mowing. No studies have assessed pollinator mortality during mowing specifically for road verges, but an experiment in fields of *Phacelia tanacetifolia* and fields of *Trifolium repens* found that honeybees did not avoid approaching mowing machinery, so many honeybees were killed or injured, though the proportion killed was strongly affected by the type of mowing machinery (Fluri and Frick, 2002).

Other studies are limited to Lepidoptera but provide evidence that they benefit from low mowing frequencies, delaying mowing until late summer and only partially mowing verges. Two large-scale field experiments assessed optimum mowing regimes for butterflies. In Florida, USA, Halbritter et al. (2015) found that mowing every 3 weeks resulted in 0.5 times lower flower density and 0.25 times lower flower species richness than mowing every 6 weeks or not mowing, but little difference in butterfly density (though the unmown treatment yielded the greatest number of butterflies from August onwards). In southern Finland, Valtonen et al. (2006b) found that partially-mown verges (where a substantial part of the verge always remained unmown) had double the butterfly density, 1.3 times greater butterfly species richness and 1.6 times greater diurnal moth species richness than early-summer mown verges; whilst late-summer mown verges showed intermediate results. Similarly, two further studies in southern Finland observed greater butterfly densities in road verges that are unmown, or otherwise mown in late summer (Valtonen and Saarinen, 2005) or mown no more than once or twice per year (Saarinen et al., 2005), and others have observed that verge mowing is followed by declines in butterfly densities (Haaland, 2015; Munguira and Thomas, 1992).

Studies focusing on single pollinator species can provide contradictory management recommendations. Field experiments exploring mowing regimes for monarch butterflies found that mowing spurred a regrowth of milkweed, which increased egg laying and extended the monarch breeding season compared to unmown controls, and that

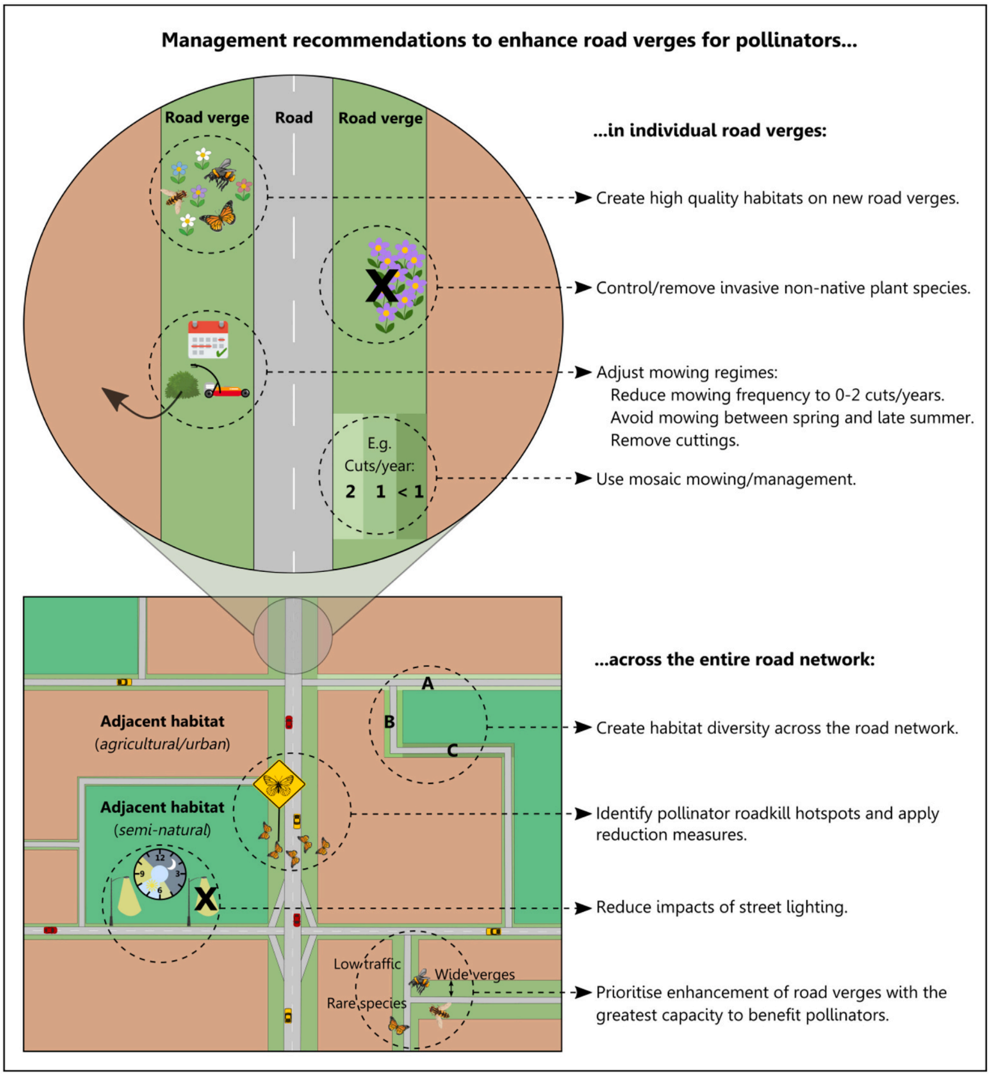

Fig. 3. Management recommendations for enhancing road verges for pollinators, based on the findings of the literature review.

mowing around mid-July was best, whilst mowing in August was too late for milkweeds to recover (Fischer et al., 2015; Knight et al., 2019). By contrast, a study of large blue butterflies *Phengaris* spp. (specialist brood parasites of ants that rely on a single hostplant species) found that mowing between mid-June and mid-September destroyed the locations with both host ants and flowering hostplants, whilst no mowing was also detrimental, and that some *Phengaris* spp. benefited most from early mowing but others from late mowing (Wynhoff et al., 2011). These studies demonstrate that bespoke management is needed when targeting a specific pollinator species of conservation concern.

3.5.3. Management to reduce vehicle-pollinator collisions

Studies suggest that improving the quality of road verge habitats can reduce butterfly road crossing (Polic et al., 2014; Ries et al., 2001) and roadkills (Skórka et al., 2013, 2015), though research is absent for other pollinator taxa. For example, Skórka et al. (2013) found that butterfly roadkills increased with the amount of verge mowing and that relative roadkills (roadkills as a proportion of the butterflies observed in the road verge) decreased with increasing plant species richness in the adjacent road verge. Ries et al. (2001) found that a much lower proportion of butterflies in higher quality prairie verges crossed roads (23%) than butterflies in grassy (low forb cover) verges (49%), which resulted in half as many relative roadkills. Two studies found no such effects (Halbritter et al., 2015; Valtonen and Saarinen, 2005), whilst one study found the opposite, but focused on a single rare butterfly species (*Speyeria zerene hippolyta*) along a single road (Zielin et al., 2016). Various other methods might be used to reduce pollinator roadkills (e.g. traffic speed restrictions) but have not been studied, though Zielin et al. (2016) found that 3 m high nets arranged parallel to the road were ineffective at increasing butterfly flight height over roads.

3.6. Q6) How do road verge, road and landscape characteristics affect pollinators in road verges?

Beyond management, other factors affect how good individual road verges are for pollinators, and their relative importance within the wider landscape, namely the characteristics of the road verge (e.g. verge width, aspect), the road (e.g. width, traffic volume) and the landscape (e.g. adjacent land-use). The effects of these road verge, road and landscape characteristics on pollinators in road verges are synthesised in Appendix C, summarised here, and must all be considered to optimise large-scale management of road verges for pollinators (e.g. where to prioritise enhancements). The most important factors are as follows. (i) Road verge habitat quality: higher quality road verge habitats support richer pollinator communities; specifically, the density of flowers and larval plants, and the species richness of flowers and plants often positively relate to pollinator density and species richness (e.g.

Table 4
Management recommendations for enhancing road verges for pollinators. Recommendations are based on interpretation of the findings of the literature review but are often "Inferred" (logically inferred, but not explicitly/empirically tested), based on the availability and limitations of evidence. The "Confidence" of each expected "Benefit for pollinators" is provided (from Table 3, methods described therein), and references to the evidence are provided in Appendix D.

Scale	Management recommendation	Description	Benefit for pollinators	Practical implications
Individual road verges	Create high quality habitats on new road verges	Follow best management practices for creating high quality pollinator habitats. For example, species-rich grasslands can be created by ensuring low soil fertility (e.g. removing/not adding topsoil) and sowing native, local provenance wildflower seed.	↑ Pollinator density ↑ Pollinator species richness *Well established* ↓ Butterfly road crossing and roadkill *Well established*	Nutrient-poor habitats may require less mowing to maintain safe vegetation height but may have more bare ground (initially and ongoing), which might affect aesthetics and soil stability.
	Control/remove invasive, non-native plant species	Maintain high quality habitats by ensuring that they do not become dominated by invasive, non-native plant species.	↑ Pollinator density ↑ Pollinator species richness *Established but incomplete*	May be very costly, though might have wider conservation and economic benefits by reducing the spread of invasive, non-native species to other areas.
	Reduce mowing frequency to 0–2 cuts/year	Reduce mowing frequency to between 0 and 2 cuts per year.	↑ Pollinator density ↑ Pollinator species richness *Established but incomplete*	May not be possible in urban areas due to aesthetics. In this case, management should aim to reduce mowing frequency as much as possible and to improve social acceptability (e.g. regularly mowing verge edges for tidiness and communicating the environmental benefits).
	Avoid mowing between spring and late summer	Avoid mowing between spring and late summer, when pollinators are most active.	↑ Pollinator density ↑ Pollinator species richness *Unresolved* ↓ Mortality of pollinators, eggs and larvae *Inferred, but inconclusive*	Not always plausible due to minimum safety requirements, for example on visibility splays and often a 1 m strip alongside the road. May be perceived as untidy due to taller vegetation.
	Remove cuttings	Remove cuttings from the road verge, or to a single area of the road verge.	↑ Flower species richness *Established but incomplete* ↑ Flower density ↑ Pollinator density *Inconclusive*	May improve road verge aesthetics and removal of soil nutrients may reduce subsequent vegetation growth and the need for verge cutting, but an appropriate location is needed to dispose of cuttings.
	Use mosaic mowing/management	Apply different mowing/management regimes along the length and/or width of a road verge. For example, split road verges into three sections: Section 1 (front of verge): mow twice per year (in early summer and from late summer onwards), Section 2 (middle of verge): mow once from late summer onwards Section 3 (back of verge): leave unmown or cut on a multi-year rotational basis from late summer onwards.	↑ Habitat diversity; balances the needs of different pollinator taxa; allows areas where pollinator eggs and larvae can persist. *Inferred, but inconclusive* Frequently mowing verge edges may ↓ pollinator road crossing and roadkill. *Inconclusive*	Can be based around current number of cuts, so no increase in costs (unless no current management), but more complex management requires greater training of ground staff. Mowing verge edges more frequently will increase visibility and safety for road users, and perceived aesthetics around tidiness.
Entire road network	Create habitat diversity across the road network	Apply different mowing/management regimes across different road verges (e.g. mow the opposite sides of roads at different times).	↑ Habitat diversity; balances the needs of different pollinator taxa; allows areas where pollinator eggs and larvae can persist. *Inferred, but inconclusive*	As for mosaic mowing/management (above).
	Identify pollinator roadkill hotspots and apply reduction measures	Use measures to reduce pollinator roadkills at roadkill hotspots. For example, improve road verge habitat quality and reduce traffic speeds (or enforce speed limits), both spatially (specific roads) and temporally (e.g. during monarch migration).	↓ Butterfly roadkill *Inconclusive*	Requires initial investment to identify pollinator roadkill hotspots, improve verge habitat quality and enforce speed limits. Reducing speed limits is often impractical, and probably socially contentious for the purpose of invertebrates, but might be justified for strategic roadkill hotspots and achieved by leveraging support for charismatic pollinator species (e.g. bees and butterflies) via an effective communication strategy.
	Reduce impacts of street lighting	Remove street lighting where possible by reducing the number of fixtures, the light intensity and the duration that street lighting is on, and using least harmful lighting technologies.	↓ Pollinator predation ↓ Suboptimal behaviour *Well established*	Needs to be balanced against safety concerns (especially in residential areas) and costs associated with changing street lighting technologies, though energy savings and reduced usage might result in long-term cost-savings.

(*continued on next page*)

Table 4 (*continued*)

Scale	Management recommendation	Description	Benefit for pollinators	Practical implications
	Prioritise enhancement of road verges with the greatest capacity to benefit pollinators	Focus beneficial management on road verges with the greatest capacity to benefit pollinators, namely wider road verges, roads with lower traffic volumes, road verges of particular conservation interest, road verges in landscapes with few other suitable habitats for pollinators, and road verges that connect conservation areas and disproportionately increase habitat connectivity at a landscape scale.	↑ Benefits for pollinators per unit investment *Inferred, but inconclusive*	Requires initial investment to identify priority road verges and additional costs and training of ground staff to deviate from standard management.

Hopwood, 2008; Phillips et al., 2019; Ries et al., 2001), and some studies on butterflies show that higher quality road verge habitats can reduce road crossing and roadkills (e.g. Ries et al., 2001; Skórka et al., 2013, 2015). (ii) Road verge width: wider road verges, which provide greater total habitat area and areas at greater distance from the road, often contain greater Lepidoptera density and species richness (e.g. Munguira and Thomas, 1992; Skórka et al., 2013). (iii) Traffic volume: some studies report fewer pollinators along roads with greater traffic volumes (Martin et al., 2018; Phillips et al., 2019), and traffic volume increases butterfly roadkills (Skórka et al., 2013, 2015, 2018). (iv) Surrounding landscape: road verges that are near higher quality pollinator habitats (e.g. semi-natural grasslands) often have more pollinators (e.g. Flick et al., 2012; Öckinger and Smith, 2007) and subsequently more pollinator roadkills (e.g. Keilsohn et al., 2018; Skórka et al., 2015), though pollinators are probably more dependent on road verges in landscapes with few high-quality habitats (e.g. intensive agricultural landscapes) (Phillips et al., 2019).

4. Synthesis & agenda for future research

Road verges have considerable potential to be used for pollinator conservation, given the significant areas that they collectively cover (e.g. an estimated 1% of UK land). Growing societal interest in managing road verges for nature (especially pollinators) has provided an immediate need for evidence to inform management. This literature review has assessed the potential benefits of road verges for pollinators (as habitats and corridors), the potential negative impacts of roads (pollution and vehicle-pollinator collisions), and the impacts of road verge management. Based on the literature review, we provide a list of conclusions about pollinators and road verges, and information about the confidence and limitations of support for each conclusion (Table 3). Overall, the literature review demonstrated that: (i) road verges are often hotspots of flowers and pollinators (*well established*), (ii) traffic and road pollution can cause mortality and other negative impacts on pollinators (*well established*), but available evidence suggests that the benefits of road verges to pollinators far outweigh the costs (*established but incomplete*), and (iii) road verges can be enhanced for pollinators through strategic management (*well established*). During the review, we have identified key research gaps. In general, there is a scarcity of research outside of Europe and North America, and on non-grassland road verge habitats, entire pollinator communities and pollinator taxa other than butterflies. Specifically, we propose seven priority questions for future research:

1. To what extent do pollinators use road verges for reproduction, nesting and overwintering, relative to other habitats?
2. To what extent do pollinators use road verges as corridors for movement and dispersal?
3. What is the combined impact of the diverse forms of road pollution on pollinators?
4. To what extent does mowing directly kill pollinators, eggs and larvae?
5. What are the population-level impacts of vehicle-pollinator collisions, pollution and different road verge management options?
6. Do road verges ever constitute an ecological trap for pollinators, and if so, under what circumstances?
7. What management strategies can be used to reduce pollinator roadkill and impacts of road pollution?

Furthermore, our approach provides a framework (Fig. 1) from which future research can explore and address issues relating to using road verges for nature conservation for other taxa.

5. Management recommendations

Finally, we consider what might be done to enhance road verges for pollinators. The characteristics of road verges (e.g. verge width), roads (e.g. traffic volumes) and the surrounding landscape (e.g. availability of semi-natural habitats) affect the capacity and importance of road verges for supporting pollinators. Therefore, management needs to consider both management of road verges per se (e.g. optimised mowing regimes), as well as strategic management of the road verge network as a whole (e.g. creating habitat diversity across the whole road network, and prioritising enhancement of road verges with the greatest capacity to benefit pollinators based on the type of road verge, road and composition of the surrounding landscape). We provide a general set of management recommendations in Fig. 3, incorporating the full range of topics that have been covered in the review, alongside practical considerations such as safety, costs and implementation of road verge management for pollinators in Table 4, as these will ultimately affect the acceptability and uptake of recommendations. Here, we describe three illustrative examples of management recommendations that are most strongly supported by the literature review.

First, management should aim to create high quality habitats on new and existing road verges by following best management practices, for example creating species-rich grassland by ensuring low soil fertility (e.g. removing/not adding topsoil) and sowing local provenance wildflower seed. This can increase pollinator density and species richness (*well established*) and reduce butterfly road crossing and roadkill (*well established*) (Table 4). From a practical perspective, nutrient-poor habitats may require less mowing to maintain safe vegetation height, but a greater cover of bare ground may affect aesthetics and soil stability. Second, management of frequently mown areas should be reduced where possible to 0–2 cuts per year to allow wildflowers and larval foodplants to grow and to reduce the risk of direct mortality of pollinators and their eggs and larvae. Doing so can increase pollinator density and species richness (*established but incomplete*) (Table 4). Whilst this may be socially contentious in urban areas due to aesthetics, management should aim to reduce mowing frequency as far as possible and to improve acceptability of reduced mowing, for example by regularly mowing verge edges for tidiness and communicating the environmental benefits to the public. Third, impacts of street lighting should be reduced where possible by removing fixtures, reducing durations that fixtures are active, or otherwise by using the least harmful lighting technologies. This will reduce attraction of nocturnal pollinators and associated predation and impacts on pollinator communities (*well established*) (Table 4), but needs to be balanced against safety concerns, especially in residential areas, as well as costs associated with changing street lighting technologies; though energy savings and reduced usage might result in long-term cost-savings.

Overall, management recommendations for pollinators need to be balanced against requirements of other taxa (e.g. for important species-rich plant communities, it may not be desirable to leave areas uncut; Jakobsson et al., 2018). Furthermore, bespoke management is recommended for road verges of particular conservation interest, based around specific habitat requirements (e.g. phenology and hostplants of the pollinator species). Finally, a strong environmental, social and financial case for investment in enhancing road verges for nature could be made by taking into consideration the benefits that people derive from pollinators and other forms of nature in road verges (Phillips et al., 2020) and by leveraging public support for the conservation of charismatic pollinator species (e.g. bees and butterflies).

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CRediT authorship contribution statement

Benjamin B. Phillips: Conceptualization, Methodology, Investigation, Visualization, Formal analysis, Writing - original draft, Writing - review & editing, Project administration. **Claire Wallace:** Investigation, Writing - review & editing. **Bethany R. Roberts:** Conceptualization, Investigation, Writing - review & editing. **Andrew T. Whitehouse:** Conceptualization, Writing - review & editing. **Kevin J. Gaston:** Writing - review & editing. **James M. Bullock:** Methodology, Writing - review & editing. **Lynn V. Dicks:** Methodology, Writing - review & editing. **Juliet L. Osborne:** Methodology, Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability statement

All data supporting the results are provided in the manuscript and appendices, and were gathered from the associated references.

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