Biological Conservation 272 (2022) 109643

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Bumblebee queen mortality along roads increase with traffic

Juliana Dániel-Ferreira [a,b,*], Åsa Berggren [a], Riccardo Bommarco [a], Jörgen Wissman [b], Erik Öckinger [a]

[a] Swedish University of Agricultural Sciences, Department of Ecology, Box 7044, SE-75007 Uppsala, Sweden
[b] Swedish University of Agricultural Sciences, Swedish Biodiversity Centre, CBM, Box 7016, SE-75007 Uppsala, Sweden

ARTICLE INFO

Keywords:
Bombus
Linear infrastructure habitats
Right-of-way
Ecological trap
Population sink
Semi-natural grasslands

ABSTRACT

Managing road verges to promote diverse and flower-rich plant communities has been proposed to mitigate the decline of pollinating insects caused by the loss of natural and semi-natural habitat. There is, however, a concern that flower-rich road verges can be ecological traps for pollinators as insects might be attracted to a habitat where there is a risk that they are killed by traffic. Therefore, we investigated the combined effects of traffic intensity and flowering plant diversity in road verges on the mortality and behaviour of bumblebee queens. The probability that an observed bumblebee queen was dead almost quadrupled when traffic increased from 100 to 6000 vehicles per day and tended to be lower when the flowering plant diversity in the road verge was high. Further, the number of nest-seeking bumblebee queens decreased dramatically with increasing traffic intensity in sites with low diversity of flowering plants, but not in sites with high diversity. Based on published data on bumblebee colony densities in different habitat types, we estimate that between 0.2 % and 32 % of all bumblebee queens present in our study landscapes were killed by traffic. We conclude that the flowering plant diversity in the road verge neither mitigates nor exacerbates the mortality from traffic. Road verges often provide pollinators with a high abundance of resources in florally poor landscapes. We therefore advise management to prioritise plant diversity along roads with low traffic intensity.

1. Introduction

Pollinators are crucial in supporting global plant diversity and thereby entire ecosystems (Hanley et al., 2015; Ollerton, 2017). Yet, pollinator abundance and diversity are steadily declining regionally and globally (Bartomeus et al., 2013; Ollerton, 2017). The drivers of these declines are multifaceted and include habitat loss and degradation, changes in land use, urbanisation, and climate change, among others (Potts et al., 2016). In Europe, the extensive loss of semi-natural grasslands is a major driver of pollinator decline (Li et al., 2020; Potts et al., 2010). The loss of semi-natural grasslands and the intensification of agriculture have led to a reduction in nesting sites, foraging habitat, and quality of food resources (Bäckman and Tiainen, 2002). Furthermore, the remaining semi-natural grassland habitats are typically isolated fragments scattered across the landscape, which decrease species' colonisation rates and increase the risk of local extinctions (Cousins et al., 2015; Monasterolo et al., 2020; Öckinger et al., 2010). If species can use linear landscape elements such as field borders and road verges as habitat, this partly can mitigate the negative effects of loss and fragmentation of semi-natural habitats (Gardiner et al., 2018).

Roads and road verges form an extensive network in many landscapes, covering large areas of land globally (Phillips et al., 2020a). Road verges can provide habitat for several species associated with semi-natural grasslands, including pollinating insects (Cole et al., 2017; Li et al., 2020; Phillips et al., 2019), and facilitate animal and plant dispersal in the landscape (Monasterolo et al., 2020; Vanneste et al., 2020). However, roads can also have detrimental effects on insect populations through mortality caused by collisions with passing traffic and by being physical or behavioural barriers to movement (Baxter-Gilbert et al., 2015; Muñoz et al., 2015). If the mortality caused by traffic leads to negative population growth rates in road verges, these would be population sinks (Pulliam, 1988). At the same time, road verges that are managed to promote flower richness might attract insects from other habitats, thereby potentially acting as ecological traps (Gilroy and Sutherland, 2007). The negative effects of roads can be particularly pronounced along wide roads with high speed limits and high traffic intensity and can result in isolated populations, reduced population sizes, and genetic bottlenecks (Baxter-Gilbert et al., 2015; Keilsohn

---

* Corresponding author at: Swedish University of Agricultural Sciences, Department of Ecology, Box 7044, SE-75007 Uppsala, Sweden.
E-mail address: juliana.daniel.f@slu.se (J. Dániel-Ferreira).

https://doi.org/10.1016/j.biocon.2022.109643
Received 19 October 2021; Received in revised form 13 June 2022; Accepted 19 June 2022

et al., 2018; Muñoz et al., 2015). Most research on negative population consequences of roads and how they can be mitigated have focused on mammals, birds, and amphibians, leaving a knowledge gap for invertebrates (Andersson et al., 2017; Muñoz et al., 2015).

Recently it has been proposed that management that promotes a diverse plant community in road verges can benefit pollinator communities, both locally and at larger spatial scales (Phillips et al., 2020b). However, given the potential negative influence of roads and traffic, it is unclear under what circumstances such management is appropriate and if road verges with high plant diversity can mitigate the negative effects of traffic on pollinating insects. Floral availability can affect populations of flower-visiting insects in contrasting ways. If insects are attracted to road verges with high plant diversity, this could lead to more individuals crossing the road and thereby increasing their mortality risk. Contrastingly, a high plant diversity could lead to longer residence times in the road verge, less frequent movements into the roads due to this, and thereby reduced mortality. Empirical studies have found evidence of both higher mortality (in butterflies) when the road verges had low levels of floral resources (Skórka et al., 2015), and higher mortality (in bumblebees) when the road verges had abundant floral resources (Keilsohn et al., 2018). This highlights the need to understand the combined effects of road verge plant diversity and traffic intensity on pollinating insect populations (Jakobsson et al., 2018; Keilsohn et al., 2018). Managers need to know whether there is a threshold when traffic has such large and detrimental effects on pollinator populations that any efforts to increase habitat quality in the verges risks creating an ecological trap (Battin, 2004), and if road verges with high plant diversity can mitigate the negative effects of traffic on pollinating insects.

Bumblebees (*Bombus* spp.) and other social insects have comparably small effective population sizes because each colony is founded by a single queen, and in most species, the queens mate with a single male before going into hibernation (Goulson, 2010). Therefore, the mortality of bumblebee queens before they have established a colony can have a large impact on population persistence. Bumblebees can suffer from traffic mortality but are not deterred from using resources in the road verges (Baxter-Gilbert et al., 2015; Phillips et al., 2021). Even though workers are known to avoid crossing roads (Bhattacharya et al., 2003), less is known about how bumblebee queens are affected by roads and road verges. While bumblebee workers are central-place foragers, newly emerged queens can disperse over distances ranging from 3 km (Lepais et al., 2010) up to several hundreds of kilometres (Fijen, 2021) before establishing a nest. Further, the movement patterns of queens are typically different before and after they have established a nest (Cavigliasso et al., 2020). Newly emerged queens do not attempt to return to the site of emergence, and show random dispersal movement by short flight sequences before they start searching for a nest (Makinson et al., 2019). In contrast, queens that have established a nest are central place foragers and primarily search for pollen, which they bring back to their nest (Cavigliasso et al., 2020; Suzuki et al., 2009). Roads verges could facilitate dispersal of queens, but not if they are killed in the process. The slower and less targeted movements of nest-seeking queens along roads could make them particularly vulnerable to collisions with cars.

We explored the combined effects of traffic intensity and road verge flowering plant diversity on the mortality and behaviour (foraging and nest-seeking) of bumblebee queens as an indirect step in determining whether road verges can be acting as ecological traps. We predicted that 1) higher flowering plant diversity in the verges leads to a higher number of bumblebee queen individuals, 2) higher flowering plant diversity in the road verges affects road mortality, either negatively or positively, 3) bumblebee mortality increases with traffic intensity, and 4) there will be a higher number of foraging and nest-seeking queens along roads with higher flowering plant diversity and low traffic intensity.

2. Methods

2.1. Study organisms

We aimed to examine how traffic intensity and the flowering plant diversity in road verges affect the important pollinator group bumblebees (*Bombus*). Bumblebees are one of the most important group of native crop pollinators in Europe and North America (Kleijn et al., 2015), and are showing declines in these continents (Goulson et al., 2008). As bumblebees are social insects, the survival of a queen is the most important determinant of the development of each colony further on in the season. In northern Europe, bumblebee colonies usually have one generation per year (Goulson, 2010). Newly hatched bumblebee queens mate in late summer, overwinter, and establish a new colony in the spring. After the queen has established the colony, the first set of sterile female workers hatches and start foraging, while the queen remains inside the nest to produce more workers. Each colony produces one or a few new queens that eventually hibernate to emerge the next spring, starting the cycle again (Goulson, 2010; Iles et al., 2018). In east mid-Sweden, hibernating bumblebee queens begin to emerge in April.

2.2. Study design and site selection

We established a factorial study design that consisted of ten matching sites, where we varied the *traffic intensity on the road* and the *flowering plant diversity in the road verge*. We selected 10 pairs of sites that were matched regarding traffic intensity (continuous), but with contrasting (factor: high vs low, see below) flowering plant diversity (Fig. 1a; Table S1). Sites with high flowering plant diversity also had higher flower cover than low plant diversity sites (see below). To select the sites, we used data from the National Road Database (NVDB: http://www.nvdb.se) which contains information about Swedish roads such as the average number of vehicles per day (traffic intensity), road width, speed limit, and road type. The Swedish Transport Administration aims at identifying road verges of high value for biodiversity, and to adapt the management of such road verges. Hence, the NVDB contains information on road verges classified as 'species-rich'. 'Species-rich' road verges are classified as such if they fulfil at least one of the following conditions regarding the plant species present: 1) have rare or threatened species, or contain several indicator species indicating a species-rich plant community, 2) contain high species diversity, 3) provide an important ecological resource (e.g. crucial in an organism's life cycle) or 4) promote species' dispersal and landscape connectivity (Lindqvist, 2012). 'Species-rich' road verges are usually mown only once by the end of the season, in contrast to regular grassy road verges which are cut up to three times. Neither type of road verge is managed using pesticides or herbicides. We used this information to select ten 'species-rich' sites (hereafter referred to as having high flowering plant diversity) along a gradient from low to high traffic intensity. We first selected ten sites with high flowering plant diversity, aiming to maximise the gradient in traffic intensity. After this, we selected ten additional sites with low flowering plant diversity (i.e. not classified as 'species-rich' by the Swedish Transport Administration) that met the same conditions and with a similar gradient in traffic intensity as the first group (Fig. 1b). To confirm that road verges identified as 'species-rich' had higher numbers of plant species used by bumblebees, we surveyed flowering plants in each site and identified all flowering forb species (i.e. excluding grasses and sedges) within six 1 m^2 plots on both sides of the road. Plant surveys were carried out twice: once during June 2019 and another in August 2019, while the bumblebee queen surveys were performed during the spring and late summer of the following year. The plots were situated 200 m apart, and the placement of the first plot was where the Swedish Transport Administration identified the beginning of the 'species-rich' area. When a species rich segment was longer than 1 km, the first plot was placed randomly along the road verge. All plots were placed in the centre width of the road verge to avoid the buffer zone (area adjacent to

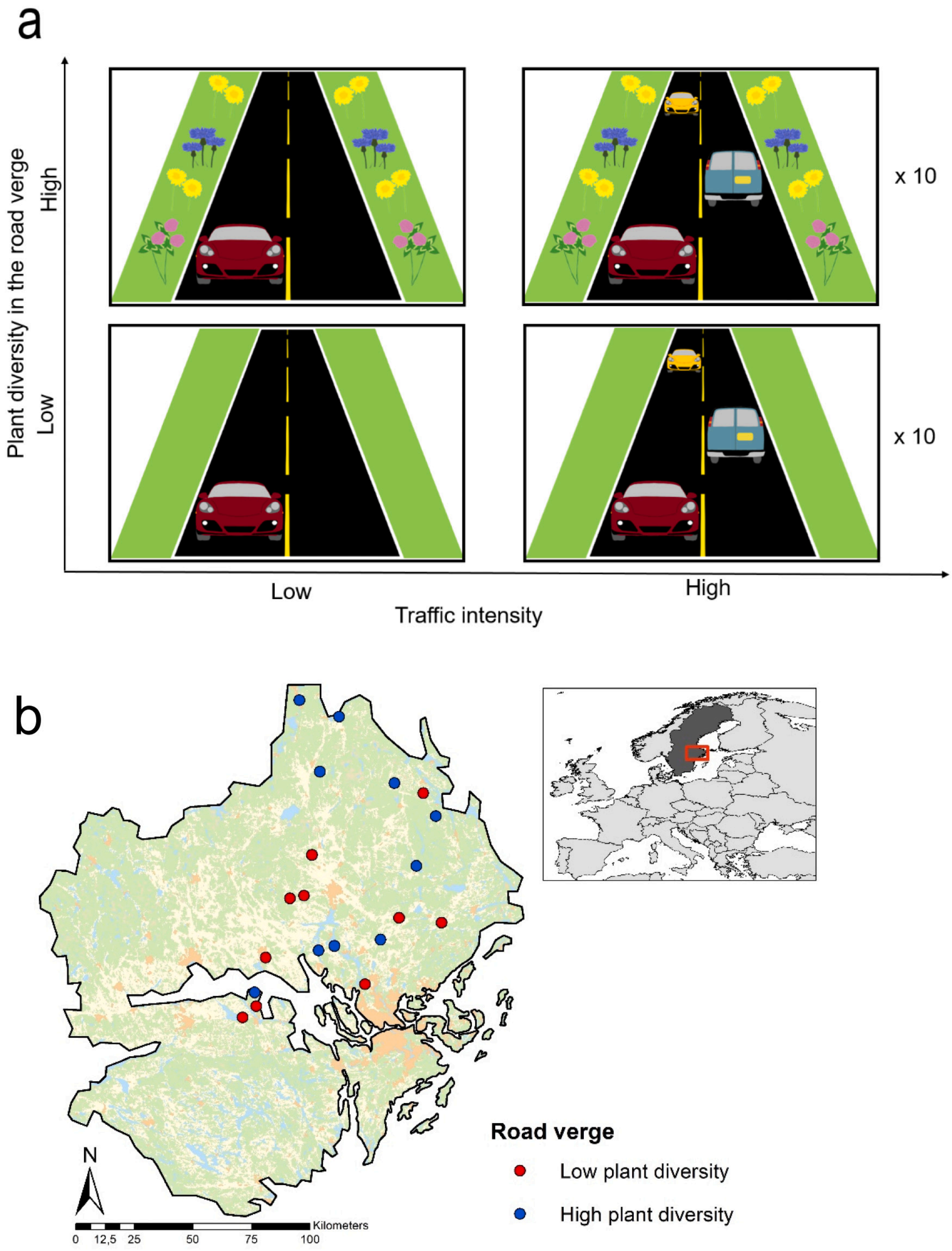

Fig. 1. a) Study design with half of the 20 sites with a high flowering plant diversity in the road verge and a traffic intensity gradient. The other half had a regular grassy road verge with low flowering plant diversity and a similar traffic intensity gradient. b) Location of the 20 study sites in east mid-Sweden.

the road aimed at intercepting road run-off) at sites with high traffic. This showed that 'species-rich' road verges had indeed a higher number of flowering plant species (mean = 15 ± 4.94 species in six 1 × 1 m plots per site) than the road verges with low plant diversity (mean = 10.1 ± 2.81 species; ANOVA $F_{1,18} = 7.43$, $p = 0.01$). Previously (using the same sites as in this study), we demonstrated that the 'species-rich' road verges had on average 29 % higher flower density (Dániel-Ferreira et al., 2022). In general, low flowering plant diversity sites were dominated by grasses while high flowering plant diversity sites had in average more flowering forb species. According to the National Road Database, average traffic intensity in our sites ranged from 125 to 6300 vehicles per day for sites with high plant diversity, and from 158 to 6198 vehicles per day for sites with low plant diversity. Given that the bumblebee queen survey took place during the covid-19 pandemic with potentially changed traffic patterns, we measured traffic intensity at our sites by counting all passing vehicles during 15 min at the same time (between 13:00 and 13:30 h) in 20 different working days to ensure the traffic intensity gradient was not affected. We found that the measured average traffic intensity agreed well with the estimate in the National Road Database (Pearson's $r_{18} = 0.97$, $p \leq 0.001$), and therefore used the values in the database for the analyses.

To standardise characteristics other than traffic intensity and road verge flowering plant diversity as far as possible, we restricted our selection to roads with a width between 6 and 7 m and a speed limit of 70 or 80 km/h. All sites were surrounded by rural landscapes dominated by a mix of forest and agriculture, with an average 32 % arable land cover (min = 0.42 %, max = 76.95 %), 42 % forest cover (min = 4.12 %, max = 77.5 %), and 18 % grassland cover (min = 3.66 %, max = 38.76 %) (in a 1 × 1 landscape). Road verge density in the landscape varied between 1.05 % and 2.81 % (Table S7).

2.3. Bumblebee queen survey

In 2020, we surveyed bumblebee queens in each study site in two sampling rounds during spring (between the 5th and 29th of May) and late summer (between the 25th of August and the 8th of September). In each sampling round, spring and late summer, the sites were visited twice. The interval between visits was at least one week, and the order of the visits to each site was randomised. The timing of the spring surveys was selected to match the time when the queens of most bumblebee species are searching for nesting sites in our study region. During late summer, queens can be observed searching for places where they can overwinter, and we performed the surveys during this period to explore the role of road verges as overwintering habitat. During the surveys, the observer walked slowly in a 1 km long transect along the road verge on one side of the road and back 1 km on the other side of the road, resulting in a 2 km transect in total. Along this transect, the observer searched visually for both living and dead bumblebee queens 1 m into the road verge and 1 m into the road. All observed bumblebees were identified to species level in the field (except for one individual that was collected for later identification in the lab) using Swedish field guides for bumblebees (Mossberg and Cederberg, 2012; Söderström, 2013). Individuals were identified as queens based on size and behaviour. The behaviour of each bumblebee was recorded. In spring, the bumblebees were seen performing one of four activities: nest-seeking, foraging, resting, or flying along the road verge. Nest-seeking bumblebees are easy to identify in the field, as they fly in a typical zigzag trajectory near the ground and land to investigate potential nesting sites (Kells and Goulson, 2003). Queens seen entering a nest were also counted as showing a 'nest-seeking' behaviour. In late summer, the queens could be mating, foraging, resting, flying along the road verge, or seeking overwintering sites. All dead individuals were counted and, if possible, identified to species. Dead bumblebee queens that could not be identified, e.g. due to decomposition or predation attempts, were also counted. The nomenclature used follows the Swedish Species Information Centre taxonomic database Dyntaxa (http://www.slu.se/dyntaxa/). Individuals belonging to *B. lucorum*, *B. cryptarum*, and *B. magnus* were pooled together into one group, *B. lucorum coll.*, as they are difficult to separate in the field. The surveys were only conducted between 09:00 and 17:00 h on days with no precipitation when the temperature was above 10 °C and sunny, and when the wind did not exceed 6 on average in the Beaufort scale. Given that most road verges are mowed during the end of the summer, we expected a similar variation in the detection probability of dead bumblebee queens across all sites.

2.4. Data analysis

We used R (R Core Team, 2020) for all analyses. All models described below use flowering plant diversity in the road verge (factor: high or low) and traffic intensity (continuous) as fixed effects. Traffic intensity was scaled in all models by subtracting the mean and dividing by the standard deviation, to allow for model convergence. For each test, we included traffic intensity and plant diversity in the road verge as explanatory variables. We tested models both with and without the interaction between traffic intensity and plant diversity using Likelihood Ratio (LR) tests between the candidate models. We ensured that the models were not over- or underdispersed, and the residual diagnostics were visually checked for all models using the package '*DHARMa*' (Hartig, 2020).

To assess differences in the number of bumblebee species and the number of living bumblebee queens between treatments, we used generalized linear models (GLM) with a Conway-Maxwell Poisson distribution using the function *glmmTMB* and the family *compois* from the package 'glmmTMB' ($n = 40$; Brooks et al., 2017). In order to detect and account for differences in the number of species and number of alive individuals between seasons, we added sampling season (factor: spring or late summer) as a fixed effect. We applied the Conway-Maxwell Poisson distribution because the corresponding models with a Poisson distribution were either under- or overdispersed (Huang, 2017). The model exploring differences in the number of species between treatments included all observed individuals (i.e. dead and alive).

To assess how the mortality of bumblebee queens was affected by flowering plant diversity in the road verge and traffic intensity, we used a generalized linear mixed effects model (GLMM) using the package 'glmmTMB' with a binomial distribution and a logit link. Bumblebee mortality was estimated as the probability that an observed bumblebee (of any species) was dead or alive using the entire data set ($n = 403$). The response variable was binary: one corresponding to dead and zero to alive bumblebee queens. The fixed effects were flowering plant diversity in the road verge, traffic intensity, and the sampling season. Sampling season was added as a fixed effect account for differences in abundance between seasons. To account for variation among species, we included species identity as a random effect. An additional random effect for site was added to account for the multiple observations in each site.

To determine the frequency of behaviours related to flowering plant diversity in the road verge and traffic intensity, we performed a GLMM with a Poisson distribution and a log link, with the number of individuals per site foraging or nest-seeking as the response variable ($n = 40$). Too few individuals were observed for the other behaviours (overwintering, mating, passing, and resting) to include them in the analyses. The type of behaviour, flowering plant diversity in the road verge, and traffic were included as fixed effects. We also included the two-way and three-way interactions between these variables (Table S3). Site was included as a random effect to account for overdispersion and to ensure that the variation among sites was taken into account. As behaviours differ between seasons (i.e. queens do not seek nests in the late summer), it was not possible to include the sampling season in the model. Instead, data from spring and late summer were aggregated.

To disentangle the three-way interaction, we analysed the effects of traffic intensity and flowering plant diversity in the road verge on the number of foraging ($n = 40$) and nest-seeking ($n = 20$) bumblebees, respectively, in two separate models. To explore whether the traffic and the plant diversity in the road verge affected the number of foraging bumblebee queens, we performed a GLM with a Conway-Maxwell Poisson distribution with the number of foraging queens per site as a response variable and the flowering plant diversity in the road verge, traffic intensity and sampling season as explanatory variables. We selected a Conway-Maxwell Poisson distribution because the corresponding model with a Poisson distribution was overdispersed. Finally, we performed a GLM with a Conway-Maxwell Poisson distribution with the number of nest-seekers (using data from spring surveys only) per site as a response variable to flowering plant diversity in the road verge and traffic intensity.

2.5. Estimating the number of bumblebee queens for the study landscapes

As each bumblebee queen has the potential to establish one colony, the death of each bumblebee queen can potentially reduce the total population density of bumblebees in the landscape. To estimate how the observed traffic-related bumblebee mortality translates to consequences for the total bumblebee population in a landscape, we estimated the density of bumblebee populations based on data from two previous and complementary studies that provided estimates of bumblebee queen and nest densities, respectively, in different habitat types (Osborne et al., 2008; Svensson et al., 2000). We used these estimates in combination with land cover data in 1 × 1 km landscapes surrounding our study sites in order to estimate the total number of bumblebee queens emerging in spring in each landscape. Assuming that bumblebee queens stay in the same 1 × 1 km landscape where they emerged after hibernation, we thereafter calculated the proportion of the total population of bumblebee queens killed by traffic along the studied roads in these landscapes. Further, we extrapolated these numbers to estimate the number of bumblebees killed by traffic in Sweden in total, based on the total length of roads with at least 2000 vehicles per day. For details regarding these estimations, we refer to the Supplementary Methods (Appendix A).

3. Results

We observed 403 bumblebee queens belonging to 18 species (Fig. S1; Table S2). Of the 403 individuals, 132 were found dead, 146 were foraging, 97 showed nest-seeking behaviour, 15 were passing, 10 were resting on flowers, 2 were lying alive next to the road, and 1 was searching for an overwintering location (Fig. S2). In late summer we found only one dead bumblebee queen in total (~1 %, 89 observations). The average number of bumblebee species (including dead and alive queens) was similar in sites with high (mean = 8.2 ± 1.4) and low (mean = 7.0 ± 1.89) flowering plant diversity (Table S4).

The number of dead individuals varied among species, with *B. terrestris* and *B. lucorum coll.* having the highest proportion of dead individuals (Fig. S1a). The proportion of dead bumblebee queens increased with increasing traffic intensity (Fig. 2a). When traffic was around 100 vehicles/day, the probability that an observed bumblebee queen was dead was approximately 0.22. This probability increased to 0.37 when the traffic intensity was around 2000 vehicles/day and to 0.78 when the traffic intensity was around 6000 vehicles/day (Table 1). There was a marginal effect of the flowering plant diversity on the probability that an observed bumblebee queen was dead (Fig. 2b; Table 1), indicating lower mortality when plant diversity was high. Furthermore, the number of observed living queens decreased with increasing traffic intensity ($z = -3.18$; $p = 0.001$) but did not vary between sites with low and high flowering plant diversity (Table S5). The interaction between traffic and flowering plant diversity in the road verge never improved model fit and were thus not used in the final models described above (Table S3).

Table 1

Results from the generalized linear mixed-effects model exploring the relationship between the probability of observing dead queens with the flowering plant diversity and traffic intensity. Shown are the Chi-square values (χ^2), degrees of freedom (df), estimates (e), standard error (s.e.), and *p*-values (*p*). *P*-values in bold are significant at the 0.05 level or lower.

	$\chi^2(df = 1)$	e	s.e.	*p*
Intercept		−0.39	0.40	
Road verge (high diversity)	3.55	−0.87	0.46	0.06
Traffic	14.86	0.83	0.22	**<0.001**
Sampling season (late summer)	16.07	−4.36	1.09	**<0.001**

There was a three-way interaction between the type of behaviour (foraging or nest-seeking), the diversity of flowering plants in the road verge, and the traffic intensity on the abundance of queens that were either foraging or nest-seeking (Table S6). In other words, the behaviour of a bumblebee queen depended on both the traffic intensity and the flowering plant diversity in the road verge. There was no difference in the number of foraging queens between low and high plant diversity sites, but traffic intensity had a marginal negative effect on the number of foraging queens (Table 2). There was an interaction between traffic intensity and flowering plant diversity in the road verge on the number of nest-seeking bumblebees (Table 3). In low flowering plant diversity sites, the number of nest-seeking queens was negatively affected by high traffic intensity, while there was no effect of traffic intensity in high flowering plant diversity sites (Fig. 3).

Table 2

Results from the generalized linear model with a Conway-Maxwell Poisson distribution exploring the relationship between the number of foraging queens with the traffic intensity and the flowering plant diversity in the road verge. Shown are the estimates (*e*), standard error (*s.e.*), z-values, and *p*-values (*p*). *P*-values in bold are significant at the 0.05 level or lower.

	e	s.e.	*z*-value	*p*
Intercept	1.12	0.29		
Road verge (high diversity)	0.17	0.32	0.54	0.59
Traffic	−0.31	0.17	−1.87	0.06
Sampling season (late summer)	0.07	0.31	0.23	0.82

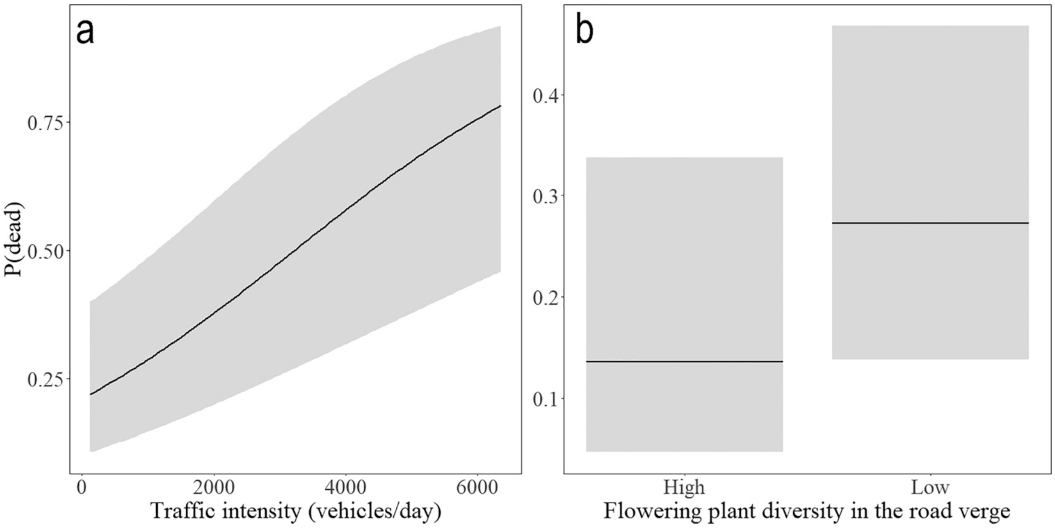

Fig. 2. a) The predicted probability that an observed bumblebee queen was dead increased with increasing traffic intensity. b) The predicted probability that an observed bumblebee queen was dead tended to be lower in sites with a high flowering plant diversity. Shown are the fitted lines and the shaded areas represent the 95 % confidence intervals.

Table 3
Results from the generalized linear model with a Conway-Maxwell Poisson distribution exploring the relationship between the number of nest-seeking queens with the traffic intensity and the flowering plant diversity the road verge. Shown are the estimates: (*e*), standard error (*s.e.*), z-values, and *p*-values (*p*). *P*-values in bold are significant at the 0.05 level or lower.

	e	s.e.	z-value	p
Intercept	−0.81	0.79		
Road verge (high diversity)	2.16	0.81	2.66	**<0.01**
Traffic	−4.35	1.08	−4.02	**<0.001**
Road verge (high diversity) × traffic	4.46	1.10	4.07	**<0.001**

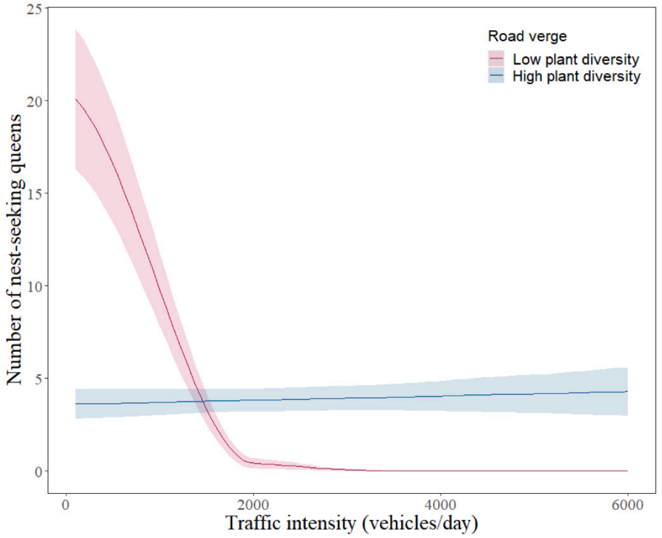

Fig. 3. The number of nest-seeking bumblebee queens per site decreased with increasing traffic intensity in sites with low flowering plant diversity in the road verge. In sites with high flowering plant diversity, there was no effect of traffic intensity on the number of bumblebee queens with this behaviour. Shown are the fitted lines and the bands represent the 95 % confidence intervals. The red line indicates sites with low flowering plant diversity and the blue line indicate sites with high flowering plant diversity in the road verge. The y-axis is rescaled from a logarithmic scale to the original scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.1. *Estimating the number of bumblebee queens in the landscapes*

The area of land cover types in the landscapes surrounding the 20 roads is presented in Table S7. Using numbers from Svensson et al. (2000), the estimated average number of bumblebee queens in our 1 km^2 landscapes was 68 (min = 24, max = 106; Table S8). When using the estimates given in Osborne et al. (2008), the number of queens per landscape was considerably higher, with an average of 744 (min = 262, max = 1051; Table S9) queens per landscape. Combined with our observations of dead bumblebee queens, this resulted in that on average between 1 % (min = 0 %, max = 10 %, median = 0.7 %; using estimates from Osborne et al., 2008) and 10 % (min = 0 %, max = 32 %, median = 7.4 %; using estimates from Svensson et al., 2000) of the bumblebee queens in a landscape were killed by traffic along the studied roads.

4. Discussion

Identifying threats to wild pollinators is essential to stop and reverse their population decline. We identified high traffic intensity as a threat to bumblebee populations as queen mortality increased with traffic intensity. Interestingly, road mortality tended to be lower when plant diversity in the road verge was high. Most nest-seeking queens were observed in road verges with low flowering plant diversity, but only in sites with low traffic intensity. As the traffic intensity increased, the number of queens searching for nesting sites in road verges decreased in sites with low flowering plant diversity. The period when queens establish their colonies is crucial in the life cycle of bumblebees and can have a great effect on population sizes. In this period, high mortality and competition for nest sites are often observed (Baer and Schmid-Hempel, 2003; Vepsäläinen and Savolainen, 2000), and additional sources of mortality can have severe consequences for bumblebee populations. Our results put light on key drivers influencing the mortality of bumblebee queens and colony survival that affect bumblebee abundance and diversity.

We found a higher proportion of dead bumblebee queens along roads with high traffic intensity. An increase from 125 to 2680 vehicles/day related to a doubled mortality risk for queens, increasing from 0.22 to 0.44. This shows that traffic can be a substantial source of mortality for bumblebee queens, and is in line with previous observations that road mortality of insects generally increases with traffic intensity (Baxter-Gilbert et al., 2015; Keilsohn et al., 2018; Martin et al., 2018; Muñoz et al., 2015). There was a tendency to lower mortality risk in sites with high flowering plant diversity. Although this effect was not statistically significant, it suggests that managing road verges for increased flowering plant diversity does not directly lead to increased road mortality, as one would expect if flower-rich road verges were ecological traps (but see Keilsohn et al., 2018). However, plant diversity did not moderate the effect of traffic on mortality (i.e. no interactive effect), and hence we found no evidence that managing road verges for increasing flowering plant diversity mitigates the negative effect of traffic on bumblebee populations. Note, however, that it could be the case that a higher diversity and abundance of flowering plants than in our 'species rich' sites could give a different response. Our results show that road mortality risk of bumblebee queens along roads increases with increasing traffic regardless of the flowering plant diversity in the road verge.

The number of nest-seeking queens decreased with increasing traffic intensity in low flowering plant diversity sites, but not in high flowering plant diversity sites. In addition, the number of foraging bumblebees tended to decrease with increasing traffic intensity. The general positive relationship between traffic intensity and mortality in combination with the sharp decrease in the number of nest-seeking queens in low flowering plant diversity road verges with increasing traffic suggests that the nest-seeking behaviour is a key factor in traffic-related bumblebee mortality. In spring, ~42 % (131 out of 314) of observed queens were dead, while in late summer when bumblebees do not search for nest sites, we observed only one dead bumblebee queen. The lower mortality of foraging queens compared to nest-seeking queens could be due to that they collide less frequently with traffic than nest-seeking queens do. This has been found for foraging bumblebee workers, which have been observed avoiding crossing roads (Bhattacharya et al., 2003).

Grass-dominated road verges with low flowering plant diversity appear to be more attractive to nest-seeking queens of both belowground and above-ground nesting species than road verges with high flowering plant diversity. This could partly be explained by a preference for grass tussocks (Kells and Goulson, 2003; Liczner and Colla, 2019), which are more abundant in verges with low flowering plant diversity, by some of the species we observed (e.g., *B. pascuorum* and *B. ruderarius*). Additionally, both the number of nest-seeking queens and the number of nests have been shown to be independent of floral abundance (O'connor et al., 2017). This suggests that the specific location of a nest is not related to the local amount of forage, but to the availability of abandoned mammal burrows and the presence of the vegetation structure needed to build a nest (Liczner and Colla, 2019; O'connor et al., 2017; but see Suzuki et al., 2009).

The number of foraging bumblebee queens was marginally affected by traffic but not by the flowering plant diversity in the road verge. However, we did not measure flower density throughout the entire season, only during the early and late summer of the previous year. It is possible that flower densities were relatively similar between high and low flowering plant diversity sites during our survey periods, and especially in spring when the number of flowering species is low. Furthermore, foraging queens that have not yet established a nest tend to be less selective regarding the habitat quality in terms of pollen heterogeneity (Cavigliasso et al., 2020), which could also have led to similar numbers of foraging queens among the sites.

The apparently high mortality of bumblebee queens due to traffic raise the question of whether road verges could be acting as population sinks or ecological traps for nest-seeking bumblebees. Ecological traps arise by the inability of animals to distinguish between high- and low-quality habitat, which leads them to settle in a poor-quality habitat where their net population growth rate is negative (Gardiner et al., 2018; Gilroy and Sutherland, 2007). Road verges can provide essential floral resources in landscapes where these are otherwise scarce (Gardiner et al., 2018; Vanneste et al., 2020). However, if flower-rich road verges attract bumblebees from the surrounding landscape and at the same time their association with roads increases the bumblebees' risk of getting killed, they could be ecological traps. We did not find higher numbers of bumblebees in road verges with high diversity of flowering plants, and the mortality tended to be lower when the diversity of flowering plants was high. Without exploring the overall demography of bumblebees in relation to roads and road verges, it is impossible to determine whether road verges are population sinks or ecological traps, but our results do not point in that direction.

We took a first step to understand the impacts of traffic mortality of queens on bumblebee populations in the surrounding landscape. Assuming at least one dead queen per road site, we estimated that the proportion of dead queens per 1 km^2 of surrounding landscape varied from a minimum of 0.2 % (i.e. the lowest estimate in any of our landscapes based on the data on colony densities from Osborne et al., 2008), to a maximum of 32 % (the highest in any of our landscapes, based on the data from Svensson et al., 2000). The contrast between these estimates reflects the uncertainty about bumblebee nest site preferences which are poorly understood (Liczner and Colla, 2019; O'connor et al., 2017; Osborne et al., 2008). The contrast also reflects the variation in the estimated colony densities for 'woodland', which cover a substantial part of the landscapes we performed our study in. Svensson et al. (2000) did not observe a single nest-seeking bumblebee in the forest habitat, which they described as mixed well-grown forest. In contrast, Osborne et al. (2008) found that the nest density in woodlands was 10.8 nests ha^{-1}. The average estimates across landscapes, (i.e. 1 % using data from Osborne et al. (2008) and 10 % using data from Svensson et al. (2000)) nevertheless give an indication that the potential impact on populations of traffic-related mortality could be substantial.

4.1. Implications for road verge management and conservation of bumblebees

We estimate that between 0.2 and 32 % of all bumblebee queens are killed on roads with a traffic intensity of 2000 vehicles per day or more in Sweden (Tables S8, S9). This would represent a minimum of 45,876 and a maximum of 596,388 dead bumblebee queens in Sweden during the month of May alone. The road mortality is likely to be even higher in countries with higher road density and traffic intensity than in Sweden (Supplementary methods). Unquestionably, this is a very rough estimation as the number of queens in a landscape is highly variable between years, geographical areas, time of the year, and depends on landscape structure and configuration (e.g. Iles et al., 2018; Rundlöf et al., 2014). Nevertheless, our results highlight that despite bumblebees being probably the most studied group of wild bees (Iles et al., 2018), we still lack a comprehensive understanding about their nesting preferences and what influences their population sizes, and thereby how important traffic is as a cause of mortality for bumblebees. Based on our estimates, we argue that road mortality should be regarded as a driver of bumblebee decline.

Managing road verges with low flowering plant diversity could also have a positive impact on bumblebee populations (Fig. 3). If road verges with low flowering plant diversity have a high mortality risk for nest-seeking bumblebee queens, a potential mitigation measure would be to maintain a low vegetation height in verges along roads with high traffic intensity during the spring. To reduce overall mortality along roads, a possibility could be to manage wide road verges with a buffer strip of low habitat quality with low vegetation height closest to the road and high plant diversity and flower density further away from the road surface.

Pollinator populations are subject to several anthropogenic stressors that drive changes in community composition and local extinctions through bottom-up effects (Bommarco et al., 2012; Potts et al., 2010; Roberts et al., 2020). Also, top-down effects that cause direct mortality, such as predation, parasitism, and pesticides, can reduce the population size of wild pollinators (Roberts et al., 2020). Additional sources of mortality, such as traffic collisions, can exacerbate population declines. Conservation efforts have usually been aiming to increase the amount and quality of the foraging habitat in the landscape. These efforts can be complemented with conservation acting on other crucial stages in the life cycle of an organism, especially when they relate to social hymenopterans, whose entire populations depend on the rates of success of single individuals such as bumblebee queens. Road mortality of bumblebees could decrease by reducing the amount of traffic, and probably also by reducing speed limits to lower the risk of collisions. The management of road verges to enhance flowering plant diversity for conservation purposes has recently gained more attention, as this may also enhance population viability (Gardiner et al., 2018). In Sweden, only ~10 % of the roads with a traffic intensity below 2000 vehicles per day have adjacent road verges with high plant diversity (Table S9), allowing enough opportunities to apply the desired targeted management. Furthermore, there is substantial evidence that road verges provide important habitat for pollinators (Baude et al., 2016; Cole et al., 2017; Heneberg et al., 2017; Rundlöf et al., 2014), especially in intensively managed agricultural landscapes with a lack of floral resources. Following this, we suggest that if management to promote flowering plant diversity is to be applied, it should be primarily targeted to road verges along roads with low traffic intensity.

Data availability

The data supporting the findings of this publication are available in the Swedish National Data Service (SND) at https://doi.org/10.5878/mrva-kt50.

CRediT authorship contribution statement

Juliana Dániel-Ferreira: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Visualization **Riccardo Bommarco:** Writing – review & editing, Funding acquisition **Åsa Berggren:** Methodology, Writing – review & editing **Jörgen Wissman:** Methodology, Writing – review & editing, Funding acquisition **Erik Öckinger:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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.

Acknowledgments

M. Johansson assisted with data collection. This study was funded by the Swedish Research Council FORMAS (contract 942-2015-988) (to EÖ, JW, RB) and Stiftelsen Oscar och Lili Lamms minne (to E.Ö.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109643.

References

Andersson, P., Koffman, A., Sjödin, N.E., Johansson, V., 2017. Roads may act as barriers to flying insects: species composition of bees and wasps differs on two sides of a large highway. Nat. Conserv. 18, 47–59. https://doi.org/10.3897/natureconservation.18.12314.

Bäckman, J.-P.C., Tiainen, J., 2002. Habitat quality of field margins in a finnish farmland area for bumblebees (Hymenoptera: bombus and Psithyrus). Agric. Ecosyst. Environ. 89, 53–68. https://doi.org/10.1016/S0167-8809(01)00318-8.

Baer, B., Schmid-Hempel, P., 2003. Effects of selective episodes in the field on life history traits in the bumblebee Bombus terrestris. Oikos 101, 563–568. https://doi.org/10.1034/j.1600-0706.2003.12395.x.

Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M., Winfree, R., 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. Proc. Natl. Acad. Sci. 110, 4656–4660. https://doi.org/10.1073/pnas.1218503110.

Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conserv. Biol. 18, 1482–1491. https://doi.org/10.1111/j.1523-1739.2004.00417.x.

Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D., Smart, S.M., Memmott, J., 2016. Historical nectar assessment reveals the fall and rise of floral resources in Britain. Nature 530, 85–88. https://doi.org/10.1038/nature16532.

Baxter-Gilbert, J.H., Riley, J.L., Neufeld, C.J.H., Litzgus, J.D., Lesbarrères, D., 2015. Road mortality potentially responsible for billions of pollinating insect deaths annually. J. Insect Conserv. 19, 1029–1035. https://doi.org/10.1007/s10841-015-9808-z.

Bhattacharya, M., Primack, R.B., Gerwein, J., 2003. Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? Biol. Conserv. 109, 37–45. https://doi.org/10.1016/S0006-3207(02)00130-1.

Bommarco, R., Lundin, O., Smith, H.G., Rundlöf, M., 2012. Drastic historic shifts in bumble-bee community composition in Sweden. Proc. Royal Soc. B. 279, 309–315. https://doi.org/10.1098/rspb.2011.0647.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400.

Cavigliasso, P., Phifer, C.C., Adams, E.M., Flaspohler, D., Gennari, G.P., Licata, J.A., Chacoff, N.P., 2020. Spatio-temporal dynamics of landscape use by the bumblebee Bombus pauloensis (Hymenoptera: Apidae) and its relationship with pollen provisioning. PLOS ONE 15, e0216190. https://doi.org/10.1371/journal.pone.0216190.

Cole, L.J., Brocklehurst, S., Robertson, D., Harrison, W., McCracken, D.I., 2017. Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. Agric. Ecosyst. Environ. 246, 157–167. https://doi.org/10.1016/j.agee.2017.05.007.

Cousins, S.A.O., Auffret, A.G., Lindgren, J., Tränk, L., 2015. Regional-scale land-cover change during the 20th century and its consequences for biodiversity. Ambio 44, 17–27. https://doi.org/10.1007/s13280-014-0585-9.

Dániel-Ferreira, J., Berggren, Å., Wissman, J., Öckinger, E., 2022. Road verges are corridors and roads barriers for the movement of flower-visiting insects. Ecography 2022 (2), ecog.05847. https://doi.org/10.1111/ecog.05847.

Fijen, T.P.M., 2021. Mass-migrating bumblebees: an overlooked phenomenon with potential far-reaching implications for bumblebee conservation. J. Appl. Ecol. 58, 274–280. https://doi.org/10.1111/1365-2664.13768.

Gardiner, M.M., Riley, C.B., Bommarco, R., Öckinger, E., 2018. Rights-of-way: a potential conservation resource. Front. Ecol. Environ. 16, 149–158. https://doi.org/10.1002/fee.1778.

Gilroy, J., Sutherland, W., 2007. Beyond ecological traps: perceptual errors and undervalued resources. Trends Ecol. Evol. 22, 351–356. https://doi.org/10.1016/j.tree.2007.03.014.

Goulson, D., 2010. Bumblebees: behaviour, ecology, and conservation. In: Oxford Biology, 2nd ed. Oxford University Press, Oxford ; New York.

Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumble bees. Annu. Rev. Entomol. 53, 191–208. https://doi.org/10.1146/annurev.ento.53.103106.093454.

Hanley, N., Breeze, T.D., Ellis, C., Goulson, D., 2015a. Measuring the economic value of pollination services: principles, evidence and knowledge gaps. Ecosyst. Serv. 14, 124–132. https://doi.org/10.1016/j.ecoser.2014.09.013.

Hartig, F., 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R Package Version 0330.

Heneberg, P., Bogusch, P., Řezáč, M., 2017. Roadside verges can support spontaneous establishment of steppe-like habitats hosting diverse assemblages of bees and wasps (Hymenoptera: Aculeata) in an intensively cultivated central european landscape. Biodivers. Conserv. 26, 843–864. https://doi.org/10.1007/s10531-016-1275-7.

Huang, A., 2017. Mean-parametrized Conway–Maxwell–Poisson regression models for dispersed counts. Stat. Model. 17, 359–380. https://doi.org/10.1177/1471082X17697749.

Iles, D.T., Williams, N.M., Crone, E.E., 2018. Source-sink dynamics of bumblebees in rapidly changing landscapes. J. Appl. Ecol. 55, 2802–2811. https://doi.org/10.1111/1365-2664.13175.

Jakobsson, S., Bernes, C., Bullock, J.M., Verheyen, K., Lindborg, R., 2018. How does roadside vegetation management affect the diversity of vascular plants and invertebrates? A systematic review. Environ. Evid. 7. https://doi.org/10.1186/s13750-018-0129-z.

Keilsohn, W., Narango, D.L., Tallamy, D.W., 2018. Roadside habitat impacts insect traffic mortality. J. Insect Conserv. 22, 183–188. https://doi.org/10.1007/s10841-018-0051-2.

Kells, A.R., Goulson, D., 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. Biol. Conserv. 109, 165–174. https://doi.org/10.1016/S0006-3207(02)00131-3.

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Ward, K.L., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat. Commun. 6, 7414. https://doi.org/10.1038/ncomms8414.

Lepais, O., Darvill, B., O'connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L., Goulson, D., 2010. Estimation of bumblebee queen dispersal distances using sibship reconstruction method. Mol. Ecol. 19, 819–831. https://doi.org/10.1111/j.1365-294X.2009.04500.x.

Li, P., Kleijn, D., Badenhausser, I., Zaragoza-Trello, C., Gross, N., Raemakers, I., Scheper, J., 2020. The relative importance of green infrastructure as refuge habitat for pollinators increases with local land-use intensity. J. Appl. Ecol. 57, 1494–1503. https://doi.org/10.1111/1365-2664.13658.

Liczner, A.R., Colla, S.R., 2019. A systematic review of the nesting and overwintering habitat of bumble bees globally. J. Insect Conserv. 23, 787–801. https://doi.org/10.1007/s10841-019-00173-7.

Lindqvist, M., 2012. Method for Surveying Road Side Verges With High Biodiversity Values (No. Report 2012: 149). Swedish Transport Administration.

Makinson, J.C., Woodgate, J.L., Reynolds, A., Capaldi, E.A., Perry, C.J., Chittka, L., 2019. Harmonic radar tracking reveals random dispersal pattern of bumblebee (Bombus terrestris) queens after hibernation. Sci. Rep. 9, 4651. https://doi.org/10.1038/s41598-019-40355-6.

Martin, A.E., Graham, S.L., Henry, M., Pervin, E., Fahrig, L., 2018. Flying insect abundance declines with increasing road traffic. Insect Conserv. Divers. 11, 608–613. https://doi.org/10.1111/icad.12300.

Monasterolo, M., Poggio, S.L., Medan, D., Devoto, M., 2020. Wider road verges sustain higher plant species richness and pollinator abundance in intensively managed agroecosystems. Agric. Ecosyst. Environ. 302, 107084 https://doi.org/10.1016/j.agee.2020.107084.

Mossberg, B., Cederberg, B., 2012. Humlor i Sverige: 40 Arter att älska och Förundras över. Bonnier fakta.

Muñoz, P.T., Torres, F.P., Megías, A.G., 2015. Effects of roads on insects: a review. Biodivers. Conserv. 24, 659–682. https://doi.org/10.1007/s10531-014-0831-2.

O'connor, S., Park, K.J., Goulson, D., 2017. Location of bumblebee nests is predicted by counts of nest-searching queens. Ecol. Entomol. 42, 731–736. https://doi.org/10.1111/een.12440.

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S., Bommarco, R., 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol. Lett. 13, 969–979. https://doi.org/10.1111/j.1461-0248.2010.01487.x.

Ollerton, J., 2017. Pollinator diversity: distribution, ecological function, and conservation. Annu. Rev. Ecol. Evol. Syst. 48, 353–376. https://doi.org/10.1146/annurev-ecolsys-110316-022919.

Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J., Sanderson, R.A., 2008. Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. J. Appl. Ecol. 45, 784–792. https://doi.org/10.1111/j.1365-2664.2007.01359.x.

Phillips, B.B., Gaston, K.J., Bullock, J.M., Osborne, J.L., 2019. Road verges support pollinators in agricultural landscapes, but are diminished by heavy traffic and summer cutting. J. Appl. Ecol. 56, 2316–2327. https://doi.org/10.1111/1365-2664.13470.

Phillips, B.B., Bullock, J.M., Osborne, J.L., Gaston, K.J., 2020a. Ecosystem service provision by road verges. J. Appl. Ecol. 57, 488–501. https://doi.org/10.1111/1365-2664.13556.

Phillips, B.B., Wallace, C., Roberts, B.R., Whitehouse, A.T., Gaston, K.J., Bullock, J.M., Dicks, L.V., Osborne, J.L., 2020b. Enhancing road verges to aid pollinator conservation: a review. Biol. Conserv. 250, 108687 https://doi.org/10.1016/j.biocon.2020.108687.

Phillips, B.B., Bullock, J.M., Gaston, K.J., Hudson-Edwards, K.A., Bamford, M., Cruse, D., Dicks, L.V., Falagan, C., Wallace, C., Osborne, J.L., 2021. Impacts of multiple pollutants on pollinator activity in road verges. J. Appl. Ecol. 58, 1017–1029. https://doi.org/10.1111/1365-2664.13844.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007.

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. Nature 540, 220–229. https://doi.org/10.1038/nature20588.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Nat. 132, 652–661. https://www.jstor.org/stable/2461927?seq=1.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, B.R., Cox, R., Osborne, J.L., 2020. Quantifying the relative predation pressure on bumblebee nests by the european badger (Meles meles) using artificial nests. Ecol. Evol. 10, 1613–1622. https://doi.org/10.1002/ece3.6017.

Rundlöf, M., Persson, A.S., Smith, H.G., Bommarco, R., 2014. Late-season mass-flowering red clover increases bumble bee queen and male densities. Biol. Conserv. 172, 138–145. https://doi.org/10.1016/j.biocon.2014.02.027.

Skórka, P., Lenda, M., Moroń, D., Martyka, R., Tryjanowski, P., Sutherland, W.J., 2015. Biodiversity collision blackspots in Poland: separation causality from stochasticity in roadkills of butterflies. Biol. Conserv. 187, 154–163. https://doi.org/10.1016/j.biocon.2015.04.017.

Söderström, B., 2013. Sveriges humlor — en fälthandbok. Entomologiska föreningen i Stockholm.

Suzuki, Y., Kawaguchi, L.G., Munidasa, D.T., Toquenaga, Y., 2009. Do bumble bee queens choose nest sites to maximize foraging rate? Testing models of nest site selection. Behav. Ecol. Sociobiol. 63, 1353–1362. https://doi.org/10.1007/s00265-009-0789-3.

Svensson, B., Lagerlöf, J., Svensson, B.G., 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agric. Ecosyst. Environ. 77, 247–255. https://doi.org/10.1016/S0167-8809(99)00106-1.

Vanneste, T., Govaert, S., Kesel, W.D., Berge, S.V.D., Vangansbeke, P., Meeussen, C., Brunet, J., Cousins, S.A.O., Decocq, G., Diekmann, M., Graae, B.J., Hedwall, P.-O., Heinken, T., Helsen, K., Kapás, R.E., Lenoir, J., Liira, J., Lindmo, S., Litza, K., Naaf, T., Orczewska, A., Plue, J., Wulf, M., Verheyen, K., Frenne, P.D., 2020. Plant diversity in hedgerows and road verges across Europe. J. Appl. Ecol. 57, 1244–1257. https://doi.org/10.1111/1365-2664.13620.

Vepsäläinen, K., Savolainen, R., 2000. Are spring mass migrations of bumblebees and wasps driven by vole cyclicity? Oikos 91, 401–404. https://doi.org/10.1034/j.1600-0706.2000.910221.x.