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Research

Road verges are corridors and roads barriers for the movement of flower-visiting insects

Juliana Dániel-Ferreira, Åsa Berggren, Jörgen Wissman and Erik Öckinger

J. Dániel-Ferreira (<https://orcid.org/0000-0002-0268-0498>) ✉ (juliana.daniel.f@slu.se), Å. Berggren (<https://orcid.org/0000-0002-4998-5723>) and E. Öckinger (<https://orcid.org/0000-0001-7517-4505>), Swedish Univ. of Agricultural Sciences, Dept of Ecology, Uppsala, Sweden. – J. Wissman (<https://orcid.org/0000-0001-8456-8178>), Swedish Univ. of Agricultural Sciences, Swedish Biodiversity Centre, Uppsala, Sweden.

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Roads and road verges can potentially have opposite impacts on organisms that move through the landscape. While road verges can be habitat for a large number of species, and have been proposed to act as dispersal corridors, roads can act as barriers to movement. This duality of roads and road verges has however rarely been assessed simultaneously, and it is unknown to what degree it depends on the amount of traffic on the road and on the habitat quality of the road verge. We used fluorescent powdered dye to track movements of flower-visiting insects along roads with varying traffic intensity, and in verges with contrasting habitat quality (flowering plant species richness and flower density). Insect movements along road verges were more frequent than movements into the adjacent habitats, indicating that verges act as corridors. The frequency of movements that required crossing the road was lower compared to the frequency of movements that did not, suggesting that roads are barriers. The movement patterns were independent of traffic intensity, but the barrier effect was stronger when the road verge had a higher density of flower resources. The effect of roads as a barrier and of the road verges as corridors were independent of each other. Our results suggest that flower-visiting insects tend to remain longer in road verges with high density of flowers and we therefore suggest that managing road verge habitats for an increased plant diversity will mitigate the known negative impacts of roads on insect populations.

Keywords: bees, butterflies, dispersal, habitats, hoverflies, landscape, linear infrastructure connectivity

Introduction

The amount of traditionally managed semi-natural grasslands in Europe and their quality and connectivity have drastically decreased due to conversion to forest or arable land, or by increasing their productivity by use of artificial fertilizers (Cousins et al. 2015). Consequently, plant and insect diversity linked to these semi-natural habitats has decreased and species have gone regionally extinct (van Swaay et al. 2006, Goulson et al. 2008). This is an alarming trend given that insects are the backbone



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of food webs, and provide humans with multiple ecosystem services such as pollination, biological control and nutrient cycling (Wagner 2020). Typically, a decrease in habitat area leads to lower carrying capacity of individual habitat patches and reduced connectivity between populations. The isolated populations have higher extinction risk from low re-colonisation rates and high mortality of dispersing individuals (Edelsparre et al. 2018). Therefore, one of the most important factors for population persistence is that individuals can disperse between habitat patches (Auffret et al. 2017). Because of this, habitat corridors that connect isolated patches have been used as conservation measures as they increase connectivity between remnant habitat patches (Haddad et al. 2003).

The ability to disperse is dependent on both the physical characteristics of the landscape and on how individuals perceive their environment (Tischendorf and Fahrig 2000). Connectivity, defined as the degree to which a landscape facilitates or impedes movements (Taylor et al. 1993), can be viewed from both the landscape and the individual's perspectives. Structural connectivity relates to the physical aspects of the landscape that might facilitate or impede movement, and while it is a generally useful concept for landscape managers, it does not always explain the dispersal behaviour of individuals (Baguette and Van Dyck 2007, Turlure et al. 2011). Functional connectivity incorporates the behavioural response of the organism to landscape structure, as well as the mortality risk in different landscape elements. Roads and other linear infrastructure can affect functional connectivity because they can act as physical and behavioural barriers to movement and affect mortality risk (Tischendorf and Fahrig 2000, Andersson et al. 2017). The mortality risk can vary due to traffic intensity, width and speed limit of the road, the type of habitat adjacent to the road and the behaviour of individuals when encountering the road (Saarinen et al. 2005, Muñoz et al. 2015, Martin et al. 2018, Fitch et al. 2021). While there are numerous studies exploring the effects of roads and traffic on the movements of larger animals, the number of studies focusing on insects is limited and their results are inconclusive (Muñoz et al. 2015, Phillips et al. 2019, 2020).

Plant communities in road verges tend to resemble semi-natural grasslands due to similar management regimes that aim to maintain the vegetation in an early successional stage. These linear habitats can have both a high local plant and insect diversity (Gardiner et al. 2018, Phillips et al. 2019), and have been shown to act as corridors for butterflies as well as ground-living insects (Berggren et al. 2001, Villemey et al. 2016). The potential use of linear habitat elements as corridors can depend on their length, width and contrast to surrounding habitats (Öckinger and Smith 2008, Li et al. 2021), as well as their habitat quality and the traits of the species, like degree of specialisation (Söderström and Hedblom 2007, Gilbert-Norton et al. 2010, Phillips et al. 2020, Li et al. 2021). It is, however, unknown if the role of road verges as corridors depend on the diversity of their plant community, and how this in combination with traffic intensity

on the roads can affect insect movements in the landscape (Jakobsson et al. 2018).

The aim of this study was to investigate how roads and adjoining road verges influence the movements of flower-visiting insects, and how these patterns are modified by traffic intensity and the habitat quality of the road verges. To study this, we mimicked pollen transfer between flowers by applying fluorescent dye to experimentally placed flowers in high and low quality road verges on both sides of roads that varied in traffic intensity. We predicted that for flower-visiting insects 1) road verges are acting as dispersal corridors while the roads act as barriers, 2) the use of the corridor increase if the road verge has a high density of flowering plants and 3) the barrier effect depends on traffic intensity, so that roads with high traffic intensity reduce crossing the most (Fig. 1).

Methods

Study design and site selection

We established a study design that consisted of ten matching sites (i.e. in total 20 sites) with a similar gradient in traffic intensity but with contrasting flowering plant species diversity and flower density (hereafter referred to as 'habitat quality') in the road verge (Fig. 2). Using this design, we examined how traffic intensity on the road and habitat quality of the road verge affected the movement of day-flying flower-visiting insects. To select the roads we used the Swedish National Road Database (NVDB: <www.nvdb.se>). The database contains general information about Swedish roads such as

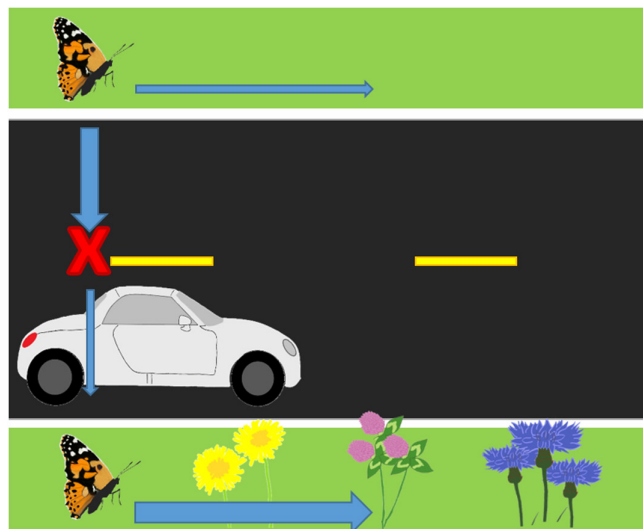


Figure 1. Graphical representation of the working hypotheses: 1) road verges are acting as dispersal corridors and roads as barriers, 2) the corridor effect of the road verge is stronger for verges that have a higher density of flower resources and 3) the barrier effect of the road increases with traffic intensity. Movements along the road verges and across the road are represented by arrows of different thickness and represent the magnitude of the movement frequency.

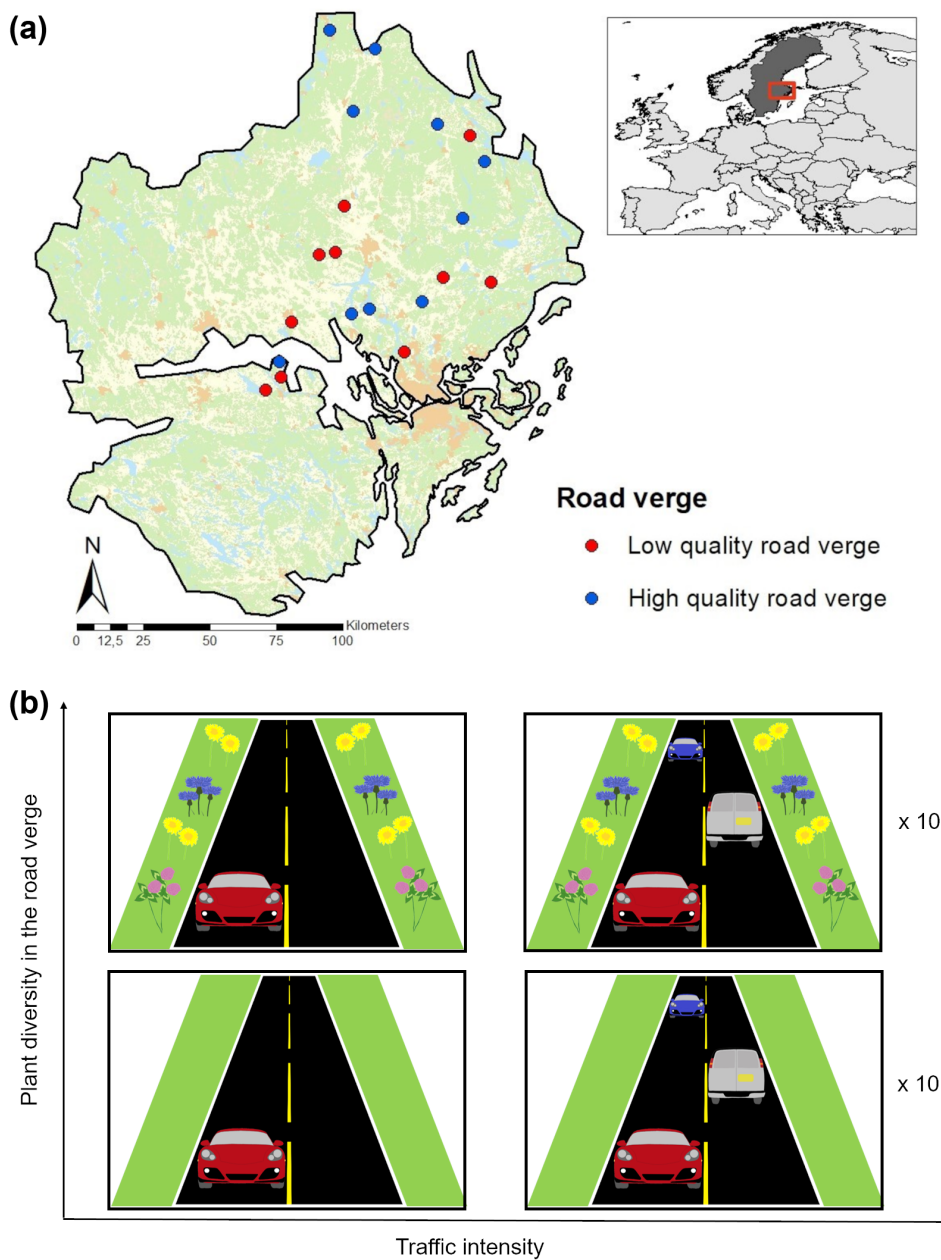


Figure 2. (a) Location of the 20 study sites in Sweden. Sites marked with red are sites with a low number of flowering plant species in the road verge (low quality sites), and sites marked with blue had a higher number of species in the road verge (high quality sites). (b) Study design. Half of the sites had a lower number of flowering plant species in the road verge and a gradient in traffic intensity, while the other half had higher number of flowering plant species in the road verge and a similar gradient in traffic intensity.

number of passing vehicles per day, number of lanes and speed limit. First, we selected ten high habitat quality sites that combined had a gradient in traffic intensity ranging from approximately 100 to 6300 vehicles per day according to the NVDB database. The traffic intensity estimates in NVDB undergo a strict data quality assessment and are thus regarded as reliable. These were sites identified as 'species rich road verges' by the Swedish Transport Administration. The verges are classified as 'species rich' if they fulfil at least one of four conditions in terms of plant species: 1) holds

indicator, rare or threatened species, 2) contains high species diversity 3) provides an important ecological resource (e.g. for reproduction life cycle or protection) or 4) promote species' dispersal and landscape connectivity (Lindqvist 2012). All potential sites were required to have a similar road width (between approx. 6–7 m) and speed limit (either 70 or 80 km h⁻¹), since these variables can affect mortality rates and thus affect the results (Muñoz et al. 2015). After this, ten matching sites with similar traffic intensity gradient, road width and speed limit, but with low habitat quality of the road

verge (i.e. regular road verges) were selected. This resulted in 20 sites similar in characteristics except 10 had low quality road verges and 10 had high quality road verges. All potential sites were visited before the start of the experiment in the summer of 2019 to confirm the habitat quality of road verges. Thus, we ensured that the selected high quality sites had abundant plant species that provided flower resources throughout the season and that the low quality sites were mostly grass-dominated. To ensure similarity of the adjacent habitat, we used the Swedish national survey of semi-natural pastures and meadows (TUVA: <www.jordbruksverket.se/tuva>) in which information about the management status of semi-natural pastures of high nature value is stored. When it was not possible to acquire roads with the aforementioned conditions that had a neighbouring pasture of high nature value, we selected roads adjacent to ley or clear-cuts.

Estimating frequency of movements

We investigated if the relative frequency of movements of flower-visiting insects across the road, along the road verge and perpendicular to the road into the adjacent habitat were affected by traffic intensity and by the quality of the road verge by tracking the transfer of fluorescent dye between flowers. We placed eight groups of potted plants of the species *Scabiosa columbaria* (variety 'Butterfly blue') along the road verges on both sides of the road and into the adjacent habitat at one side of the road (Fig. 3a). We selected this plant species because it is attractive to many flower-visiting insects (Comba et al. 1999), it was commercially available, and easy to acquire in large numbers. *S. columbaria* (commonly named 'small scabious' or 'pincushion flower') is native to Sweden although relatively rare. It can be found in dry pastures, banks or thickets (Stenberg 2018). The plant groups were placed where the surrounding habitat was open and dominated by herbaceous vegetation, except for one site where the groups were placed in young coniferous forest (number of sites in which the adjacent habitat was grassland = 15, clear-cuts = 2, ley = 2, forest = 1). The distance between the plants along the road verge and into the adjacent habitat was equal to two times the width of the road (i.e. if the road was 6 m wide, the plants were 12 m apart). The number of flower heads in all plant groups was maintained as constant as possible, either by 1) having several potted plants that in total had around 30 flower heads, or by 2) cutting off extra flower heads when one potted plant had too many (mean flower heads/group = 31.42, median = 30, min = 18, max = 57). Two colours of fluorescent dyes were used to track insect movements: red and blue (Radglo TP-series, Radiant Color Corp., Houthalen, Belgium). On one side of the road, we marked 15 flower heads with blue dye. Directly opposite and across the road, we marked 15 flower heads with red dye (Fig. 3). The flower heads were marked at 6:00 h and left exposed for ~12 h in each site. Any insect that visited a marked flower head transferred dye particles to the next (and subsequent) flowers they visited. Hence, by examining unmarked flower heads for red or blue fluorescent dye

particles at the end of the day, we could track the movements of flower-visiting insects from the marked flowers across the road, along the road verge and into the adjacent open habitat perpendicular to the road. This was repeated across the 20 sites between 10 June and 30 June in 2019. Between 17:00 and 18:00 h, all unmarked flower heads were cut and carefully placed separately in a paper bag for later examination in the lab. Because the process of cutting and bagging flower heads took a significant amount of time (~180 flower heads per site), we randomized the order in which each group would be cut in each site. The paper bags were placed in an oven and left to dry in 60°C for 24 h. This was done to avoid the flower heads developing mould before being processed. Each individual flower head was examined for the presence or absence of fluorescent dye using an UV lamp. The number of flower heads with dye per group of plants was recorded for both colours. The experiment was conducted only during weather periods with low risk of rain to avoid the fluorescent dye from being washed off the flower heads. In one of the sites, the plants were exposed for less than 12 h (from 6 to 15.45) due to rainfall. The analyses without this site did not affect the general results (Supporting information).

Flower-visiting insect abundance and flower density

Given that differences in flower density in the road verges between sites, quality of the adjacent habitat and traffic intensity in the road could all affect the abundance of flower-visiting insects, we estimated insect abundance and flower density for all sites. We visually counted all butterflies, bees and syrphid flies visiting the marked flowers at each side of the road once for 15 min (equalling 30 min per site). This allowed us to compare insect abundance among our sites and to control for the fact that more insects could potentially transfer more dye. To estimate the availability of flower resources, we placed six (three on each side of the road) quadratic sample plots (1 × 1 m) in each site. The plots were 200 m apart, and the placement of the first plot was where the Swedish Transport Administration had marked the beginning of the 'species rich' area. If a long road segment was marked, the first plot was placed randomly within the marked segment. In the plots all flowers or equivalent units (individual flowers, number of flower heads, number of inflorescences or number of racemes; Persson and Smith 2013) were counted and all species of nectar-bearing plants within the plots were identified. This was carried out once per site in June 2019. Finally, we estimated the width of the road verges in each site by selecting a 1 km fragment of the road and measured the width of the road verge five times (every 200 m) in each side to be able to control for the effect of habitat area on insect abundance and flower density (Table 1, Supporting information).

Data analysis

We used R (<www.r-project.org>) for all analyses. To determine whether the quality of the road verge and the traffic intensity affected the movement of flower-visiting insects we

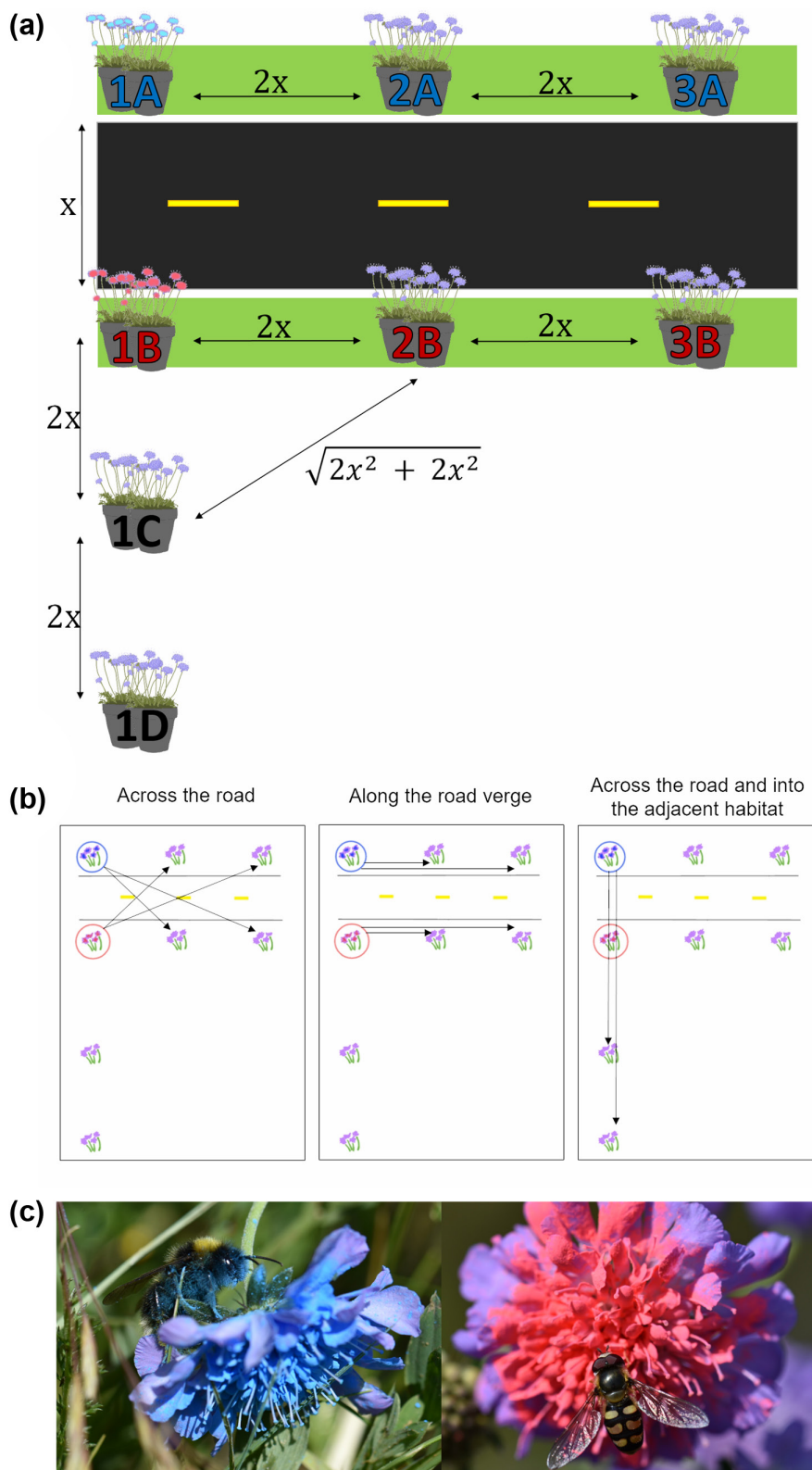


Figure 3. (a) In each of the 20 sites, we placed eight groups of pots with flowers of *Scabiosa columbaria*. The groups along the road verge and into the adjacent habitat were separated by a distance of two-times the width of the road (x = width of the road). Group 1A had flower heads that were marked with blue fluorescent dye, while the flower heads on the opposite side of the road (group 1B) were marked with red. (b) Graphical representation of the three types of movements studied: across the road, along the road verge and across the road and into the adjacent habitat. (c) An individual of *Bombus terrestris* visiting a plant marked with blue dye and an individual of *Euclyptus corollae* visiting a plant marked with red dye.

Table 1. Description of the experimental sites of high and low habitat quality (10 in each category). The quality assessment was based on the number of flowering plant species in the road verge.

Road verge status	No. of flowering plant species (median)	Mean road width (m \pm SD)	Traffic intensity (min/max vehicles/day)	Mean road verge width (m \pm SD)
High quality	11	6.16 \pm 0.31	125/6356	4.49 \pm 0.70
Low quality	6.50	5.97 \pm 0.09	158/6168	4.17 \pm 0.60

performed two separate analyses. First, we used the entire data set to test whether the movements along the road verge (either on the same side as the marked flowers, or along the other side after crossing the road) were more frequent than movements perpendicular to the road and into the adjacent habitat. This analysis was aimed at determining whether road verges were serving as corridors for the individuals, and if the road was acting as a barrier. We used a generalized linear mixed model (GLMM, package 'lme4', Bates et al. 2015) with number of marked/unmarked flower heads per plant group as a binary response variable (successes: number of marked flower heads per group, failures: number of unmarked flower heads per group, number of trials: total number of flower heads per group). As explanatory variables we used direction (movements along the road verges or into the adjacent habitat), side in which the movement took place (same side or across the road), distance (m) to the marked plant group, flower density at each side of the road, insect abundance in each side (log-transformed) and two random effects. We included the number of flower-visiting insects as a co-variate in these models, as this can affect the probability of a certain flower head being marked. The total number of flower-visiting insects was tied to the side of the road where insects were counted (i.e. if an insect visited a blue marked flower and then crossed the road and visited an unmarked flower on the red side, the insect abundance value used was the one recorded on the blue side). Flower density was added into the model as we predicted that road verges with higher habitat quality would be more likely to be used as corridors for flower-visiting insects than road verges of low habitat quality. Site as a random effect was added to account for the fact that there were multiple measures arising from using two fluorescent dye colours in each site. Overdispersion was detected in the model (package 'DHARMA', Hartig 2020) and thus accounted for by including an observation level as a random effect (Bolker et al. 2009). Fixed effects (distance and flower density) were scaled (subtracted the mean and divided by the standard deviation) to allow for model convergence.

In the second part of the analyses, we divided the data set into three kinds of movements: across the road, along the road verge and across the road into the adjacent habitat (Fig. 3b). To explore how traffic intensity and the habitat quality of the road verge affected the movements across the road, we modelled the number of marked/unmarked flower heads as a binary response to traffic intensity (scaled), quality of the road verge, the difference in flower density between the two sides of a road (Δ flower density), distance to the marked group (scaled), number of flower-visiting insects (log-transformed) and a random effect for site. We included Δ flower

density as an absolute and not a relative value to explore whether differences in flower density between the two sides of the road influenced the frequency of movements across the road. The same model but without Δ flower density was used for the other two types of movement (along the road verge, and across the road and into the adjacent habitat) separately. For each of these models we included the interaction between traffic intensity and road verge quality. If the interaction did not show any importance (i.e. statistical significance at the 0.05 level, and AICc values did not improve when including the interaction) to the outcome of the model, it was later removed from analysis. All models included a term for distance to the marked group of plants to control for the detectability of the fluorescent dye decreasing with distance (Van Rossum et al. 2011), and to control for the discrepancies in distance to the marked plant for movements along the road verge and across the road. The distance from an unmarked to a marked group of plants located across the road was calculated as the Euclidean distance between two points (i.e. Pythagorean distance).

Results

Site characteristics

Road verges denoted high quality sites had on average 3.6 more plant species in the road verge, as measured in six 1×1 m plots per site, than low quality sites (t -value = 2.6, $p = 0.02$), and had on average 29% more flowers ($t = 3.44$, $p = 0.002$). This confirmed that the classification from the National Road Database could be used as a proxy for resource availability for pollinating insects. We did not find any difference in insect abundance between low- and high quality sites ($F_{1,18} = 1.69$, $p = 0.21$), or with increasing traffic intensity ($F_{1,18} = 0.15$, $p = 0.70$).

We collected a total of 240 observations (20 sites \times (6 groups to be marked with blue + 6 groups to be marked with red)), and processed a total of 3770 flower heads of *Scabiosa columbaria*. Blue dye had been transferred by insects to 397 of these, and red dye to 652 flower heads. The most frequent visitors of *S. columbaria* flower heads were hoverflies (83 visits), followed by bumblebees (26 visits), butterflies (21 visits) and solitary bees (9 visits). The number of insects visiting the marked flower heads was not correlated with the flower density in each site (Pearson's $r_{18} = -0.11$, $p = 0.65$). The interaction term between traffic intensity and the quality of the road verge was not significant in any of the models and did not improve AICc values, and it was thus removed from all analyses.

Roads with high traffic intensity had on average wider road verges (Pearson's $r_{18} = 0.46$, $p = 0.04$), but this is unlikely to have affected the results as there was no difference in road verge width between high and low quality sites (ANOVA $F_{1,18} = 1.09$, $p = 0.311$).

Movement frequencies

In general, movements along the road verges were more frequent than movements into the adjacent habitat (Fig. 4a; $\chi^2 = 12.05$, $p \leq 0.001$), indicating that the road verge acts as a dispersal corridor. Further, the frequency of movements that did not require crossing the road was higher than the frequency of movements that did (Fig. 4b; $\chi^2 = 16.98$, $p < 0.001$), indicating that the road acts as a barrier to movements. There was a negative relationship between

the distance to the marked plant group and the proportion of marked flowers, but no effect of flower density nor insect abundance (Table 2). Including traffic intensity in the model did not change the general results (Supporting information).

The frequency of movements across the road was lower in sites with road verges of high habitat quality than in sites with verges of low quality (Fig. 5). The probability of movements across the road was lower when the movement originated from the side with lower flower density. Neither traffic nor quality of the road verge affected movements along road verges and across roads to the adjacent habitat. The number of 'pollinated' (dye) plants decreased with increasing distance from the marked plants for movements along the verges and across the road into adjacent habitat, but not for road crossings (Table 3).

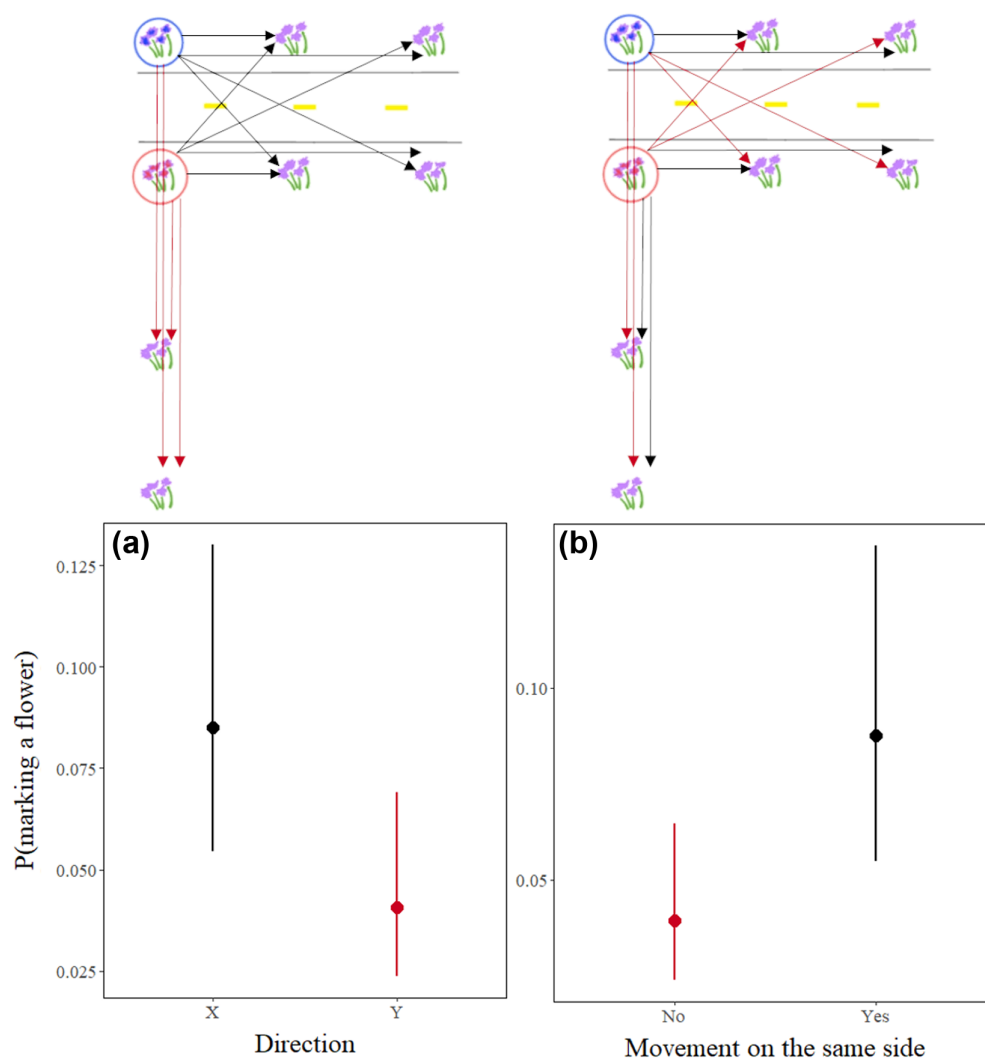


Figure 4. (a) Flower-visiting insects were more likely to move along the road verges (i.e. direction 'X', indicated in black) than into the adjacent habitat (i.e. direction 'Y', indicated in red). The upper panels show the types of movements included in each category. (b) Flower-visiting insects were also more likely to visit a flower on the same side of the road than across the road. The error lines represent the 95% confidence intervals. The presented probabilities are the estimates from the model including all the covariates (direction, side of the movement, distance to marked plant group, flower density at each side and two random effects).

Table 2. Results of the generalized linear mixed model exploring the role of road verges as corridors (direction) and of the road as barriers to movement (same side). Shown are the χ^2 values, degrees of freedom (df), estimates (e), standard error (SE) and p-values (p). p-values in bold are significant at the 0.05 level.

Predictors	χ^2 (df = 1)	e	SE	p
(Intercept)		-3.00	0.37	
Same side (yes)	16.98	0.85	0.21	< 0.001
Direction (Y)	12.05	-0.78	0.23	< 0.001
Distance to marked (m)	13.3	-0.39	0.11	< 0.001
Flower density	0.00	0.01	0.15	0.95
Insect abundance	0.61	0.39	0.50	0.43

Discussion

Identifying potential movement barriers and corridors is key to understanding the functional connectivity of landscapes. We estimated how roads and their associated road verges influence movement patterns of flower-visiting insects through observations of transfer of fluorescent dye particles between flower heads. Our approach allowed us to evaluate the potential corridor and barrier effects independent of each other. The results showed that road verges act as movement corridors for flower-visiting insects, that roads are barriers to

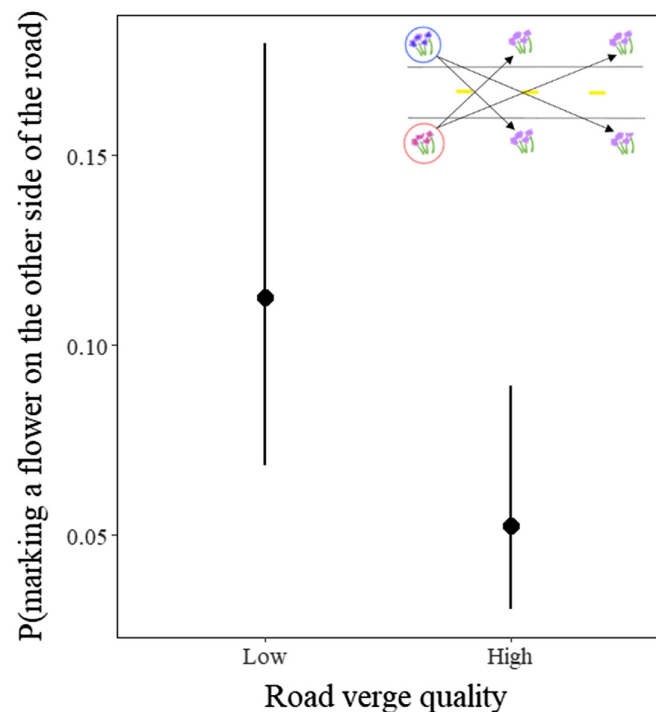


Figure 5. Flower-visiting insects crossed the road less often when the road verge was of high habitat quality than when it was of low habitat quality. The error lines represent the 95% confidence intervals. The presented probabilities are estimates from the model testing whether movements across the road were influenced by the quality of the road verge and the traffic intensity. The model also included distance to the marked plant group, number of flower-visiting insects and a random effect.

their movement and that these effects can be moderated by the habitat quality of the road verges. Overall, the effects of roads as barriers and of the road verges as corridors were independent of each other.

By mimicking pollen transfer using fluorescent dye powder, we found that flower-visiting insects moved more frequently along the road verges than perpendicular to the road into the adjacent habitat. This suggests that road verges are acting as movement corridors irrespective of their flower resource density. Given that habitat quality has been found to affect insect dispersal probability and movement in linear landscape elements (Söderström and Hedblom 2007, Habel et al. 2020), we expected a higher movement frequency along the road verges with high habitat quality. However, our findings were more in line with previous research showing that corridors do not necessarily need to provide high habitat quality in order to promote movements between habitat patches (Haddad and Tewksbury 2005).

The movements assessed in our study were foraging movements over relatively short distances, i.e. 'routine movements' sensu Van Dyck and Baguette (2005), as opposed to directed movement aimed at displacement. Öckinger and Smith (2008) suggested that corridors mostly influenced short-distance movements. The contribution of routine movements to dispersal is thought to decline with increasing habitat fragmentation (Van Dyck and Baguette 2005). Hence, it is still unclear to what extent road verges influence long-distance dispersal of pollinating insects. Nevertheless, if road verges are mainly aiding dispersal by promoting routine movements, then increasing their habitat quality would have an important effect on inter-patch movements for more sedentary and specialised species.

Recently, Habel et al. (2020) argued that high habitat quality corridors are particularly beneficial for specialist species. Patches with higher plant diversity may contain species preferred by specialists, and also provide an attractive source of foraging resources for a wider array of generalists (Lázaro and Totland 2010). In our study, low habitat quality road verges were not entirely lacking flowering plants (and we increased their quality by experimentally adding flowers), and they could therefore potentially fulfil the minimum quality requirements for some species. Road verges with high habitat quality might have been used to a higher degree by more specialised species less prone to leave their habitat. Unfortunately, as we did not directly observe movements, our experimental approach did not allow us to confirm the level of habitat specialization of the species visiting the marked flowers. Still, the visiting insect observations suggest that most individuals present in our sites were generalists. Munguira and Thomas (1992) found that while most of the butterfly species present in road verges in the UK were generalists, it was also possible to observe some rare species.

We also found that the propensity to cross the road decreased when the road verge had more resources, but as above, higher flower density did not increase the frequency of movements along the road verge. Hence, our interpretation is

Table 3. Results of linear mixed effects models for each type of movement explored. Movements (modelled as number of marked flower heads per group) across the road, along the road verge and into the adjacent habitat were modelled as a response to the habitat quality of the road verge (high, low), traffic intensity, distance to the marked group of plants and the number of insects seen visiting the marked flowers under 30 min/site. Shown are chi-square values (χ^2), degrees of freedom (df), estimates (e), standard error (SE) and p-values (p). p-values in bold are significant at the 0.05 level.

	Movements across the road				Movements along the road verge				Movements across the road and into the adjacent habitat			
	χ^2 (df=1)	e	SE	p	χ^2 (df=1)	e	SE	p	χ^2 (df=1)	e	SE	p
Intercept		-1.66	0.32			-1.57	0.38			-3.71	1.01	
Road verge (high quality)	4.41	-0.83	0.40	0.04	0.35	-0.29	0.49	0.55	0.01	-0.10	0.87	0.91
Traffic	1.51	0.24	0.20	0.22	0.17	0.10	0.25	0.68	0.06	-0.12	0.49	0.81
Distance to marked (m)	0.08	0.02	0.07	0.78	76.10	-0.49	0.06	< 0.001	22.55	-0.66	0.14	< 0.001
Number of visiting insects (log)	3.07	-0.64	0.37	0.08	0.53	0.25	0.34	0.47	0.01	-0.15	1.37	0.91
Δ flower density	5.65	-0.19	0.08	0.02								

that insects tend to stay longer in road verges with high density of flowers. This suggests that increasing the flower density in road verges will not increase their function as movement corridors, but might decrease road mortality of flower-visiting insects (Skórka et al. 2013). It has been previously observed that linear landscape elements that do not contain floral resources fail to direct the movements of butterflies compared to those which contained nectaring plants (Cant et al. 2005), suggesting the existence of a floral density threshold that determines the viability of road verges as movement corridors.

Movements that did not require crossing the road (i.e. either along the road verge or perpendicular to the road) were more frequent than movements across the road, indicating that the road acts as a barrier to movements. This effect was independent of traffic intensity. This is in line with a recent study (Fitch et al. 2021) in which the authors used a similar approach using fluorescent dye and found that road width, and not traffic intensity nor speed limit, best explained the movement patterns of pollinators. Effects of roads as behavioural barriers have been observed for bumblebees (Bhattacharya et al. 2003), and there is evidence that hoverflies avoid crossing areas where there is a break in vegetation cover (Wratten et al. 2003). Recent evidence shows that mortality due to traffic can have a significant detrimental effect on pollinator populations (Baxter-Gilbert et al. 2015, Keilsohn et al. 2018). Our results indicate that many flower-visiting insects avoid crossing the road surface, a behaviour known as road surface avoidance (Jaeger et al. 2005). While not directly, this indicates that roads, irrespective of traffic, are acting as barriers to movement for flower-visiting insects. Road surface avoidance is dependent on the width of the road (Jaeger et al. 2005), which suggests that the effect of roads as barriers for flower-visiting insects should increase with increasing road width. This might partly depend on insect perceptual range, i.e. to what extent insects can detect habitat at the opposite side of the road and estimate its quality (Lima and Zollner 1996, Olden et al. 2004). Road width and traffic intensity may interact, as species that cross roads are forced to spend more time on wider roads (that also in general have

more traffic) and thereby increase the risk of collision. Since we standardized road width in this study, we could not test this. Future studies should test whether there is a threshold width where the barrier effect of roads is increasing, in order to identify roads with high risk of mortality as a first step in mitigation actions.

Conclusions and implications for management of road verges

Our study provides an approximate representation of the movements of day-flying flower-visiting insects in road environments. We found that while roads are barriers to movement, flower-visiting insects use road verges as movement corridors. Interestingly, the barrier effect of the road was not tightly linked to traffic intensity. This suggests that roads might influence movement behaviour rather than mortality, and as a consequence the sheer presence of a road creates a barrier to pollinator movements. A first step in order to maintain landscape connectivity would be to avoid the construction of new roads that create new barriers in the landscape.

While the frequency of movements across the road was higher when habitat quality in the road verge was low, this did not seem to affect the corridor function of the verges. Due to the large variation in responses to traffic and road verge quality, it has been difficult to apply mitigation strategies for insects in road environments (Zielin et al. 2016). Our results suggest that road verges of high quality increase functional connectivity for day-flying flower-visiting insects by reducing collision risk. However, our findings need to be applied with caution. More knowledge is needed to detangle the effects of traffic intensity, speed and road surface on the movement and mortality of insects, and on how to design roads and road verges to reduce the barrier effect. With this in mind, we suggest that managing road verge habitats to enhance plant diversity, e.g. by sowing native plants, reduce cutting frequency during the growing season, adequate time removal of cut debris (Phillips et al. 2020) will also benefit flower-visiting insects.

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Author contributions

Juliana Dániel-Ferreira: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Åsa Berggren:** Methodology (equal); Writing – review and editing (equal). **Jörgen Wissman:** Methodology (equal); Writing – review and editing (equal). **Erik Öckinger:** Conceptualization (lead); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

The data supporting the findings of this publication are available in the Swedish National Data Service (SND) at <<https://doi.org/10.5878/h758-5n57>>.

Supporting information

The supporting information associated with this article is available from the online version.

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