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Research Paper

Trait and habitat filters shape absences of wild bee and butterfly species from road verges

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ABSTRACT

Road verges can provide resources for pollinating insects, but it remains unclear if these resources are accessible to all species, or if some ecological traits can prevent certain species from using road verge habitats. We sampled wild bees and butterflies in 37 road verges in southern Sweden, with contrasting mowing regimes and along a gradient of traffic intensity. We compiled data on the pools of the regionally occurring species of wild bees and butterflies, and on ecological traits related to body size, feeding specialization and nesting habitat or overwintering stage. First, we tested if any of the selected ecological traits explained why some species were absent from road verges. Among the species that occurred in road verges, we then tested how the ecological traits influenced their response to management regime, verge width and traffic intensity. Along 7400 m of road verges, we observed 39% of bee species and 43% of the regionally occurring bee and butterfly species. Cavity-nesting bees were more likely to be absent from road verges than soil-nesting bees, but none of the ecological traits explained which of the regionally occurring butterfly species were absent from road verges. Among solitary bee and butterfly species that occurred in road verges, wider road verges reduced the absence probability more in dietary specialists than in generalist species. In bumblebees, wider road verges reduced the absence probability more in small-bodied than in large-bodied species. Our results indicate that road verges are suitable habitats for many but by far not all bee and butterfly species, and that certain species are prevented from using road verges because of their ecological traits. This needs to be considered when road verges are designed or managed to promote biodiversity.

Introduction

Despite large conservation efforts, the biodiversity associated with temperate semi-natural grasslands is still declining (Seibold et al., 2019). Road verges have been proposed to support populations of species associated with these semi-natural grasslands, or even act as replacement habitats in landscapes where most other grassland habitats have been lost (Gardiner et al., 2018). In particular, pollinating insects can have high abundance and species richness in road verges (Meinzen et al., 2024; Wojcik & Buchmann, 2012). Nonetheless, despite comparable levels of species richness, the identity of the species that are present in or absent from road verges can differ compared to semi-natural grasslands (Dániel-Ferreira et al., 2023).

The ability of species to use road verges as habitat can be influenced by the composition of the plant community, management of the road verge and the traffic on the road (Phillips et al., 2020). For example, the diversity of flower-visiting insects could benefit from the restoration or establishment of native vegetation in road verges (Brown et al., 2024) and be affected by the frequency and timing of road verge mowing (Horstmann et al., 2024; Phillips et al., 2019). The traffic on the roads could also affect insect populations and communities in road verges, both through direct mortality due to collision with vehicles (Dániel-Ferreira et al., 2022; Skorka et al., 2013), and through chemical, noise or light pollution (Boyes et al., 2021; Meinzen et al., 2024; Mitchell et al., 2020; Phillips et al., 2021). In addition, flower-visiting insects might avoid apparently suitable habitats next to roads, potentially

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because they perceive the environment as being too hostile (Blomqvist et al., 2025). Due to differences in species traits and preferences, can be assumed that some species might be more susceptible to certain road and road verge characteristics than other species. However, so far this is still poorly understood.

Analysing if certain groups of species from the regional species pool are unlikely to use a certain habitat can increase our understanding of community assembly processes (Pärtel et al., 2011). It is also of applied value by for example identifying target habitats for conservation or restoration (Morel et al., 2022; Noreika et al., 2020), and for gaining insights into the factors behind species absence from a seemingly suitable habitat (Moeslund et al., 2017). The examination of how ecological traits explain the absence of regionally occurring species in a specific habitat could shed light on the mechanisms that shape the local community composition.

For flower-visiting insects in road verges, a potential driver explaining species occurrence could be the presence and abundance of specific plant species that these insects use for pollen, nectar, or oviposition (Larsson & Franzén, 2007; León-Cortés et al., 2003). This means that diet and larval host plant generalists are more likely to be present because they have a wider range of potential food plants. Absence of specific plants and flowers could in turn be linked to the road verge management and mowing regimes (Jakobsson et al., 2018). If mowing removes most of the flowers which the insects are specialized to, or removes the larval host plants for specialized herbivores, the road verge will be less suitable as habitat for these species. Whether a species can exploit the resources provided in the road verge also depends on the species' mobility. Central place foragers, such as bees, return to their nest between each foraging bout and are restricted to foraging in patches within flight distance from their nest (Michener, 2007). The flower resources in road verges could thus be unavailable to bees if there is no suitable nesting habitat in the road verge, or if the distance to suitable nest sites is too great (Olsson et al., 2015). This could especially be the case for species with small foraging ranges. This means that species absences from road verges is likely to be determined by an interaction between species traits and road verge characteristics.

Another potential factor affecting insect occurrences in road verges is mortality through collisions with vehicles. This threat could affect species differently depending on their traits, For example, it has been estimated that the direct road mortality through vehicle collisions was higher for bees than for butterflies (Baxter-Gilbert et al., 2015). Among butterflies, it has been suggested that small-bodied species are more likely to be killed through collisions with vehicles than large-bodied species (Skorka et al., 2013), but also that the collision risk increases with a species' mobility (Remon et al., 2018).

Despite the clear potential for life-history traits to influence the occurrence of flower-visiting insects in road verge habitats, the extent to which they manifest in real world environments is still unclear. We have previously shown that species richness of butterflies in road verges depends on mowing regimes, plant species richness and traffic, and that the species richness of bees in road verges depends on flower abundance, traffic and road verge width (Horstmann et al., 2024). Road verges can clearly provide habitat for flower-visiting insects, but to understand the value of these habitats for conservation, it is also necessary to understand which factors that prevent certain species from utilising this habitat. Assessing the trait composition of species that are absent from road verges with contrasting characteristics, such as management regimes and traffic volumes, can be a first step towards understanding the mechanisms that shape community composition in these habitats.

Here, we combine data on road verge characteristics with data on species traits for the regional species pool to understand how the absence of regionally occurring species in the road verges is explained by species traits, i.e. if these traits act as filters in shaping local communities. We specifically ask: i) Are there any species traits that make bee or butterfly species unlikely to occur in road verges?, ii) Do traffic, road verge management or verge width have particularly pronounced effects on groups of species that share some specific traits?, iii) To what extent do rare and threatened bee and butterfly species use road verges as habitat, and iv) are these species more strongly affected by traffic, management or verge width than other species?

Methods

Study design and site selection

The study was performed in Skåne county in southernmost Sweden. We initially selected 40 road verges with contrasting management regimes, crossed with a gradient in traffic intensities, but situated in similar landscape types (Fig. 1). Land cover in the region is dominated by arable land (40 %) and forest (44 %), with 5 % permanent grasslands and 10 % urban and other developed land, including roads and other infrastructure (Statistics Sweden, 2023). To select road verges, we used the environmental and infrastructure data from the National Road Database (Trafikverket, 2024). We selected road verges that were either mowed once or twice per season, with a width of at least 2 m (1.9 m in one case) and where the speed limit on the adjacent road was between 50 and 90 km/h.

We extracted data on the traffic intensity in all road verges from the National Road Database, measured as the average number of vehicles per day assessed several times over a year. We calculated the land cover of arable land, forest, open land and surface water in a 2 km buffer around prospective road verges using data from the National Land Cover Database (Naturvårdsverket, 2020) with QGIS version 3.10. Open land can broadly be interpreted as grassland habitat, consisting mainly of livestock pasture, but also includes other open (but non-arable) land cover categories, such as wetlands and urban green space. To account for potential landscape effects, we only considered road verges located in landscapes with a maximum of 50 % forest and a minimum of 30 % arable land, and without valuable grassland habitat within a 350 m buffer, using data from the national TUVA database of meadows and pastures of high nature value (Jordbruksverket, 2024). Road verges were selected with contrasting traffic intensities and mowing regimes. Verges were mown either once or twice per season, with hay material left in place. The selected road verges are between 1.9 and 13.9 m wide (median of 5.6 m), and were located at least 2 km apart. In two road verges, we had to slightly relocate the study sites compared to the initial selection, and then had 22 % and 26 % arable land in the surrounding landscapes (instead of at least 30 %). Due to inconsistent mowing, we had to exclude three road verges from our analyses, resulting in 37 study sites, of which 16 were mown once per year and 21 were mown twice per year. In those verges mown twice per year, the 1.5 m closest to the road was mown during the survey period (see below).

Survey of bees and butterflies

In each road verge, we established four 50 m long transects, located directly adjacent to one another and directly alongside the road (i.e. along a 200 m stretch of road per site). We conducted transect walks to survey butterflies four times and wild bees three times between May and July 2021. Except for the fourth butterfly survey round, surveys on butterflies and wild bees were always conducted on the same day. We only conducted the surveys between 10 am and 5 pm, when wind was moderate (max. Beaufort 5), the vegetation was dry, and when air temperature was at least 13°C if cloud cover was less than 50 %, or at least 17°C with higher cloud cover. Between survey rounds, we alternated the time of day during which we visited the road verges. For butterflies and burnet moths (Zygaenidae; from here on included in 'butterflies'), the observer walked 5 minutes along each of the four transects at a steady pace and caught and identified (using Söderström 2019) all individuals within 2.5 m on each side and 5 m in front of them to species level. For wild bees, the observer spent 10 minutes walking along each of the four transects, catching all individuals within 1.5 m on

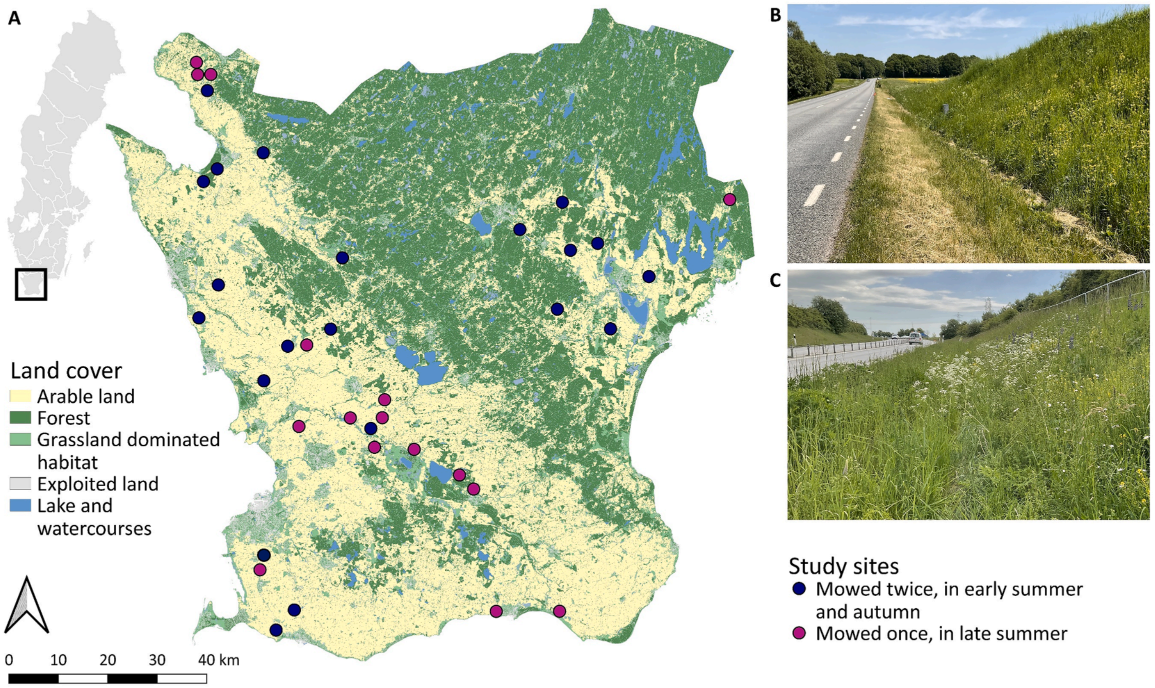

Fig. 1. **A)** Location of the 37 study sites on road verges in southern Sweden. 21 of the road verges are mowed twice a year, in early summer and autumn, but only once during our study period (see photo in **B)** from a road verge during our study period). 16 of the road verges are mowed once per year, in late summer, but only after our study period (see photo in **C)** for a road verge during our study period). Within each of the two mowing regimes, the road verges were selected along a gradient of traffic intensity. Land cover was taken from Sweden's 2018 land cover database (Naturvårdsverket, 2020). Photos: Svenja Horstmann.

each side and in front. For road verges narrower than the planned transect width, the whole road verge was covered. Bees were either identified directly in the field or collected for later identification in the lab. Observation time was stopped for identification of butterflies and bumblebees, and for collection of solitary bees that were later identified in the lab. All collected individuals were identified to species level using identification keys from the SLU Swedish Species Information Centre (Cederberg et al. 2018); as well as from Schmid-Egger and Scheuchl (1997), Amiet et al. (2001, 2004, 2007, 2014), and Bogusch and Straka (2012). The numbers of domestic honeybees *Apis mellifera* was low, and they were excluded from our survey, since its distribution in the landscape to a large extent depends on where beekeepers choose to place their hives rather than on road verge characteristics.

Survey of food plants and larval host plants

To assess if preferred pollen and nectar plants for wild bees were present in the road verges, we identified all flowering vascular plants within the same four transects in each of the road verges used for the bee and butterfly inventories, but now covering the whole width of the road verge. We identified all nectar-producing plants that were flowering at the time of visiting to the species or genus level at the same time as the wild bee inventories, between May and July 2021.

To identify if butterfly larval host plants were present in the road verges, we also conducted a full vascular plant inventory. In each road verge and across the same four transects in which we conducted the butterfly and wild bee surveys, we surveyed the presence of vascular plants once per study site, at the end of June and in July 2021 or 2022. We did so in 10 plots of each 1 m^2, located across the four transects with a fixed distance between all plots. When the narrowest part of the road verge measured <2.5 m, we positioned all 10 plots 50 cm from the road edge. When the road verge was wider, we distributed five plots 50 cm from the road edge and five plots into the centre of the remaining road verge area, alternating between these two positions. This method allowed us to cover the part of the road verge close to the road as well as further away, if applicable. After the plot survey, we walked in the middle of the road verge and checked if any important host and food plants were present in the road verge outside of the vegetation plots. We used a list of plants that we compiled with our own expert knowledge (Table S1). We identified vascular plants (hereafter only ‘plants’) to species level when possible.

Regional species pool

We downloaded the list of all bee and butterfly species observed during the years 2000 to 2023 in the region Skåne (area: 11 300 km^2), from the Swedish Species Gateway (Artportalen). These data were accessed on 2 February 2024. To exclude apparently misidentified species and species that are not regularly breeding in this region (i.e. migrants and species with only temporary populations), we excluded any species with fewer than five records from Skåne during this period. For bees, we pooled the species *Seladonia* (syn. *Halictus*) *confusus* and *S. tumulorum* in both the field data and the regional species pool data, since we could not reliably distinguish them, and they have similar ecological traits. We also considered *Bombus lucorum* and *B. cryptarum* as “*B. lucorum* complex” and treated them as one species. The third species in the complex, *B. magnus*, had not been recorded in the region. To exclude species that are highly unlikely to occur in road verge habitats, we excluded butterfly species categorized as “wetland specialists” by van Swaay et al. (2006) that occurred in the study region (*Boloria aquilonaris, Coenonympha tullia, Colias palaeno*). These three species are all associated with peat bogs. Finally, we excluded species that are only active in early spring or in late summer to early autumn, and hence could not have been observed even if they were present, due to the timing of our surveys.

Trait data

For both bees and butterflies, we compiled information on traits related to diet (larval host plant for butterflies and pollen forage plants for bees) and body size (reflecting mobility; wingspan for butterflies and body length for bees). For butterflies we additionally compiled information on overwintering stage, and for bees we compiled information on nest sites and whether or not they are kleptoparasitic, meaning that they parasitize the nest of another species. We also distinguished between bumblebees (*Bombus* spp.) and other bees (here referred to as solitary bees; see definition below).

Butterflies

We compiled data on butterfly wingspan (as an indicator of body size), as well as larval host plants and overwintering stage (i.e. egg, larva, pupa or adult) from Eliasson et al. (2005). Data for Zygaenidae was extracted from the Swedish species information database Artfakta (SLU Artdatabanken 2024). For butterfly species with well-known host plants and that only feed on a few (maximum six) plant species, we listed all known larval host plant species. For butterfly species that can use several host plant species from a single plant genus (e.g. *Viola spp*. for some Nymphalidae), we included all species in that genus as potential host plants for this butterfly species. For butterfly species that can feed on several plant species from one plant family (e.g. Poaceae for several grass-feeding butterfly species), we included all species in that plant family as potential larval host plants. This information was used to assess if host plants used by a certain butterfly species were present or absent from a specific road verge. We also classified butterflies as oligophagous if they feed on plants within a single plant genus, and polyphagous if they feed on plants from several genera, following Öckinger et al. (2010). Two species (*Vanessa atalanta* and *V. cardui*) were migrant species that rarely hibernate in Sweden and were excluded from respective analyses.

Solitary bees

Here, we refer to all bee species that are not bumblebees (*Bombus* spp. *sensu lato*) as “solitary bees”, even if this includes some primitively eusocial species in the family Halictidae. We compiled data on body length, nest site and whether or not a species is kleptoparasitic (binary), from Artfakta (SLU Artdatabanken 2024). Nest site was coded as soil-nesting or cavity-nesting. For non-kleptoparasitic species, we also compiled data on pollen foraging specialization (lecticism; oligolectic = collecting pollen from plants within a single plant family; polylectic = collecting pollen from plants in more than one plant family). For oligolectic species we also compiled data on the identity of their respective pollen plants, either as a single plant species, one plant genus or one plant family. For kleptoparasitic bee species (hereafter specifically referred to as parasitic solitary bees), we compiled data on their host species, except for two species, *Sphecodes longulus* and *S. crassus*, with unknown host, which were excluded from the analyses.

Bumblebees

We compiled data on whether or not a species is kleptoparasitic, from Artfakta (SLU Artdatabanken 2024), and on body size from Gérard et al. (2018). As measure of body size, we used the inter-tegular distance (ITD), which is frequently used as a body size measure in bees (e.g. Greenleaf et al. 2007). Note that we used different types of body size measures for solitary bees and bumblebees, due to data availability. We complied data on nest site preference (i.e. nesting most frequently above ground or below ground) from Mossberg and Cederberg (2012). All bumblebee species in the dataset were polylectic and hence this trait was not included in any bumblebee analyses. Due to the low number of observed kleptoparasitic bumblebee species ($n = 4$), we excluded them from the analyses.

Red list status

We compiled the threat status of each bee and butterfly species from the national Swedish Red list (SLU Artdatabanken 2020). We included this information as a binary categorical variable, i.e. “Red-listed” (including Red list categories CR = Critically endangered, EN = Endangered, VU = Vulnerable and NT = Near threatened) or “Least concern” (LC).

Statistical analyses

We asked if certain species-specific traits act as filters in determining species occurrence patterns in road verges. Hence, we analyzed if these traits affect the probability that butterfly and wild bee species from the species pool are absent from all road verges in general, or only from certain road verges. Road verge specific variables that we considered included the mowing regime (once in late summer and twice, in early summer and autumn), traffic intensity (92–5661 vehicles per 24 h,), mean road verge width (1.9–13.9 m) and proportion of open land cover in a 2 km buffer (4.7–65.0 %). To investigate the role of species traits, we analyzed the following four species groups separately: butterflies, solitary bees, parasitic solitary bees, and bumblebees. We also analyzed if red-listed butterflies and solitary bees were more likely to be absent than species of least concern. Traits analyzed for each group are listed in Table 1, and details are described in Supplementary Material Appendix 1.

Statistical analyses were conducted using the ‘glmmTMB’ package (Brooks et al. 2017) in R 4.3.1 (R Core Team 2021). There was no substantial correlation between predictor variables included in the same model, i.e. no correlation (Pearson correlation coefficient > 0.6; Table S2–4; see Dormann et al. 2013 and model diagnostics were conducted using Q-Q plots, scaled residual plots, zero-inflation and outlier tests using the ‘DHARMa’ package (Hartig & Lohse 2022). Our analysis followed a consistent modelling approach across all three species groups, for which we used the same two filters (as described below) to select relevant data for our analyses. For each model, we used a binary response variable indicating absence (1) or presence (0). Absent species were defined as species that were a) either absent from either all road verges, i.e. not observed during our surveys, or b) absent from a given road verge, depending on the analysis. Two-way interactions between environmental variables and trait variables were used as the highest hierarchical level in all our analyses. Model fitting is described in Supplementary Material Appendix 1.

Regional trait filter: Do ecological traits explain why certain regionally occurring species are absent from road verges?

Here we analyzed if species traits (see Table 1) explained why some species from the regional species pool were completely absent from road verges. Data included all species from the regional species pool and were aggregated at the species level. For the analyses, we fitted generalized linear models with binomial error distribution. Predictor variables were

Table 1
A list of all group-specific species traits or trait-related factors that were included in the analyses.

Group	Traits/ trait-related factors	Type
Butterflies	Wingspan	Numeric (mm)
	Host plant presence	Factor (Presence/Absence)
	Host plant specialization	Factor (Oligophagous/ Polyphagous)
	Overwintering stage	Factor (Adult/Pupa/Larva/Egg)
Solitary bees	Body length	Numeric (mm)
	Lecticism	Factor (Oligolectic/Polylectic)
	Nesting location	Factor (Cavity/Soil)
	Pollen plant presence	Factor (Presence/Absence)
Parasitic solitary bees	Body length	Numeric (mm)
	Host species presence	Factor (Presence/Absence)
Bumblebees	Nesting location	Factor (Above-/Below-ground)
	Inter-tegular distance (ITD)	Numeric (mm)

all group-specific species traits as additive effects (see Table 1 and Appendix 1 for trait details). Road verge characteristics were not included and as such, this filter focusses solely on how traits determine the absence probability from any road verge.

Local trait filter: Do ecological traits explain species' response to road and road verge characteristics?

With this filter, we investigated if traits could explain species absences from specific road verges, depending on road and road verge characteristics. Data included only those species that we observed in any of the studied road verges (hereafter referred to as the "road verge species pool"), and were aggregated at species and road verge level. For the analyses, we fitted generalized linear mixed effects models with binomial error distribution, with road verge and species identity as crossed random effect. Predictor variables were group-specific species traits (Table 1) and road verge characteristics and their interactions (see Table 1 and Appendix 1 for details about traits and model selection).

Finally, we analyzed if nationally ***Red-listed species*** were more likely than species of least concern to be absent from road verges depending on road verge conditions. We included all species from the regional species pool. Instead of testing for interactions between traits and road verge variables, we only tested for two-way interactions between threat status (binary variable: red-listed = 1, least concern = 0) and road verge characteristics. We observed no red-listed bumblebees and only two individuals of a red-listed parasitic solitary bee species (*Nomada guttulata*) on the same road verge, so we ran these models only for butterflies and non-parasitic solitary bees.

We choose a GLMM approach rather than e.g. the combination of RLQ and fourth-corner analyses, which can also be used to identify trait-environment relationship from community-level data (Dray et al. 2014). The reason was that we wanted to test specific hypotheses regarding how road traffic, road verge with and management influences the presence or absence of insect species. Further, the GLMM approach is robust to data with many zeros, as was the case especially in the analyses accounting for the regional species pool.

We realize that our results could be sensitive to the occurrence of singletons, i.e. species only represented by a single individual, which might just have occurred in a road verge by chance. On the other hand, our research questions relate to absence probabilities, and the observation of just a single individual of a species in a road verge is evidence that the species occurred there. For this reason, we ran all analyses both with the full data set, and with singletons excluded. We present the results from the analyses with the full data in the main text, and the results from the analyes excluding singletons in the supplementary information (Tables S12 and S13 and Figures S1 – S3).

Results

The regional species pools consisted of 74 butterfly species and 196 bee species. In total, we observed 32 butterfly (43 % of the species from the regional species pool) and 74 bee species (38 % of the regional species pool) in at least one of the 37 road verges (Tables S5, S5 and S7. More specifically, among the solitary bees, we observed 48 non-parasitic (37 % of the regional species pool) and 10 parasitic (22 % of the regional species pool) species in the road verges. In addition, we observed 12 non-parasitic (out of 13 species in the regional species pool, i.e. 92 %) and 4 parasitic bumblebee species (57 % of the regional species pool) in the road verges.

Butterflies

None of the analyzed species traits influenced if a species from the regional species pool was completely absent from road verges (Regional trait filter; Table S10). For species that occurred in road verges (Local trait filter), we observed that butterflies whose host plants were absent from a specific road verge were themselves highly likely to be missing, but this was modified by wingspan. More specifically, butterflies with small wingspan and whose host plants were absent from a specific road verge, were particularly likely to be absent. This effect was much less pronounced for butterflies with large wingspan ($z = 3.290$, $P < 0.001$, Table S8, Fig. 2A). Oligophagous (host plant specialist) and polyphagous (host plant generalist) butterflies differed in their response to road verge width ($z = 2.001$, $P = 0.045$; Fig. 2B, Table S8). Both groups were less likely to be absent from wide than narrow road verges, but this effect was stronger for oligophagous than in polyphagous species, for example, the absence probability of polyphagous species declined from 0.87 in road verges that were 3 m wide to 0.75 in road verges that were 10 m wide, while the absence probability of oligophagous species declined from 0.95 in road verges that were 3 m wide to 0.75 in road verges that were 10 m wide. A higher proportion of grassland habitats in the surrounding landscape reduced the chances that species would be absent, but this effect was similar for all species, independent of their traits ($z = -2.131$, $P = 0.033$, Table S8). There was an interaction between host plant presence and road verge management. Even though butterfly species whose host plants were missing from a specific road verge were generally more likely to be absent from that road verge, this effect was more pronounced for verges that were mowed twice (absence probability 0.90 vs. 0.83 in road verges that were mowed ones, and 0.93 vs. 0.77 in road verges that were mowed twice; $z = -2.049$, $P = 0.040$; Fig. 2C, Table S8). The results were similar when excluding singletons (Tables S12 and S13, Fig. S1).

Solitary bees

When analysing how ecological traits influenced the probability that regionally occurring species (Regional trait filter) was observed in road verges, we found that cavity nesting solitary bees (average absence probability = 0.77) were more likely to be absent from road verges than soil nesting solitary bees (average absence probability = 0.56; $z = -2.266$, $P = 0.023$; Fig. 3, Table S10). This difference was also evident when analysing how ecological traits influenced how species that occurred in the road verges responded to road verge characteristics (Local trait filter) even though the difference was smaller (average absence probability of cavity nesting bees = 0.97, average absence probability of soil nesting bees = 0.93; $z = -2.004$, $P = 0.041$; Table S8). Also, bees were more likely to be absent from road verges where their food plants were lacking, but effect was similar for all species, independent of their traits ($z = -2.489$; $P = 0.013$; Table S8). When excluding singletons, the results were similar, with the exception that there was also an interaction between feeding specialization and road verge width, such that the absence probability of polylectic (generalist), but not oligolectic (specialist) bees decreased with road verge width (Table S12, Fig. S2).

Parasitic solitary bees

Overall, the occurrence of parasitic solitary bees was low. None of the analyzed species traits influenced if a species from the regional species pool was missing from all road verges (Regional trait filter; Table S10). In the local trait filter, parasitic bee species were more likely to be missing from a road verge if their host species was also absent, especially at high traffic intensities ($z = -2.267$, $P = 0.023$; Table S8) and in road verges mowed twice per year ($z = -2.485$, $P = 0.013$; Table S8). However, these effects disappeared when removing singletons from the analysis (Table S12).

Bumblebees

Twelve of the thirteen bumblebee species in the regional species pool occurred in at least one of the road verges, and hence we could not analyse how ecological traits influenced whether a species occurred in

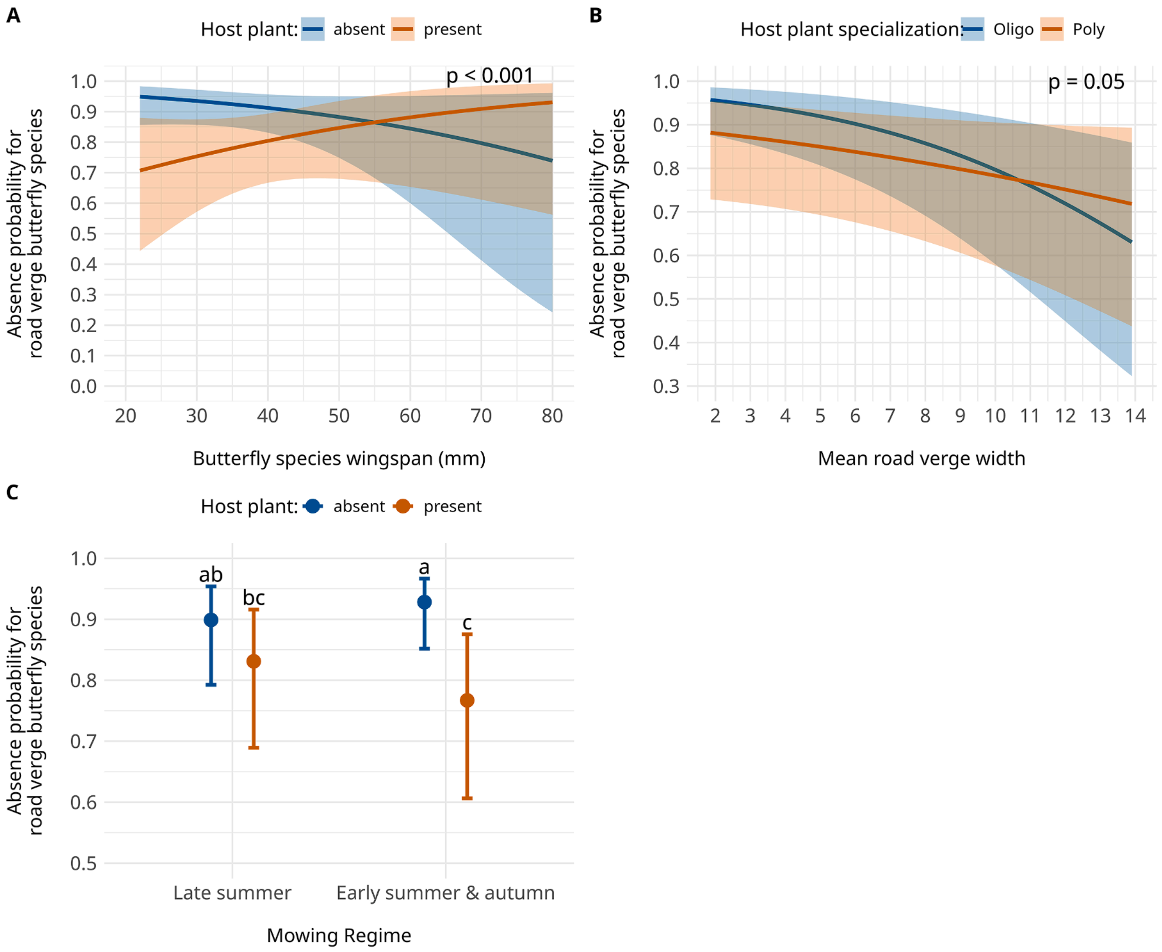

Fig. 2. Absence probability for butterfly species of road verge species pool relating to A) the interaction between host plant availability and wing span ($p < 0.001$), B) the interaction between road verge width and host plant specialisation ($p = 0.048$), and C) The interaction between host plant availability and mowing regime($p = 0.040$). Lines with bands represent predicted mean values and 95 % confidence intervals. Colours correspond to trait characteristics.

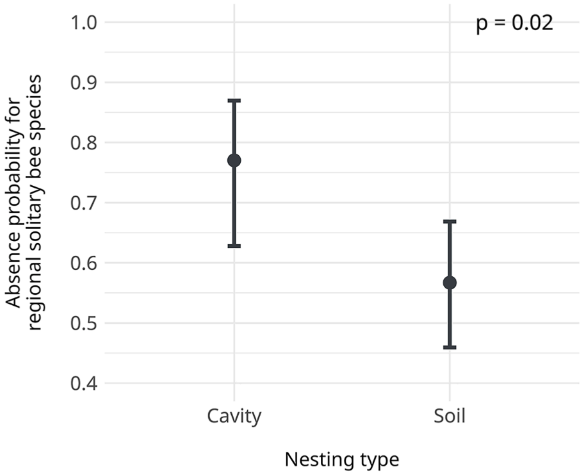

Fig. 3. Absence probability for solitary bee species of the regional species pool depending nesting location (cavity above ground or in the soil; $p = 0.023$). Dots with error bars represent predicted mean values and 95 % confidence intervals.

road verges using the Regional trait filter. Among species occurring in the road verges (Local trait filter), there was a near-significant interaction between nesting location and traffic intensity ($z = 1.948$, $P = 0.051$, Table S8). Bumblebees nesting above ground always had a high absence probability (0.85 - 0.9) regardless of traffic intensity, while bumblebees nesting below ground tended to be more likely to be missing at high than at low traffic intensities (absence probability of below ground nesting bumblebees: 0.3 at 100 vehicles per 24 h, but 0.7 at 5600 vehicles per 24 h). In the alternative model including ITD instead of nesting location, there was an interaction between ITD and road verge width ($z = 2.001$, $P = 0.045$), such that bumblebees with a smaller ITD were more likely to be missing from narrow than wide road verges (absence probability of small-bodied species = 0.9 in road verges that were 2 m wide, but = 0.7 in road verges that were 13 m wide; Fig. 4), while there was no such effect for bumblebees with larger ITD. The results were similar when excluding singletons (Table S12, Fig. S3).

Red-listed species

We found 5 nationally red-listed bee species: *Lasioglossum xanthopus* (EN; 14 observations across 8 sites), *L. nitidiusculum* (NT; one observation), *L. aeratum* (NT; one observation), *Colletes marginatus* (NT; one observation) and *C. fodiens* (NT 20 observations across 6 sites) and 6 red-listed butterfly species: *Adscita statices* (NT; 16 observations across 3 sites), *Cupido minimus* (NT; 20 observations across 4 sites), *Satyrium w-album* (NT; one observation), *Zygaena filipendulae* (NT; 60 observations across 8 sites), *Z. lonicerae* (NT; 32 observations across 2 sites) and *Z. viciae* (NT; 2 observations across 2 sites) in the road verges. This is 15 % of the red-listed bee species and 33 % of the red-listed butterfly species occurring in the region (34 and 18 species, respectively). We observed no red-listed bumblebees in any of the road verges.

Red-listed butterfly species and species of least concern were equally

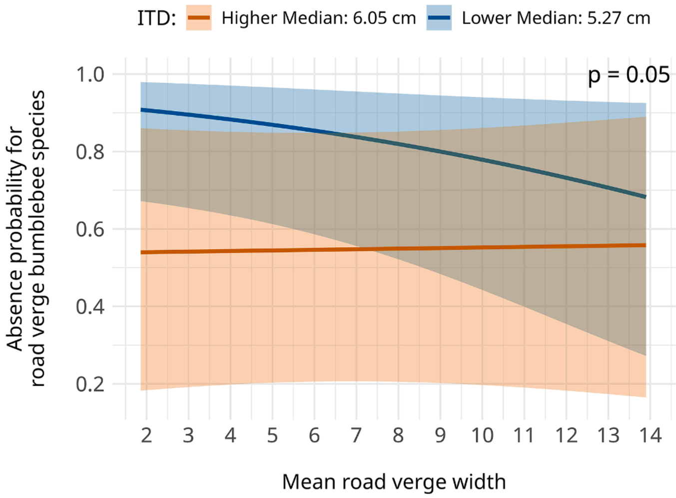

Fig. 4. Absence probability for bumblebee species of the road verge species pool, depending on the interaction between road verge width and body size measured as the inter-tegular distance (ITD; $p = 0.045$). Lines with bands represent predicted mean values and 95 % confidence intervals. Colours correspond to trait characteristics.

likely to be absent from road verges (Regional trait filter; $z = 1.580$, $P = 0.114$, Table S11), and none of the road verge characteristics influenced the absence probability of red-listed species (Table S11).

Among solitary bees, the probability that a red-listed species was absent from the road verges tended to be higher than for species of least concern ($z = -1.809$, $P = 0.071$, Table S11), but and none of the road verge characteristics influenced the absence probability of red-listed species (Table S11). When excluding singletons, there was a near-significant interaction between red-list status and road verge width, such that the absence probability of species of least concern but not of red-listed species tended increase in narrower road verges ($z = 1.837$, $P = 0.066$).

Discussion

Along 7400 m of road verges that we surveyed in this study, we observed 38 % of the bee species and 43 % of the butterfly species from the regional species pool. Among these, we observed 15 % of the red-listed bee species and 33 % of the red-listed butterfly species that occur in the region. This highlights the potential of road verges as habitat for flower-visiting insects, as a complement to semi-natural grasslands and other high nature value habitats (Dániel-Ferreira et al. 2023; Meinzen et al. 2024; Phillips et al. 2019; Wojcik & Buchmann 2012). Here, we show that, even though the effects were generally weak, the value of road verges as habitat differs among insect species depending on their traits. Hence, the negative effects of traffic and the positive effects of increased verge width affect species differently, and ultimately not all bee and butterfly species might be able to use road verges as habitats at all.

Butterfly occurrence depends on host plant availability and specialization

Several studies have found a high diversity of butterflies in road verges (Dániel-Ferreira et al. 2023; Munguira & Thomas 1992; Ries et al. 2001), and we observed a relatively large proportion of the species from the regional species pool in the studied road verges. None of the assessed traits explained why some butterflies were absent from all road verges. Given that their host plant is present, a broad range of butterfly species can thus use road verges as habitat, regardless of their traits. Indeed, road verges with a high diversity of plant species, and hence a high diversity of potential host plants, often have a higher number of butterfly species (Horstmann et al. 2024). The link between host plant presence and butterfly occurrence was particularly strong in butterflies with a small wingspan. These butterflies are typically less mobile (Sekar 2012), and hence less likely to fly far from habitats where their larval host plants occur.

Nesting ability determines the occurrence of solitary bee species

We found that cavity nesting bees were more likely to be absent from road verges than soil-nesting species. This is probably linked to the fact that road verges are dominated by open, herbaceous vegetation with only few trees and other woody plants that could provide nest sites for cavity-nesting species, and also the surroundings were dominated by agriculture. Also, it is possible that the material used for constructing the road embankment i.e. gravel and sand, is suitable as nesting substrate for many soil-nesting bees (Antoine & Forrest 2021). However, soils in road verges can have high concentration of pollutants like heavy metals (Akbar et al. 2006), and soil-nesting insects can suffer from vibrations from the traffic (Phillips et al. 2021), so to what extent soil-nesting bees are actually reproducing successfully in road verges or are just using road verges for collecting resources remains to be assessed.

Bumblebee species respond differently to verge width and traffic

Except for the red-listed and localized *Bombus muscorum*, all social bumblebee species occurring in the region were observed in the studied road verges. Although road verges in general appear to provide suitable habitat for the majority of bumblebees, traffic intensity and road verge width influenced species composition by traits. Blomqvist et al. (2025) found that bumblebee workers tend to avoid roads with intensive traffic. Here, we found a similar pattern (although not statistically significant) in that bumblebee species nesting below ground were more likely to be absent at high traffic intensities, while above ground nesting species were more often absent from all road verges, independently of traffic intensity. A potential explanation is that similarly to above ground solitary bee species, also above-ground nesting bumblebees are less likely to find suitable nest sites in road verges, while below-ground nesting species can at least nest along roads with low traffic intensity but avoid nesting in more busy roads. Interestingly, Dániel-Ferreira et al. (2022) also found that traffic-related mortality of bumblebee queens was highest in the two below-ground nesting species *Bombus terrestris* and *B. lucorum*, suggesting that direct traffic-related mortality could at least partly explain the negative effects of traffic on below-ground nesting bumblebees.

Due to strong correlations, we could not test the effects of nesting location and body size in the same models, but in the alternative analysis using ITD, small-bodied bumblebees were more likely to be absent from narrow road verges than form wide road verges, while large-bodied bumblebees were more frequent in any type of road verge. Body size is related to foraging range in bees (Greenleaf et al. 2007; Westphal et al. 2006). The vast majority of bumblebees observed in the road verges were foraging workers. We have no information on the density of bumblebee nests in our study landscapes, but if most bumblebees avoid nesting near roads, this could explain why small-bodied bumblebees with more restricted foraging ranges are generally less frequent in road verges, and perhaps especially in narrow verges with smaller amounts of flowers.

Traffic and road verge characteristics as environmental filters

Both butterfly and wild bee species richness have previously been found to be lower in narrower road verges (Horstmann et al. 2024). Here, we found that the species that are absent from narrow road verges are not a random subset of all species. Instead, in both butterflies and solitary bees the absence probability was linked to food plant specialization. While both host plant specialist and host plant generalist butterflies were more likely to occur in wide than in narrow road verges, this effect was stronger for the host plant specialists. This is consistent with the general pattern that host plant specialist butterflies are less likely than generalists to occur in small habitat fragments (Öckinger et al. 2010). In solitary bees, both pollen feeding specialists and generalists were very unlikely to occur in the narrowest road verges, but in the widest road verges, generalists were more likely to be present than specialists. We hypothesized that narrow road verges would be particularly prone to disturbances from the road traffic, but the observation that feeding specialists are more likely than generalists to be absent from the narrowest road verges instead suggests that the habitat area could be the main driver of the effects of road verge width. In our study, the narrowest road verges were <2 m wide. A potential mechanism could be that the plants on which the specialist bees or butterflies depend occur less frequently, or have too small populations to support viable insect populations, in narrow road verges. An alternative explanation could be that specialized butterflies and solitary bees, and also small-bodied bumblebees which showed a similar pattern, in general have more patchy distributions in the landscape and hence are less likely to be observed at any given site in the landscape, even if the habitat is suitable (c.f. Ranius et al. 2011).

Intensive traffic has clear negative effects on insect abundance and species richness in road verges (Horstmann et al. 2024), and previous studies have estimated that between 0.6 % and 7 % of the adult butterflies in road verges die from collisions with vehicles (Munguira & Thomas 1992; Skorka et al. 2013). While the overall dangers associated with traffic could plausibly be a contributing factor to the absence of 57 % of the butterfly and 62 % of the wild bee species in the region from our set of road verges, we found no evidence that relative differences in traffic intensity influenced the occurrence of butterfly or solitary bee species differently depending on their traits. We found that bumblebees, but not butterflies, showed trait-dependent responses to traffic intensity. This is in contrast to some previous studies that have found that either small-bodied (Skorka et al. 2013) or large-bodied butterflies (Remon et al. 2018) have an elevated mortality risk. One potential explanation for these differences is that traffic mortality risk is not influenced by body size *per se*, but rather by some other correlated trait, perhaps movement behaviour. Also, it should be remembered that we analyzed presence/absence in relation to species traits. It is still possible that species with certain traits have a higher mortality rate, but that this mortality is only affecting the abundance and not the occurrence of the species. We have no good explanation to why bumblebees, but not solitary bees or butterflies showed trait-dependent responses to traffic intensity. Since we do not know if the negative effects of traffic are mainly caused by direct mortality, avoidance or reduced habitat quality (Meinzen et al. 2024), further studies on the mechanisms behind the traffic-related effects on insects are needed.

Road verges as breeding habitat

Bee and butterfly populations in other linear habitat elements, like uncultivated field margins, often seem to be dependent on spill-over of individuals from nearby larger and permanent grasslands (Ekroos et al. 2013; Öckinger & Smith 2007). Hence, an important question is to what extent species observed in road verges also reproduce there, or how a lack of opportunity for reproduction contributes to local absences of species that occur in the species pool. Although we did not study reproduction specifically, our results give some insights. Among solitary bees, the observation that more cavity nesting than soil nesting species were absent from road verges supports the hypothesis that most solitary bees observed in road verges are also able to reproduce in these environments, especially since many solitary bees have foraging ranges of a few hundreds of meters from their nests (Greenleaf et al. 2007). However, the quality of road verges as breeding habitat remains to be determined.

We previously found that butterfly species richness in the same road verges was linked to the diversity of the plant community (Horstmann et al. 2024). Of the 32 butterfly species observed in the road verges, 27 were only ever found in road verges where their respective larval host plants occurred. This suggests that the majority of butterfly species observed in the road verges could at least potentially have reproducing populations there. However, a few species occurred in road verges where none of their larval host plants were observed, meaning that they were likely to use the road verges only for foraging or as movement corridors (c.f. Öckinger & Smith 2008). Also, a high grassland cover in the surrounding landscape increased the occurrence probability of butterflies in general, regardless of their traits, which reinforces the suggestion that not all butterflies observed in road verges had their entire life cycle there. To what extent these populations are self-sustaining, or are sink populations that depend on immigration for their long-term persistence remains to be investigated (Gardiner et al. 2018; Meinzen et al. 2024).

Road verges as habitat for red-listed species

In the 37 road verges, we observed 15 % of the regionally occurring nationally red-listed bee species and 33 % of the butterfly species. In three of these five bee species, we only observed a single individual in one site, but two of the species *Lasioglossum xanthopus* and *Colletes fodiens* appeared to have relatively high abundances in 8 and 6 sites, respectively. Among the six observed red-listed butterfly species, one species was only observed once, whereas *Adscita statices, Cupido minimus, Zygaena filipendulae* and *Z. lonicerae* all occurred in several sites and had locally high abundances. This shows that road verges can indeed act as habitat for some rare and red-listed species. Previous analyses show that some insect species may even have a large proportion of their total population in road verges and other infrastructure habitats (Helldin et al. 2015; Noordijk et al. 2011). However, biodiversity targeted management (i.e. mowing only once per year) or low traffic intensities did not increase the probability that red-listed species would occur there. Together with previous findings that plant and butterfly species that are specialized on semi-natural grasslands tend to be missing from road-verges and other infrastructure habitats (Dániel-Ferreira et al. 2023), this highlights that even though road verges can support biodiversity conservation, they cannot ultimately replace other high-quality habitats.

Conclusions

We analyzed if species traits in combination with local habitat characteristics can explain why species, that potentially could occur there, are missing from a certain road verge or from road verges at large. This approach can help us understand if flower-rich road verges can be a suitable habitat for all flower-visiting insects.

We found that road verges can be used by a wide range of flower-visiting insect species, including rare as well as common species. Our results show that road verges are used as foraging habitat by most bumblebee species occurring in the region, and by many butterflies, as long as their larval host plants occur there. Overall, the previously observed negative response to traffic intensity in butterflies and solitary bees (Horstmann et al. 2024; see also Munguira & Thomas 1992; Phillips et al. 2019; Skorka et al. 2013) was similar across species independent of their traits. It should also be noted that the observed trait-dependent effects were relatively weak and confidence intervals were large in most analyses, meaning that there was considerable variation in responses among species sharing the same traits. This indicates that other traits than those analyzed here might influence species' responses to traffic and road verge characteristics.

Our results indicate that many flower-visiting insect species have the potential to reproduce, and not only forage, in road verges, provided that nesting resources or larval host plants are present. Road verge management should thus be adapted to not only provide abundant flowers but also ensure that there is a high diversity of plants that can act as larval host plants for butterflies and other specialised plant-feeding insects. Addition of woody plants, and especially dead wood, near road verges might increase their quality for cavity-nesting bees. It is, however, important to note that, for butterflies, the lack of semi-natural grasslands in the surrounding landscape increased the absence probability, independently of species traits, suggesting that the value of road verge as habitat for flower-visiting insects is also dependent on high quality habitat. To optimize the use of road verges as conservation habitat, it is thus crucial to account for maintenance and restoration of semi-natural grasslands in spatial planning.

CRediT authorship contribution statement

Erik Öckinger: Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Svenja Horstmann:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lina Herbertsson:** Writing – review & editing, Methodology. **Björn K. Klatt:** Writing – review & editing, Methodology. **Alistair G. Auffret:** Writing – review & editing, Methodology, Investigation, Formal analysis.

Declaration of competing interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2026.03.008.

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