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RESEARCH ARTICLE

Traffic intensity and vegetation management affect flower-visiting insects and their response to resources in road verges

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Abstract

1. Road verges can support high densities of flowers and could therefore provide new opportunities for the conservation of flower-visiting insects. One way of optimizing road verges for vascular plant diversity is to adjust mowing regimes, but to date it is unclear how this affects flower-visiting insects. Furthermore, for mobile organisms like wild bees and butterflies, there is a risk that the benefit of increased habitat quality in road verges is limited by the proximity to traffic, but this is poorly studied.
2. In a crossed study design, we separated mowing time and frequency (early summer and autumn, or only late summer) from road verge habitat classification (valuable for biodiversity according to transport authority, or regular). We did so along a gradient of traffic intensity, to investigate if a mowing regime designed to enhance plant diversity can also benefit wild bees and butterflies, and if traffic limits the conservation potential of road verges.
3. Road verges that were mown only in late summer had higher flower densities, and there was a positive relationship between flower density and wild bee abundance and species richness. Butterfly abundance and species richness only benefitted from a late summer mowing in valuable but not in regular road verges.
4. Traffic intensity had a substantial negative impact on abundance and species richness of wild bees and butterflies. Higher traffic intensities limited the positive relationship between plant and butterfly species richness that we observed at lower traffic intensities. Increasing width of the road verges buffered negative effects of the traffic on wild bee as well as butterfly abundances, and on wild bee species richness.
5. *Synthesis and applications*. Road verges can play a valuable role for the conservation of wild bees and butterflies, but there is a need to consider both traffic intensity and resource availability when implementing management strategies. To support wild bee and butterfly diversity, we recommend actions to enhance plant species richness and flower resource availability, and to focus these conservation efforts on roads with low traffic intensity, or on wide road verges.

KEYWORDS
habitat quality, linear infrastructure habitat, linear landscape elements (LLE), marginal grasslands, mowing regime, pollinator conservation, roadside habitat, traffic volume

1 | INTRODUCTION

To reach national and international goals on halting the loss of biodiversity, there is a need to incorporate habitats into conservation-oriented management that extend beyond the traditional focus of biodiversity conservation (IPBES, 2016). One such example are road verge habitats, i.e. strips of land adjacent to roads that are usually dominated by grassland or shrubland vegetation. Road verges are mown to maintain an open early-successional vegetation for traffic safety reasons, but this management inadvertently creates a habitat that can resemble traditionally managed, species-rich semi-natural grasslands (Gardiner et al., 2018). While semi-natural grasslands are among the most species-rich habitats in Europe, their area and consequently the biodiversity associated with these grasslands has declined severely due to agricultural intensification and abandonment (Krauss et al., 2010; Prangel et al., 2023; Strijker, 2005). Many plant species associated with semi-natural grasslands also occur in road verges (Dániel-Ferreira et al., 2023; Vanneste et al., 2020), and since they are typically managed with relatively low intensity compared to other grassland habitats, road verges can have high densities of flowers and flower-visiting insects (Phillips et al., 2020), and even similar levels of species richness of bumblebees and butterflies as semi-natural grasslands (Dániel-Ferreira et al., 2023). In addition, road verges cover vast areas of land; for example in Sweden, the area of grassland habitat in road verges is similar to the total area of high-nature value grasslands (Jordbruksverket, 2012, 2016).

The combination of conceivably attractive habitat and the large area it covers have put road verges forward as potential conservation opportunities for the diversity of flower-visiting insects. Road verges can provide feeding resources for flower-visiting insects (Halbritter et al., 2015; Noordijk et al., 2009), as well as larval host plants for butterflies (Valtonen et al., 2006) and nesting and overwintering habitat for wild bees (Hopwood, 2008; Schaffers et al., 2012). As such, the pollinator assessment report by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) lists road verge management as an immediate opportunity for improving current conditions for flower-visiting animals, including insects (IPBES, 2016). However, species in road verge habitats can be exposed to multiple harmful conditions, e.g. through traffic mortality, pollution and mowing (reviews by Muñoz et al., 2015; Phillips et al., 2020). Traffic-associated mortality of butterflies increases with traffic intensity (Skórka et al., 2013), as can the mortality of bumblebee queens (Dániel-Ferreira et al., 2022). Several studies show that flower-visiting insects are killed through vehicle collisions, but research on the impact of traffic on entire communities of flower-visiting insects is scarce (but see Dániel-Ferreira et al., 2022; Phillips et al., 2020).

The potential of road verges to provide habitat for grassland species depends to a large extent on how they are managed, but most studies on road verge management so far have concentrated on the effects on plants alone (review by Jakobsson et al., 2018). In many European countries and the US, road verges are often mowed once or twice per season (Jakobsson et al., 2018). In Sweden, road verges with high biodiversity values are put under targeted vegetation management that involves adjusting the timing and frequency of mowing, mainly in order to promote plant diversity. However, plants and insects can respond differently to grassland management (Berg et al., 2019) and it is not clear if a management that benefits plants is always positive for flower-visiting insect richness. Given the increasing focus on managing road verges to support grassland biodiversity, and the dangers posed to insects by traffic and the potential trade-offs involved in promoting both plant and insect communities, it is imperative for future biodiversity policy and management that these complexities are investigated together. In this study, we collaborate with the Swedish Transport Administration (Trafikverket) to understand how, and where, to adapt road verge management to promote the conservation of bees and butterflies. Applying two different mowing regimes in regular road verges and those classified as valuable for plant diversity, and along a gradient of traffic intensity, we ask if (a) there is a positive effect of plant diversity-targeted management on wild bees and butterflies, and (b), how traffic intensity modifies the effect of road verge quality for wild bees and butterflies.

2 | MATERIALS AND METHODS

2.1 | Study design and site selection

Our study was carried out in Skåne county in southernmost Sweden, which is dominated by arable and forest land cover (39.7% and 43.7%, respectively; SCB, 2020; Figure 1). In Sweden, road verges are generally mowed twice per season and the hay is not removed. However, the Swedish Transport Administration is working on identifying road verge habitats that are important for biodiversity conservation, for example by containing rare plant species or a high number of indicator plant species (for details, see Lindqvist, 2018). We will use the term 'valuable' for such road verges. Valuable road verges receive a biodiversity-targeted mowing regime, which typically means that they are mowed only once, usually in August (hereafter 'late summer' mowing). When mown, the entire width of the road verge is mowed. Other, hereafter 'regular' road verges entail all road verges that have not been identified as valuable and are mowed twice each season, once before mid-June and once in late September (hereafter 'early summer' and 'autumn' mowing). During the early summer mowing of regular road verges, only the immediate

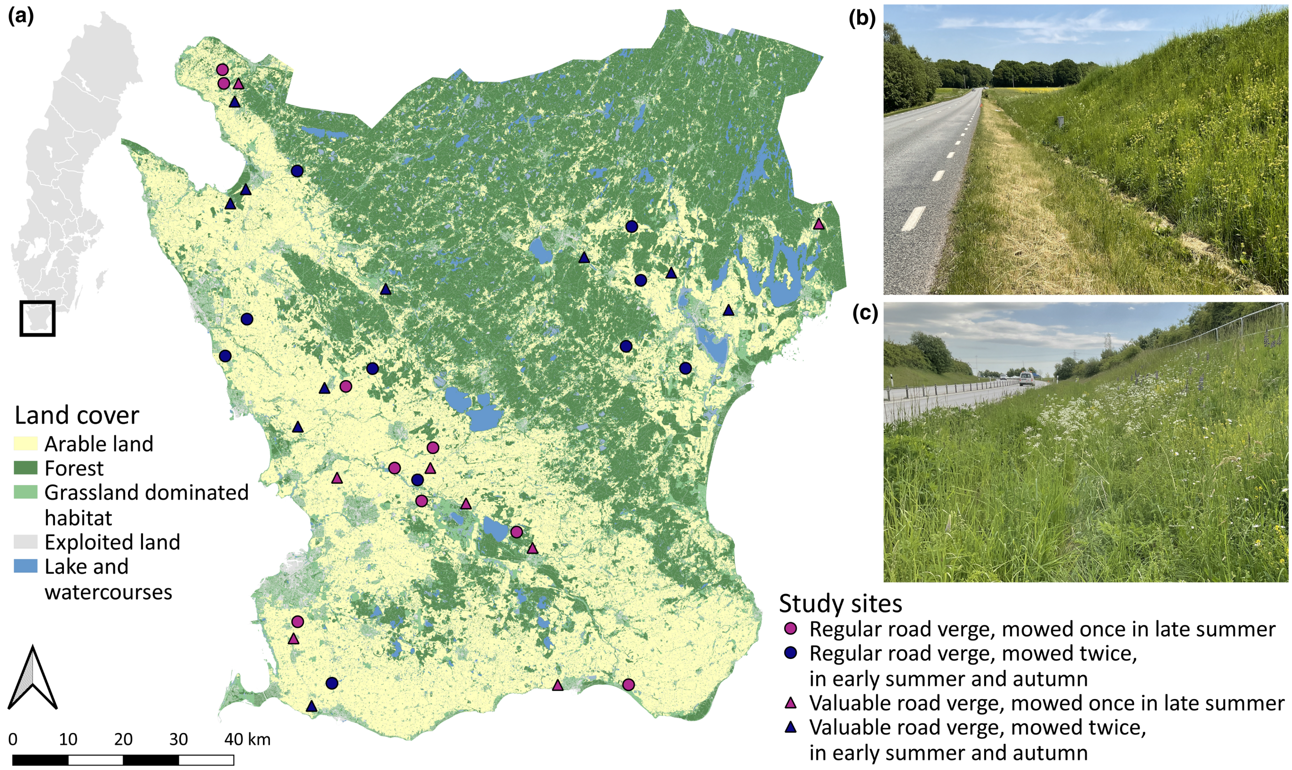

FIGURE 1 (a) Location of the 37 road verge sites in southern Sweden, showing the crossed study design to separate effects of road verge classification and mowing regime on biodiversity. Within each of the four categories for each combination of classification and mowing regime, the study sites were selected along a gradient of traffic intensity. Land cover was taken from Sweden's 2018 land cover database (Naturvårdsverket, 2020). Photos of (b) a regular road verge that was mowed in early summer, and (c) a valuable road verge that will be mown in late summer after our study period. Photos: Svenja Horstmann.

roadside verge (i.e. the first 1.5 m next to the road) is mown, while the autumn mowing is applied over the whole width, including the outer verge. The hay is usually not removed in either valuable or regular road verges.

In collaboration with the Swedish Transport Administration, we created a crossed study design allowing us to separate the effects of road verge classification from the effects of mowing regime and to study these effects on wild bees, butterflies and vascular plants along a gradient of traffic intensity (Figure 1). We selected 10 road verges in each of the following four categories: (i) Valuable verges mowed in late summer, (ii) valuable verges mowed in early summer and autumn, (iii) regular verges mowed in early summer and autumn, and (iv) regular verges mowed in late summer. Category (ii) refers to road verges that have only recently been classified as valuable by the Swedish Transport Administration and are still being mowed in early summer and autumn, whereas the Swedish Transport Administration purposely changed the mowing regime of some of our selected sites to create category (iv).

To select road verges, we used the environmental and infrastructure data from the National Road Database (https://nvdb2012.trafikverket.se/), filtering for road verges that were classified as valuable (named 'artrik vägkant' in Swedish) and longer than 200 m, along roads with speed limits of 50 km/h or higher. We also extracted the traffic intensity of all selected road verges from the National Road Database, measured by the Swedish Transport Administration as average number of vehicles per day assessed several times over 1 year ('ÅDT total' on https://nvdb2012.trafikverket.se/; Trafikverket, 2013). To account for potential landscape effects, we used road verges situated in rural landscapes and filtered for roads surrounded by a maximum of 50% forest and minimum 30% arable land in a 2 km buffer, and without valuable grassland habitat within 350 m, using QGIS (version 3.10). For this, we used the National Land Cover Database (Nationella marktäckedata: Naturvårdsverket, 2020; Table S1) and the TUVA database of meadows and pastures of high-nature value (https://etjanst.sjv.se/tuvaut/). Among all potential road verges, we then selected 20 valuable road verges at least 2 km apart, half of them mown in late summer and half still in early summer and autumn, along a similar gradient of traffic intensity within each category (see Figure S1 in Supporting Information). To find matching regular road verges, we selected roads located between 2 and 20 km away from the selected valuable road verges that fit all traffic and landscape criteria mentioned above (information about all selected sites in Table S2). Due to incorrect mowing, we had to exclude three road verges from our analyses and change category for one, resulting in 8 valuable road verges mowed in late summer, 10 valuable road verges mowed in early summer and autumn, 11 regular road verges mowed in early summer and autumn and 8 regular road verges mowed in late summer (listed from category (i) to (iv)). Two sites had to be slightly relocated and then had 22% and 26% arable land in the surrounding landscape (instead of at least 30%). Our study did not require ethical approval or permissions for fieldwork.

2.2 | Vascular plant and flower inventory

At each study site, we surveyed the presence of vascular plants in 10 plots of each 1 m^2, located across a 200 m long stretch of the road verge, with a fixed distance between all plots. When the narrowest section of the road verge measured less than 2.5 m, we positioned all 10 plots 50 cm from the road surface. In cases where the road verge was wider, we distributed five plots 50 cm from the road surface 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, and was independent of the mowing regime (Figure S2). We identified vascular plants (hereafter only 'plants') to species level when possible (using Krok et al., 2013; Mossberg & Stenberg, 2018; Rothmaler, 2017, 2021). We did this once per study site, at the end of June and in July 2021 or 2022.

We assessed flower diversity within the 200 m long stretch of road verge that we used for the vascular plant inventory. For this, we used four non-overlapping segments of each 50 m length, covering the whole width of the road verge. Within each segment, we assessed every currently flowering plant to species or genus level and estimated their abundance in flower units on a scale from 1 to 6 (1: 1–10, 2: 11–50, 3: 51–150, 4: 151–500, 5: 501–1000, 6: >1001). This was estimated separately for the first 1.5 m of the road verge, and from 1.5 m until the road verge's far edge. We did this three times in each road verge between May and July 2021.

2.3 | Wild bee and butterfly inventory

In the same segments as for the flower inventory, we conducted transect walks to survey butterflies four times and wild bees three times between May and July 2021. Data on butterflies, wild bees and flowers were always collected on the same day, except for the fourth round of the butterfly survey. Wild bees and butterflies were only surveyed between 10 am and 5 pm, when vegetation was dry, wind was moderate (max. Beaufort 5) and with at least 13°C if cloud cover was less than 50%, or at least 17°C with higher cloud cover. Between rounds, we alternated the time of day during which we visited the sites. For butterflies and burnet moths (Zygaenidae; from here on included in 'butterflies'), the observer walked 5 min along each transect at a steady pace and caught and identified (using Söderström, 2019; Tolman & Lewington, 2009) 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 min walking along each transect, catching all individuals within 1.5 m on each side and in front. All transects were located directly alongside the road. For road verges narrower than the planned transect width, the whole road verge was covered. 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 'Artdatabanken' at https://artfakta.se/artinformation/taxa/apiformes-2002991/artnyckel/23522; as well as Amiet et al., 2001, 2004, 2007, 2014; Bogusch & Straka, 2012; Schmid-Egger & Scheuchl, 1997). If we failed to catch wild bees, we noted their presence without identification. For butterflies we could not catch, we identified on sight if possible, otherwise noting only their presence. For both bees and butterflies, we did not include individuals that only flew across the road verge without interacting with it.

2.4 | Statistical analyses

2.4.1 | Model building

In this study, we ask if (a) there is a positive effect of plant diversity-targeted mowing regime on wild bees and butterflies, and (b), how traffic intensity modifies the effect of road verge quality for wild bees and butterflies. As measures of diversity, we used abundance, species richness and evenness. Wild bee and butterfly abundance in a road verge was defined as all individuals counted across all transects and all visits. For species richness and evenness of wild bees and butterflies per road verge, we only included individuals that we caught and identified to species level (92% of all wild bees, 99% of all butterflies). To calculate the Shannon evenness index for butterflies and wild bees in each road verge, we divided the Shannon diversity (package 'vegan': Oksanen et al., 2020) by the natural logarithm of the species richness. Thus, evenness indicates the relative abundance of species in the community with values between 0 and 1, with higher values representing more even communities. In one road verge, we only caught one species of butterfly and excluded this site from the butterfly evenness model, because the resulting evenness value of 1 is inconclusive when interpreting a seemingly perfectly even community with just one species.

To answer our questions, we first built six models (for abundance, species richness and evenness of both wild bees and butterflies), which included the following main explanatory variables: mowing regime (late summer versus early summer and autumn), road verge classification (valuable or regular), traffic intensity (a gradient from 92 to 5661 vehicles per day, log-transformed), and either plant richness or flower density (see model selection for details). We also included the width of each road verge as an explanatory variable (the mean of measurements at the midpoint and each end of each transect; Figure S2). In each model, we included the following two-way interactions: either flower density or plant richness × traffic intensity, road verge width × traffic intensity, and mowing regime × road verge classification.

Additionally, we built two models to test how plant richness and flower density varied with mowing regime, habitat classification and the interaction between these two variables, as well as traffic intensity. For plant richness, we included mean road verge width to account for the expected positive relationship between area and species richness. We used flower density instead of abundance to account for differences in road verge width, since we always assessed flower abundance across the entire width. To calculate flower density per transect, we summed the minimum abundance of all species within each flower abundance category (e.g. 1 for category 1: 1–10 flowers, 11 for category 2: 11–50 flowers, etc.) across the whole width and then divided the sum by the mean width of each respective transect. To calculate the flower density per road verge, we summed the flower density of all four respective transects and then used the mean flower density of all three assessment rounds in the analyses. To calculate the plant richness, we excluded individuals that we could only identify to genus level if there was another individual of the same genus present (less than 1%).

Finally, we examined potential differences in plant community composition across our four road verge categories. We conducted an NMDS with three dimensions to achieve a stress of <0.2 and a permutational MANOVA (both using package 'vegan' and based on Bray-Curtis distance: Oksanen et al., 2020), followed by pairwise comparisons between the four road verge categories (package 'RVaideMemoire': Herve, 2023). Community composition is based on species occurrences within each site's vegetation plots, with possible occurrences between 0 and 10 times per species per road verge. Furthermore, we built a model to test if the relative abundance of graminoids (hereafter 'grasses') was explained by the interaction between mowing regime and road verge classification. We calculated the relative abundance of grasses by dividing the sum of all grass species occurrences by the sum of all plant species occurrences in each road verge.

We conducted the statistical analyses in R, version 4.3.1 (R Core Team, 2021). There was no substantial correlation between predictor variables, i.e. no correlation >0.7 (Table S3, see Dormann et al., 2013). For each response variable, we tested for spatial autocorrelation with Moran's *I* autocorrelation coefficient using an inversed distance matrix (package ape: Paradis & Schliep, 2019; Table S4). If applicable (i.e. where Moran's *I* was significant at the 0.05 level), we included the first axis of a principal coordinates of neighbour matrix (PCNM) applied to site coordinates as covariate in the model (package 'vegan': Oksanen et al., 2020).

2.4.2 | Model fitting and selection

Based on our aim of identifying general differences (and no threshold values) with varying traffic intensities or flower densities, we log-transformed these two variables to allow model convergence, without critically altering the adequacy of the model interpretation. The log transformation implies the assumption of non-linear effects (the difference from 100 to 200 vehicles per day has a larger effect than from 5100 to 5200).

Prior to the model selection process, we conducted model diagnostics using histograms, fitted versus observed residual plots and Q–Q plots for linear and negative binomial GLMs, and residual plots for GLMs with beta regression (Cribari-Neto & Zeileis, 2010; base R and 'DHARMa' package: Hartig & Lohse, 2022). We tested count data for overdispersion (package 'performance': Lüdecke et al., 2021) and then fitted models with normal or negative binomial error distributions (all non-normally distributed count data were overdispersed; see Table S5 for details, package 'MASS'). For the data on evenness and relative abundance of grasses, we fitted beta regression models, which are appropriate for data restricted in the interval between 0 and 1 (Cribari-Neto & Zeileis, 2010; package 'betareg': Zeileis et al., 2021).

We used a backwards model selection to identify if either flower density or plant richness is a better explanatory variable in any of the six wild bee and butterfly models and to detect if the proposed potential interaction effects or rather additive effects provide a better fit for our data. Potential interactions included mowing regime × road verge classification (for all models), traffic intensity × road verge width as well as traffic intensity × either flower density or plant richness (wild bee and butterfly models only). We chose the model with the lowest Akaike information criterion for small sample sizes (AICc; package 'MuMIn': Bartoń, 2022; Table S5).

3 | RESULTS

3.1 | Plants

We identified 217 plant species (Table S6), with the species richness per study site varying between 20 and 55 species. Flower density varied between 157 and 1276 flower units within the 200 m transects (corresponding to log-transformed values of 5.06 and 7.15; Table S2). Road verges under the biodiversity-targeted mowing regime (mowed once in late summer) had on average a much higher flower density than those mowed in early summer and autumn, but also have been mowed only after our study period while the early summer mowing took place during our study period. Road verges have a predicted mean of 638 flower units when mowed in late summer and 429 when mowed in early summer ($p = 0.02$; Figure 2; for all model results, see Table S7). Flower density and plant species richness did not differ between valuable or regular road verges. Furthermore, plant species richness did not show any relationship with mowing regime or road verge width. At the community level, we found differences in the composition between regular road verges mowed only in late summer and valuable road verges mowed both in early summer and autumn, but not between the other pairwise comparisons of road verge categories ($p = 0.01$; Figure S3; Table S8). We found no difference in the relative abundance of grasses (Figure S4).

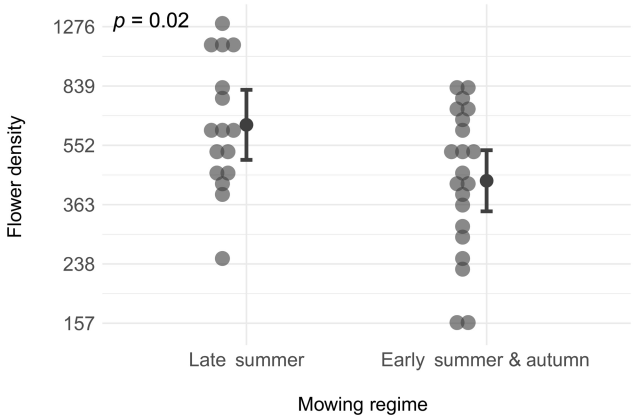

FIGURE 2 Differences in flower density (total abundance in three visits divided by width of road verge) in road verges in southern Sweden ($n=37$) depending on mowing regime. Only the early summer mowing occurred during our study period. Flower density was log-transformed for the analyses. Dots represent raw data, dots with error bars represent the predicted mean value and 95% confidence intervals.

3.2 | Butterflies

In total, we observed 1990 butterflies of 32 species (Table S9). Butterfly abundance and species richness was predicted by an interaction between mowing regime and road verge classification. In valuable road verges mowed in late summer, that is not at all during our study period, we found an estimated mean abundance almost twice as high as in regular road verges mowed in late summer (85 vs. 46; $p<0.02$; Figure 3a; for all model results, see Table S7). Also, species richness was higher in valuable than in regular road verges that were mowed in late summer, with an average of 10 species compared to 6 in regular road verges ($p=0.02$; Figure 3b).

Butterfly abundance was additionally predicted by an interaction between road verge width and traffic intensity. Along roads with high traffic, butterfly abundance was much lower in narrow than in wide road verges ($p<0.01$; Figure 3c). We also found a positive relationship between butterfly species richness and road verge width (even though the transect width remained the same), with an estimated mean richness of 7 for 3.6 m width and 9 for 8.5 m width ($p<0.01$; Figure 3d). Furthermore, we found an interaction between traffic intensity and plant species richness; butterfly species richness increased with plant species richness, but only along roads with lower traffic intensities ($p<0.01$; Figure 3e). We found no significant effects of our studied predictors on community evenness of butterflies.

3.3 | Wild bees

We observed 1682 wild bees of 76 species (Table S10). Abundance and species richness of wild bees increased with increasing flower density ($p<0.01$ and $p=0.04$, respectively; Figure 4a,b; for all model results, see Table S7), and were higher in valuable than in regular road verges ($p<0.01$ for both; Figure 4e,f). For example, with an increase in flower density from 240 to 699, wild bee abundance is estimated to double from 24 to 48, and species richness to increase from almost 8 to 11. Similar to butterfly abundance, the final models for wild bee abundance and species richness included an interaction between traffic intensity and width of the road verge. Wild bee abundance and species richness declined with increasing traffic intensity in narrower road verges, but wider verges could apparently mitigate this negative effect of traffic ($p<0.001$ and $p=0.05$, respectively; Figure 4c,d).

The best model for wild bee evenness included interactions between traffic intensity and road verge width, and between traffic intensity and plant species richness (Figure S5). Community evenness was relatively high throughout. Along busy roads, wild bee communities were more even in narrower than in wider road verges ($p=0.02$; for all model results, see Table S7). Furthermore, in road verges with low plant species richness, wild bee evenness increased with traffic intensity, whereas it decreased with traffic intensity in road verges with high plant species richness ($p<0.01$). Therefore, evenness was highest if traffic intensity was low and plant species richness high or if traffic intensity was high and plant species richness low.

4 | DISCUSSION

We found clear negative effects of traffic on wild bee and butterfly communities in road verge habitats. While flower-visiting insects benefited from increasing density of flowers and plant species richness, these effects were reduced along roads with high traffic intensity. This was especially the case in narrow road verges, where the negative effects of traffic were particularly pronounced.

4.1 | Limited effects of biodiversity-targeted management

Groups of flower-visiting insects have different needs and may therefore require specific management. In our study, abundance and species richness of wild bees were predicted by flower density, and butterfly abundance and richness by the combination of mowing regime and road verge classifications. For plants, a longer time after altering the management than in our study is necessary to notice benefits of and draw conclusions about different mowing regimes (Ladouceur et al., 2023).

4.1.1 | Butterflies and vascular plants

Reduced mowing frequency has previously been shown to benefit butterfly abundance in road verges (Halbritter et al., 2015; Saarinen et al., 2005; Valtonen et al., 2006). We only observed this in road verges classified as valuable. This result seems to be caused by a

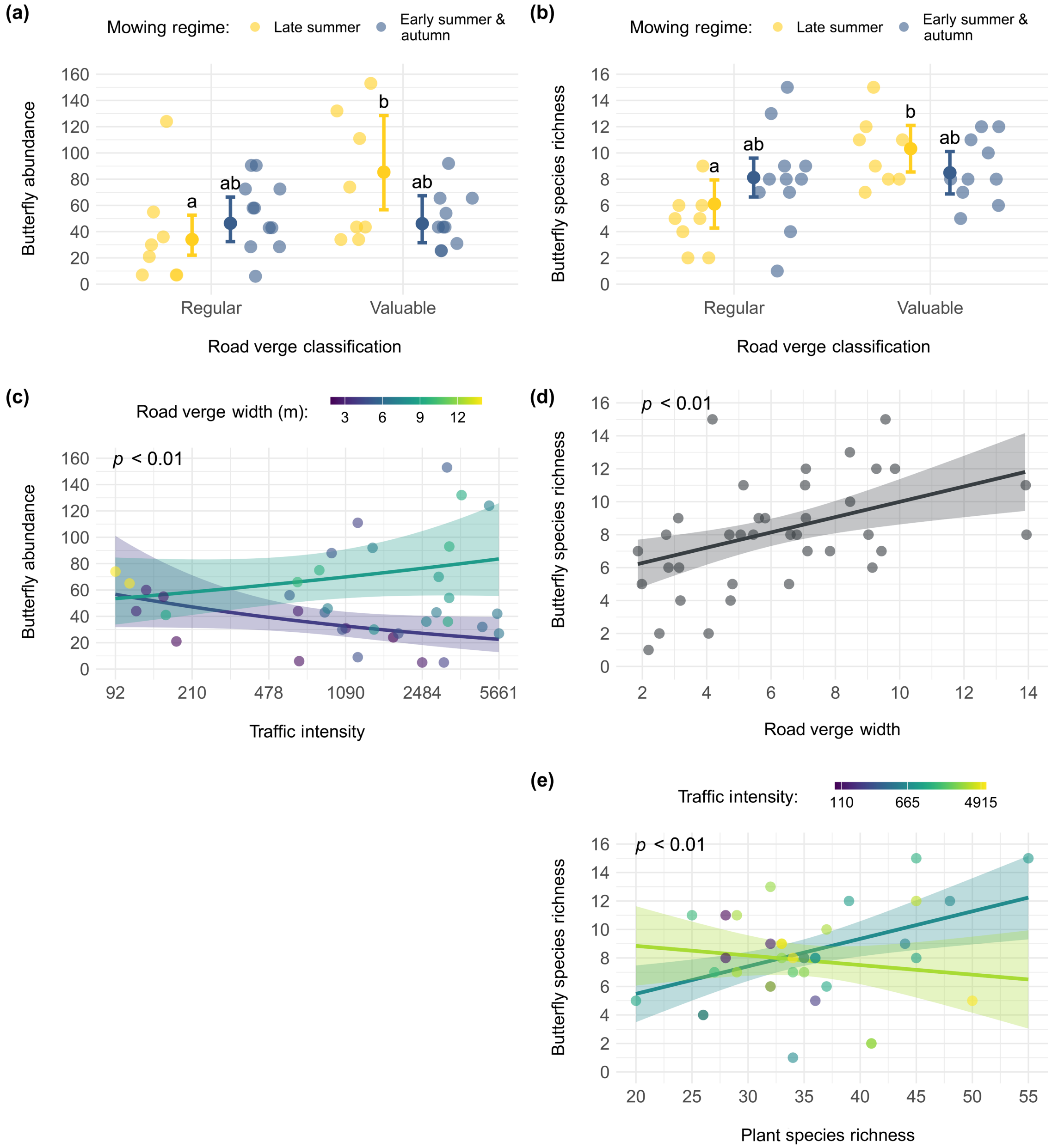

FIGURE 3 Predicted effects on butterfly abundance (left) and richness (right), depending on (a,b) the interaction between mowing regime and road verge classification, (c) the interaction between road verge width and traffic intensity for butterfly abundance, (d) the road verge width as additive effect for butterfly species richness, and (e) the interaction between traffic intensity and plant species richness. Traffic intensity was log-transformed for the analyses. Dots represent raw data, lines and 95% confidence intervals in plots c and e and dots with error bars in plots (a, b) represent predicted values and 95% confidence intervals. Colours in plot (c) correspond to values illustrated in the colour gradient of road verge width, with colours of the lines and 95% confidence intervals selected to reflect the median of the narrower and wider half of all road verges. Colours in plot (e) correspond to values illustrated in the colour gradient of traffic intensity, with colours of the lines and 95% confidence intervals selected to reflect the median of the lower and higher half of all traffic intensities along road verges.

larger variation in butterfly abundance in valuable than in regular road verges that were mowed only in late summer. A potential explanation is differences in the plant community composition, which in turn affect butterfly diversity. We found no difference in plant species richness, no difference in the relative occurrence of grasses between the four road verge categories and mostly overlapping plant community compositions between the four road verge categories, except for between regular road verges mowed only in late summer and valuable road verges mowed both in early summer and autumn. However, butterfly abundance and species richness did not differ between these two road verge categories. We did not expect to see an effect of mowing regime on plant communities. Our regular verges with late summer mowing underwent that mowing regime for the first time during our study, while the duration of late summer mowing in valuable road verges is varied and unknown (but most likely only a few years). On the other hand, plant communities take

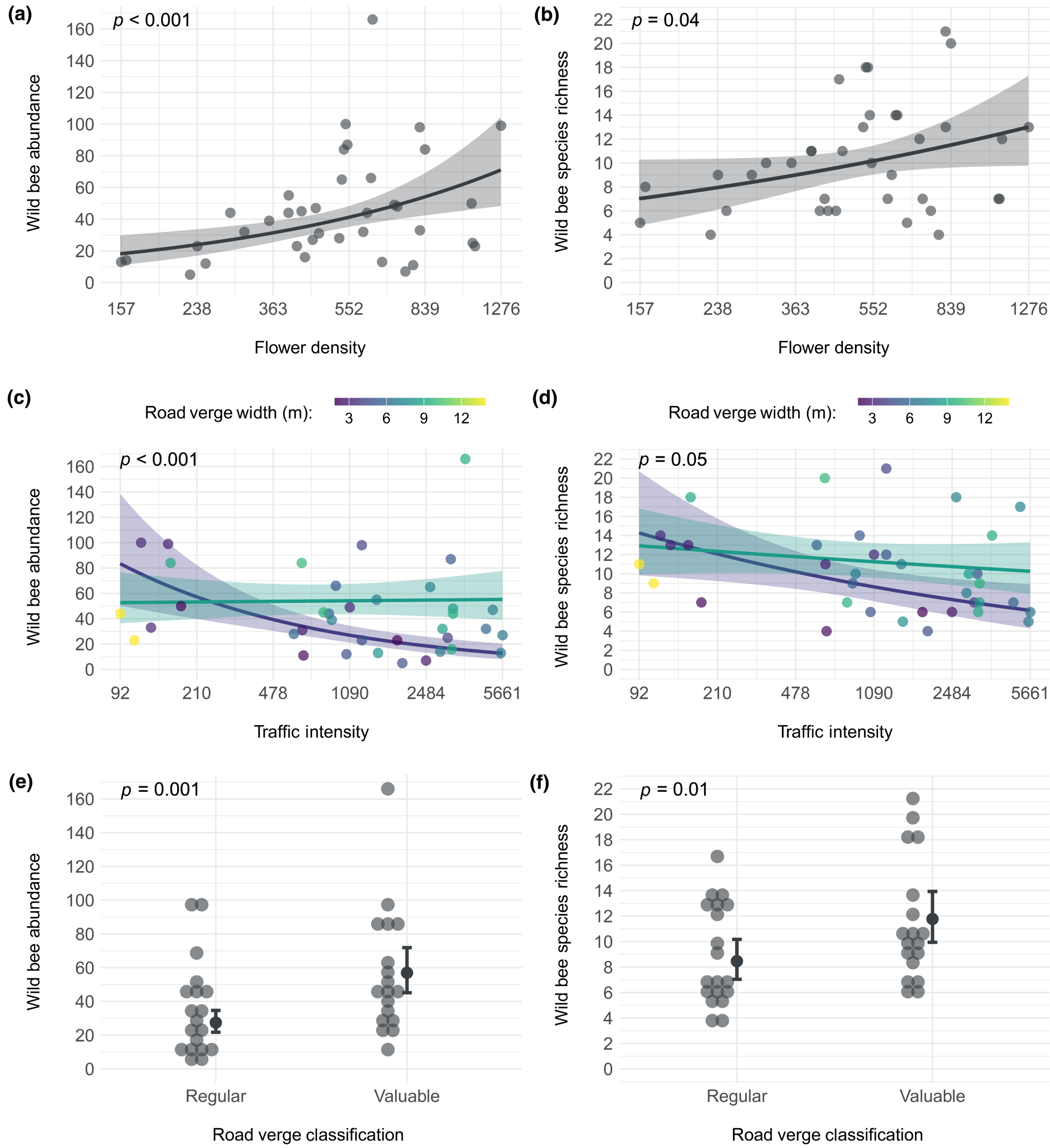

FIGURE 4 Predicted effects on wild bee abundance (left) and species richness (right) in (a, b) relation to flower density, (c, d) the interaction of traffic intensity and (e, f) road verge width and the road verge classification. Traffic intensity and flower density were log-transformed for the analyses. Dots represent raw data, lines and 95% confidence intervals in plots (a–d) and dots with error bars in plots (e, f) represent predicted effects. Colours in plots (c, d) correspond to values illustrated in the colour gradient of road verge width, with colours of the lines and 95% confidence intervals selected to reflect the median of the narrower and wider half of all road verges.

several decades to respond to altered management (cf. Ladouceur et al., 2023). Thus, we focussed on plant richness as explanatory variable for the butterfly diversity.

We suggest that the different responses of butterfly communities to mowing in valuable and regular road verges are likely due to other factors that we did not measure, but that are directly or indirectly incorporated in the Transport Administration's selection criteria for valuable road verges (Lindqvist, 2018). Due to these criteria, valuable road verges are more likely to be similar to semi-natural grasslands than regular road verges. Land-use history can affect biodiversity in road verges (Auffret & Lindgren, 2020; Horstmann et al., 2023), with older road verges often being remnants of historical grasslands. Remnant grassland habitats generally have low nutrient values compared to modern grasslands, promoting diversity (Plue & Baeten, 2021). For relatively nutrient-rich regular road verges, infrequent mowing may result in domination of nitrophilous plants and fewer nectar resources for butterflies (Erhardt, 1985; Jakobsson et al., 2018; Noordijk et al., 2009).

4.1.2 | Wild bees and flower density

While the mowing regime did not directly impact wild bees, the flower density was higher when mowing occurred in late summer compared to in early summer and autumn. Flower density, in turn, was positively correlated with both wild bee abundance and species richness. Mowing road verges during the flowering season can result in fewer pollen and nectar resources in the road verge, leading to a subsequent decline in flower-visiting insects (Phillips et al., 2019). Indeed, only verges mowed in early summer and autumn were actually mown during the course of our field study, so the observed patterns were most likely due to a reduction of the flower cover after mowing (Figure S6). On the other hand, subsequent regrowth can offer important feeding resources later in the season (Noordijk et al., 2009). Wild bee abundance and species richness was generally higher in road verges classified as valuable than in regular ones. Again, due to the selection criteria of the Swedish Transport Administration, valuable road verges are more likely to be similar to semi-natural grasslands than regular road verges. This suggests that valuable road verges on average offer more feeding or nesting resources for bees, and hence this classification works well for indicating conservation value for wild bees.

4.2 | High impact of traffic on flower-visiting insects

4.2.1 | Traffic intensity alters the relationship of plants and butterflies

We show that traffic has a substantial negative influence on butterfly diversity in road verges, and even eliminates the positive association with plant richness. Generally, a high diversity of plants correlates with a high diversity of flower-visiting insects (e.g. Biesmeijer et al., 2006; Fründ et al., 2010) and this is also the case for road verge communities (Horstmann et al., 2023). Accordingly, we found a positive relationship between plant and butterfly species richness. Alarmingly however, this was only the case along roads with a low traffic intensity, whereas high traffic intensity limited the positive effect of plant richness. This is particularly concerning because high traffic in our study system was fairly moderate in comparison to studies in other countries (e.g. see Keilsohn et al., 2018; Phillips et al., 2019). Some butterfly species might not tolerate the conditions created through higher traffic intensities. These butterflies may avoid such road verges as foraging or egg-laying habitats, or alternatively, the high mortality risk associated with the traffic results in these road verges becoming sink habitats. Butterfly (Ries et al., 2001; Skórka et al., 2013, 2015) and bumblebee queen (Dániel-Ferreira et al., 2022) mortality has been shown to increase with traffic intensity, while at the same time fewer butterflies cross the roads if the road verge habitat quality is high (Ries et al., 2001; Skórka et al., 2013, 2015). For road verges with a diverse plant community, high traffic intensities might therefore limit the conservation potential for flower-visiting insects.

4.2.2 | Wide road verges can buffer traffic effects

Higher traffic intensity strongly reduced the abundance of wild bees and butterflies in narrow road verges, but this negative effect was neutralized in wider road verges. Our results also suggest that for wild bees, traffic does not only influence abundance but also species richness. Furthermore, in narrow road verges along busy roads there was a more even abundance distribution among the few species that were present than in wider road verges, but their abundance overall was low. Traffic might impact some species more than others. Species that are more mobile might be subjected to higher traffic mortalities (Halbritter et al., 2015; Munguira & Thomas, 1992), while species that are less mobile might suffer more from exposure to pollution (Phillips et al., 2019). Due to the combination of abundant pollen and nectar resources and the proximity to traffic, road verges have been discussed as a potential ecological trap, whereby species are attracted to road verge habitats associated with a lower fitness or higher mortality (Battin, 2004; Gardiner et al., 2018; Keilsohn et al., 2018).

Understandably, wider road verges provide more habitat than narrower road verges, but it is also the case that a larger proportion of narrower road verge habitat is disturbed by traffic. Thus, narrow verges along busy roads might be an unattractive habitat due to turbulence from the passing traffic (Dargas et al., 2016). A study found that 84% of flower-visiting insects of a specific flower stopped foraging, likely due to turbulence from passing vehicles (Dargas et al., 2016). We show that wider verges buffer the negative effect of traffic, possibly allowing flower-visiting insects to use the resources directly adjacent to the road as long as they can retreat to the less disturbed outer verge. Our results are in line with other studies that show that wider road verges often support a higher butterfly abundance and richness (Munguira & Thomas, 1992; Skórka et al., 2013).

Besides disturbance, the area directly adjacent to the road surface may be subjected to higher levels of pollution and nutrient inflow from exhaust fumes, affecting plant communities and flower-visiting insects; Phillips et al. (2019) found that flower-visiting insect abundance in road verges increased with longer transect distance from a road. In our study, we always conducted the transect walks adjacent to the road, regardless of how wide the verge was. This means that in wider verges, the abundance of flower-visiting insects was higher even adjacent to the road, irrespective of the traffic intensity.

4.3 | Implications for biodiversity conservation

Our study highlights the conservation potential, but also the limitations, of road verges for flower-visiting insects. The positive relationships between flower density and wild bee diversity and between plant species richness and butterfly diversity highlight the critical role of diverse plant communities and abundant floral resources in road verges for communities of flower-visiting insects. However, mowing only once and in late summer does not appear to be a universally successful biodiversity-targeted management for flower-visiting insects compared to twice, in early summer and autumn. Instead, the effectiveness of the mowing regime might depend on productivity and prevalent plant communities (also see Jakobsson et al., 2018; Noordijk et al., 2009). We therefore recommend implementing targeted management actions that enhance plant species richness and flower resource availability, according to road verge characteristics such as verge width and soil type. Importantly, we show that not all road verges, particularly those with high traffic intensity, are suitable for interventions focussed on flower-visiting insects. We recommend focusing on areas with lower traffic intensities and on wider road verges, which in particular offer potential for enhancing flower-visiting insect habitats (also found by Phillips et al., 2019). Our findings can provide a roadmap for optimizing management to support flower-visiting insects and enhance biodiversity along roads.

AUTHOR CONTRIBUTIONS

Svenja Horstmann: Conceptualization (supporting); formal analysis (lead); investigation (lead); methodology (equal); data curation (lead); visualization (lead); writing—original draft preparation (lead); review and editing (lead). Alistair G. Auffret: Formal analyses (supporting); investigation (supporting); methodology (supporting); writing—review and editing (equal). Lina Herbertsson: methodology (supporting); writing—review and editing (equal). Björn K. Klatt: methodology (supporting); writing—review and editing (equal). Sophie Müller: investigation (supporting); writing—review and editing (equal). Erik Öckinger: Conceptualization (lead); formal analyses (supporting); funding acquisition (lead); methodology (equal); writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

Alistair G. Auffret is an Associate Editor of Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper. The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Swedish National Data Service (SND): https://doi.org/10.5878/1vk8-tp84 (Horstmann et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Each dot represents one of in total 37 road verges, showing each respective traffic intensity value across the combinations of road verge classification and vegetation management.

Figure S2. Each dot represents one of in total 37 road verges, showing each respective mean width across the combinations of road verge classification and vegetation management.

Figure S3. Non-metric multidimensional scaling (NMDS) analysis for vascular plants (stress = 0.17, dimensions = 3), in the four road verge categories. There are no evident differences in the plant species composition between all pairwise combinations except for between regular road verges mowed in late summer (yellow) and valuable road verges mowed in early summer and autumn (green) (permutational MANOVA, $p = 0.01$).

Figure S4. Differences in the relative occurrence of grasses depending on road verge classification round and mowing regime. Same letters indicate no statistically significant difference. Dots represent raw data, dots with error bars represent predicted values and 95% confidence intervals.

Figure S5. Wild bee evenness depending on traffic intensity, moderated by (A) vascular plant richness and (B) road verge width. Traffic intensity was log-transformed for analyses and the values from 5 to 8 correspond to 148, 403, 1097 and 2981 cars per day, respectively.

Figure S6. Differences in flower density depending on observation round and mowing regime. Flower density was log-transformed for analyses. Different letters indicate a statistically significant difference ($p < 0.05$). Dots represent raw data, dots with error bars represent predicted values and 95% confidence intervals.

Table S1. Reclassification of land cover categories used in the Swedish National Land Cover Database (NMD, Nationella marktäckedata) to calculate the proportional land cover of forest and arable land around the study sites.

Table S2. Information about the location and all response and predictor variables for the final 37 road verge sites included in the analyses, as well as the cover of arable land and forest, which was used to select for the study sites. For the mowing regime, "2" refers to mowing in early summer and autumn and "1" to mowing in late summer only.

Table S3. Pairwise correlation of potential predictors for the generalized linear models.

Table S4. Moran's I autocorrelation coefficient, with $p < 0.05$ indicating spatial autocorrelation (in bold).

Table S5. Selection of the final predictors for every model, including tests of two-way interaction effect between selected covariates, using the Akaike Information Criterion for small sample sizes (AICc).

Table S6. List of all plant species included in this study.

Table S7. Results of fitted models. For linear models, the t value is provided, while for negative binomial and beta-regression models the *z*-value is provided. Statistically significant *p* values

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($p < 0.05$) and respective predictor variables are indicated in bold.

Table S8. Results of permutational MANOVA for the pairwise comparisons of plant community composition between the four road verge categories.

Table S9. List of all butterfly and burnet moth species included in this study.

Table S10. List of all wild bee species included in this study.

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