# Effects of traffic intensity and road verge characteristics on moth abundance and mortality along roads

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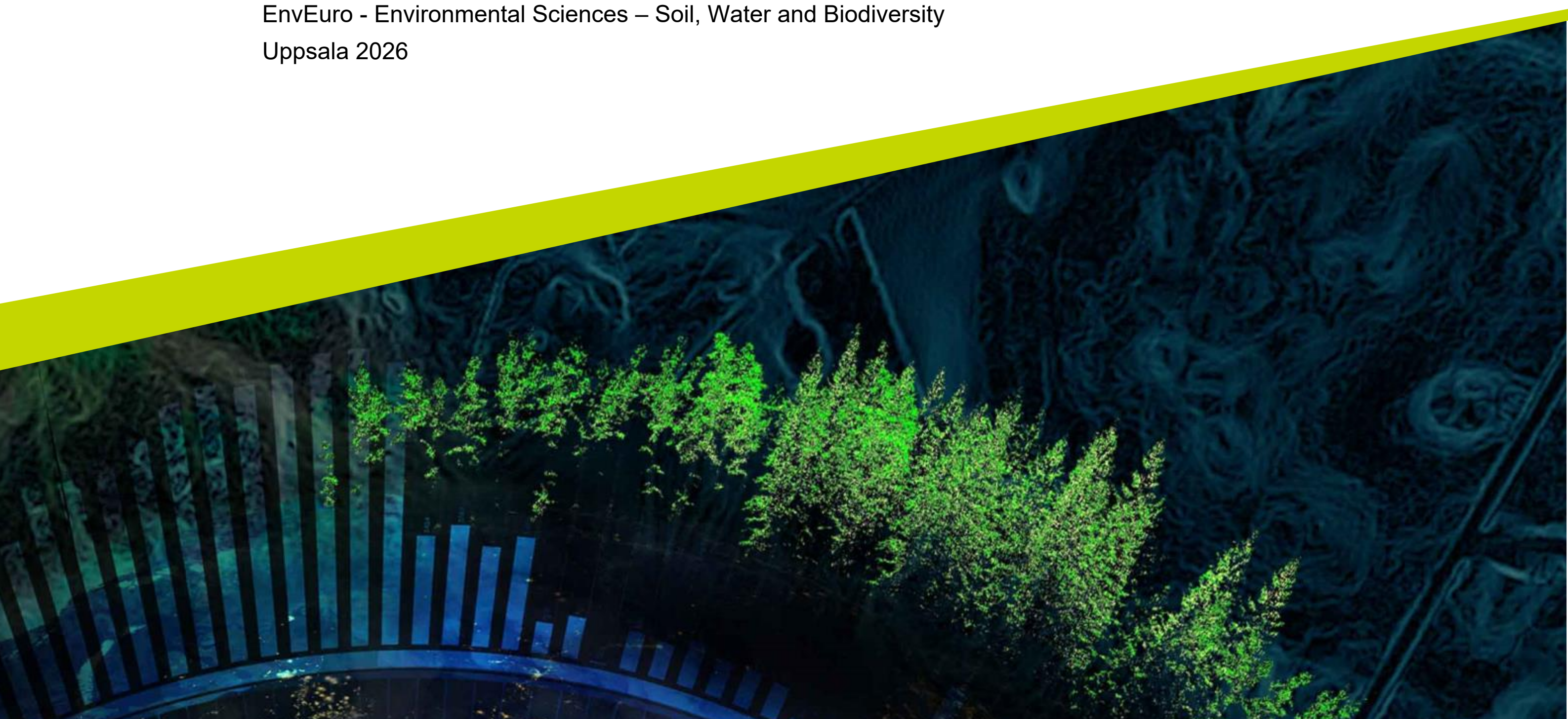

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Anna Magdalena Grubelnik

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# Abstract

Road infrastructure is an integral part of human-dominated landscapes worldwide and is partially responsible for the global decline in insects through vehicle collisions and acts as a barrier for dispersal. Road verges, however, are gaining attention as potential insect conservation sites due to their potential similarity to semi-natural grasslands. However, most research exploring this conservation dilemma has focused on diurnal insects, particularly butterflies. Since 60 % of all invertebrates and 96 % of Lepidoptera are nocturnal, insects like moths, and their mortality in road traffic are a topic worthy of exploring. Thus, this study explores the effects of traffic intensity and road verge characteristics on moth abundance and mortality along 20 roads in Sweden. Mowing management emerged as the strongest driver of moth abundance, with unmown verges supporting on average 2.56 times more moths than mown verges. Moth abundance also increased significantly across the summer season from June to August. Unlike butterflies, moth abundance was not significantly influenced by flowering plant species diversity, potentially reflecting differing ecological traits between diurnal and nocturnal Lepidoptera. While higher road verge abundance was associated with increased mortality, traffic intensity was negatively associated with moth road mortality. This may be explained by a depletion mechanism whereby highly trafficked roads support fewer moths in adjacent verges. These findings raise the question of whether well-managed road verges could act as ecological traps for moths by attracting individuals into a zone of high collision risk. Even though research on butterflies and bumblebees suggests that high-quality road verges reduce the mortality risk of insects, further research dedicated to moths is necessary. Therefore, I suggest focusing conservation measures such as suspended mowing on road verges adjacent to low-traffic roads.

*Keywords:* moths, Lepidoptera, road mortality, road verges, traffic intensity, mowing management, insect conservation, Sweden

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# 1. Introduction

Within the deterioration of our global biodiversity and ecosystem functions (IPBES 2019), insect populations are steadily declining on a global (Sánchez-Bayo & Wyckhuys 2019; Cardoso et al. 2020) and regional scale (e.g. , Hallmann et al. 2017; Powney et al. 2019). The loss of insect biodiversity and biomass is illustrated by significant regional declines which have been documented, e.g., in Britain (Powney et al. 2019) , Germany (Hallmann et al. 2017; Seibold et al. 2019), and the United States of America (Dalton et al. 2023). For instance, Hallmann et al. (2017) found a decline in average airborne insect biomass of 76 % in 27 years for protected nature areas in Germany – a result that illustrates the potential magnitude of the decline in insect populations that can eventually lead to the collapse of terrestrial and freshwater ecosystems (Goulson 2019).

Insects make up the majority of all known animal species and are intricately involved in all terrestrial and freshwater food webs and are responsible for the pollination of about 87 % of all plant species (Goulson 2019). Lepidoptera are one of the most species-rich insect orders, comprising around 158,000 known species and an estimated global diversity of 300,000 to 400,000 species, and are present in a broad range of habitats (Kristensen et al. 2007; Nieukerken et al. 2011; Stork 2018). Generally, moths are a lot more species-rich than butterflies, with only about 20,000 out of the estimated 158,000 lepidopterans being butterflies (Kristensen et al. 2007; Nieukerken et al. 2011).

Long-term declines of moth populations have been documented in some parts of Europe. In Great Britain, it has been reported that 34 % of the 390 most common macro-moths had showed significant declines between 1970 and 2016, with a 25 % decline in a species-abundance indicator (Hayhow et al. 2019; Randle et al. 2019). Similar decline rates have also been observed in the Netherlands (Groenendijk & Ellis 2011; Hallmann et al. 2020).

A decline in moths can affect the provision of ecosystem services such as pollination and natural pest control (Sánchez-Bayo & Wyckhuys 2019). Moths constitute the majority of nocturnal pollinators, and their significance and role in pollination have been understudied and underestimated (Macgregor et al. 2014; Macgregor & Scott-Brown 2020; Buxton et al. 2022). Moth pollination is important for a variety of plant species in different ecosystems (Macgregor et al. 2014). Moreover, research highlights the richness of moth-flower interactions at the community level and the potential of moths to substantially increase the pollination success in generalist flowers (Macgregor & Scott-Brown 2020). Nocturnal pollination has also been found to supplement diurnal pollination activity (Jadhav et al. 2011). Pollinator species diversity determines the quality, magnitude and resilience of the pollination ecosystem service (Vasiliev & Greenwood 2020), which is why a high diversity of pollinators can, e.g., buffer the impact of environmental changes on this ecosystem service (Brittain et al. 2013). Thus, it is important to include nocturnal pollinators like moths in pollinator conservation strategies.

Long-term decline in moth populations may, however, not only affect pollination but also have a variety of consequences for global ecosystems. Moths are a significant component of food webs in all terrestrial ecosystems and contribute to network complexity, interaction diversity and associated ecosystem stability. Thus, their decline will affect these ecosystem functions and trigger cascades across trophic webs (Wagner et al. 2021). Factors causing the continuous global decline of moth populations include habitat loss, degradation and fragmentation, agricultural intensification, deforestation, urbanisation, chemical pollution, light pollution, climate change and non-native species (Fox 2013; Wagner 2020). Due to their nocturnality and their tendency towards phototaxis (flight to light ), light pollution is a threat to moths in particular (van Langevelde et al. 2017). Artificial night-time lighting has been shown to contribute significantly to long-term changes in moth populations (Wilson et al. 2018). Adult moths are known to be vulnerable to artificial light as it can suppress the activity of adult moths, disrupt adult feeding behaviour, and have negative impacts on reproduction (van Langevelde et al. 2017; Boyes et al. 2020; Briolat et al. 2026).

Road infrastructure is an integral part of human-dominated landscapes worldwide and is among the leading causes of habitat loss, degradation and fragmentation (Keret et al. 2015). Studies have shown that roads with high traffic intensity decrease insect abundance in surrounding areas (Baxter-Gilbert et al. 2015; Keilsohn et al. 2018; Martin et al. 2018; Dániel-Ferreira et al. 2022). Baxter-Gilbert et al. (2015) estimated that road mortality may potentially be responsible for billions of pollinating insect deaths annually. Roads cause insect mortality through collisions with vehicles and can act as barriers for dispersal (Muñoz et al. 2015). Moreover, roads may act as barriers for chemical communication crucial for mate finding and thus, affect sexual selection and insect population viability (Keret et al. 2015). These risks and disturbances caused by traffic are relevant across a wide range of road types and traffic volumes (Phillips et al. 2020).

Conversely, road verges harbouring floral and vegetation resources may also act as a valuable habitat for insects in an otherwise increasingly developed, homogenous environment, as well as undeveloped, but intensively used environment (e.g., agricultural land) (Phillips et al. 2019; Meinzen et al. 2024). Road verges can be defined as “vegetated strips, generally consisting of grassland, shrubland, woodland or forest, which often form distinctly managed borders that separate roads from adjacent land” (Phillips et al. 2020:1). Vegetation in road verges often provides feeding and reproductive opportunities for pollinators including floral resources and larval hostplants (Phillips et al. 2020) and has been shown to facilitate similar or greater abundance and species richness of flowers and pollinators compared to surrounding agricultural fields, woodlands or forests (Phillips et al. 2019; 2020). They however, only show a part of the biodiversity of grassland species found in traditionally managed semi-natural grasslands (Dániel-Ferreira et al. 2023). Road verge width and flowering plant species richness have been shown to positively affect butterfly abundance in road verges (Skórka et al. 2013a). Moreover, mowing road verges has been shown to reduce pollinator abundance by reducing the availability of resources such as flowering plants (Phillips et al. 2019).

Since insects usually have low or moderate dispersal abilities, most road-killed moths are likely to be individuals living on road verges or in their vicinity (Skórka et al. 2013a). A higher abundance and thus a higher population density of moths in the road verges might further increase the chance that a moth will emigrate (Nieminen et al. 1999; Régnière & Nealis 2019) and thus cross the adjacent road and be susceptible to vehicle collision.

The majority of studies investigating the negative impact of roads and the potential of road verges as habitats have focused on diurnal insects, oftentimes butterflies (e.g., Skórka et al. 2013; Martin et al. 2018; Kantola et al. 2019; Dániel-Ferreira et al. 2022; Horstmann et al. 2024). With 60 % of invertebrates being nocturnal (Hölker et al. 2010), including about 96 % of all Lepidoptera (Ahrné et al. 2026), investigating the impacts of roads and traffic on nocturnal insects is of importance. This suggests a research gap in the literature concerning the road mortality of nocturnal moths and how road verge characteristics like plant species diversity can influence their mortality in traffic, as well as their abundance in road verges. Moreover, moths represent a far more diverse group than butterflies, and studying them may facilitate a more comprehensive understanding of the drivers of insect decline and its consequences for other organisms, communities, and ecosystem functioning (Fox 2013).

To address this research gap, I investigated the effects of traffic intensity and flowering plant species diversity on moth abundance in road verges and on moth road mortality across 20 locations in Sweden.

First, I examined the abundance of moths on road verges and its influencing factors. I hypothesized that *(H1) Moth abundance in road verges is positively related to flowering plant species diversity and road verge width*; *(H2) Mowing negatively affects moth abundance in road verges;* and *(H3) The number of moths killed by traffic is positively related to traffic intensity and to the abundance of moths in the road verges.*

# 2. Methods

This thesis is based upon data that was collected during a study conducted by Juliana Dániel-Ferreira (see Dániel-Ferreira et al. 2021; 2022). The following paragraphs provide the methodological background for the full study, covering the study design, site selection and moth survey conducted by Juliana Dániel-Ferreira, as well as my own contributions, which comprised the identification of moths on sticky traps and data analysis.

## 2.1 Study organism

Moths as well as butterflies, belong to the order Lepidoptera within the class Insecta. Butterflies are placed as a discrete group of families towards the middle of the moths, suggesting that they evolved later as a branch within the Lepidoptera order rather than early in its history. Thus, the separation is somewhat artificial (Townsend et al. 2019).

Moths are divided into macro- and micro-moths. This differentiation is more a matter of convention and practice rather than one rooted in taxonomy (Townsend et al. 2019). Families of moths that tend to feature smaller species are usually characterized as micro-moths, making up about three-quarters of all lepidopterans (Kristensen et al. 2007), while families with larger species are characterized as macro-moths. Micro-moths usually have a forewing length of 10 mm or less, but there is also an overlap in size with macro-moths (Sterling et al. 2012; Townsend et al. 2019).

Moths reproduce by laying eggs on host plants that hatch into caterpillars (also often called larvae). Larvae mostly feed on plant material, mainly leaves. Other food sources include flowers, fruit, roots, stems, or rootstocks. Adults emerge from the pupa formed during the larval stage. Male moths mainly locate females for mating by following pheromones released by unmated females. Depending on the species, females lay between 100 and 1000 eggs or more, which are usually laid on larval food plants. The adult stage is also important for dispersal, with some individuals migrating long distances and others moving only a few hundred meters. The adult lifespan varies from a few days to two or three weeks and some moths even overwinter as adults (Townsend et al. 2019).

To understand which factors attract moths towards road verges, it is important to also look at adult feeding behaviour. Many moth species are generalist nectarivores as adults (Macgregor & Scott-Brown 2020). They feed on nectar similar to butterflies with a tube-like tongue called proboscis (Townsend et al. 2019). Some moth families are important nocturnal pollinators, including *Sphingidae, Noctuidae, Geometridae, Erebidae,* and *Pyralidae* (Winfree et al. 2011; LeCroy et al. 2012; Hahn & Brühl 2016; Townsend et al. 2019). Especially members of the family *Noctuidae* stand out in their function as pollinators. For instance, Devoto et al. (2011) identified all key flower-visiting moths carrying significant pollen loads in their study as noctuids. There is also a number of micro-moth species involved in pollination, belonging to families such as *Crambidae, Pterophoridae, Prodoxidae*, or *Zygaenidae* (Hahn & Brühl 2016). However, many species have non-feeding adults that lack a proboscis. They solely rely on the nutrients they accumulated as larvae and focus solely on reproduction (Saarinen et al. 2005; Townsend et al. 2019)

Within nocturnal pollination, flowering plants employ mechanisms that attract moths, which in turn use floral cues to efficiently locate and compete for resources (Macgregor & Scott-Brown 2020). One of these mechanisms is floral scent, which is important in many nocturnal plant-pollinator mutualisms, and floral volatile chemistry has been characterized for different plant taxa pollinated by moths (Knudsen & Tollsten 1993; Jürgens et al. 2002; Macgregor & Scott-Brown 2020). Another important mechanism for detecting floral resources is night vision. Fully nocturnal taxa, such as moths, typically have superposition compound eyes with complex adaptations to improve light and movement sensitivity in low light conditions (Sterling et al. 2012; Macgregor & Scott-Brown 2020).

Another ecological trait of moths that should be considered when investigating their mortality in road traffic is their disturbance by artificial light sources. Phototaxis (flight to light) is a trait present in the majority of nocturnal moths (Sterling et al. 2012; Townsend et al. 2019; Boyes et al. 2020). It has been shown that nocturnal insects, contrary to common perception, are not “attracted” to artificial light. Rather than flying towards light, insects orient their dorsal side towards the brightest point in their visual field to maintain stable flight. Under natural conditions, this works reliably, but near artificial light sources. this mechanism causes continuous corrective steering, trapping the insects in an erratic orbital flight (Fabian et al. 2024).

Since adult moths are known to be vulnerable to artificial light (van Langevelde et al. 2017; Boyes et al. 2020; Briolat et al. 2026) and the roads examined in this study were rather rural without street lamps, the main source of direct light pollution that has to be considered is vehicle headlights. They can be categorized as pulsed artificial light at night (pALAN) that is unpredictable, intense, and extends into previously dark areas (Phillips et al. 2021b; Fabusova et al. 2024).

## 2.2 Study design and site selection

To aid with site selection, the Swedish National Road Database (*Nationell Vägdatabas* n.d.) was used. This database provides diverse information about public roads and road verges in Sweden. The Swedish Transport Administration performs regular surveys throughout the country to identify road verges of high conservation value (e.g., that have a higher-than-average number of plant species, provide habitat for threatened plant or insect species or contain indicator species) that provide an important ecological resource or promote species' dispersal and landscape connectivity (Lindqvist 2012). Road verges that fulfil these criteria are then managed differently from road verges that do not fulfil them. Usually, these road verges are only mown once by the end of the season whereas grass-dominated road verges are mown up to three times. This information was used to select species-rich and species-poor sites (hereafter referred to as high and low plants species diversity).

The flowering plant diversity of the selected road verges was confirmed on site before conducting the study. Flowering plants were surveyed on each side of the road by identifying all flowering forb species (excluding grasses and sedges) within six 1 $m^2$ plots. The plots were situated 200 m apart, and the first plot was placed where the Swedish Transport Administration identified the beginning of the area of high conservation value. This sampling confirmed that species-rich road verges indeed had a higher number of flowering plants than those with low plant species diversity. Road verges with high plant species diversity had, on average, a 29 % higher flower density (Dániel-Ferreira et al. 2022). Low flowering plant species diversity sites were dominated by grasses, while high flowering plant species diversity sites had more flowering forb species.

During site selection, it was ensured that the sites were of similar road width (between 5.7 and 7 m) and speed limit (70 or 80 km/h) to avoid possible bias in the data analysis. The verge width of the different sites was estimated by selecting a 1 km fragment of the road and measuring the verge width five times (every 200 m) on each side.

The 20 road sites showed similar gradients in traffic intensity and either low or high plant species diversity on the adjacent road verges. The first half of the selected sites had a gradient from low (158 vehicles/day) to high numbers of vehicles per day on the road (6169 vehicles/day) and road verges with low plant species diversity. The other 10 sites had a similar gradient in traffic intensity (125 to 6356 vehicles/day) to allow comparison with the first half and road verges with high plant species diversity (Figure 1a).

The term *plant species diversity* will be used in the remainder of this thesis. It should be noted that this term refers exclusively to flowering plant species diversity and does not include the diversity of grasses or sedges.

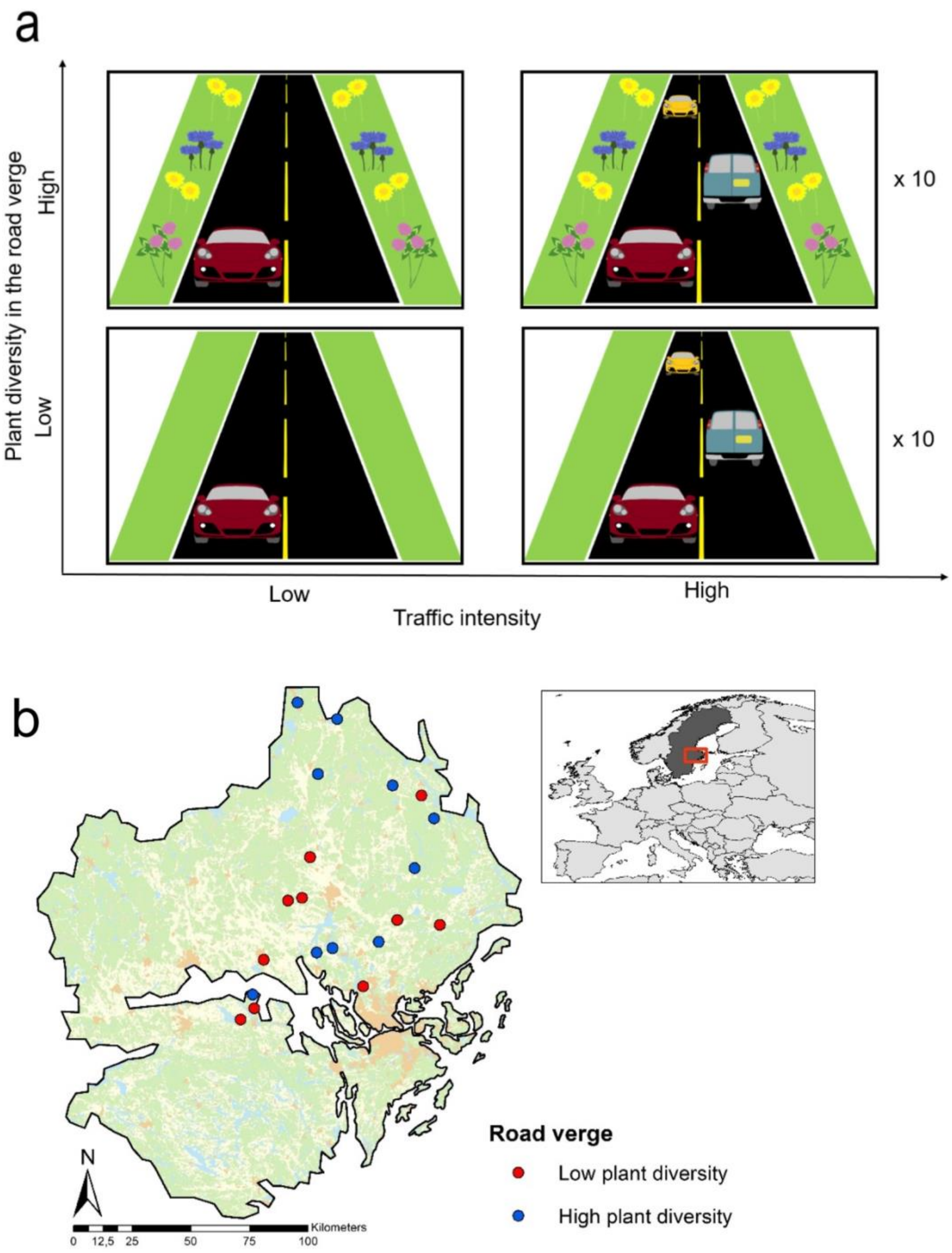

*Figure 1: (a) Study Design: Half of the sites have low plant species diversity road verges and the other half high plant species diversity road verges with similar gradients in traffic intensity (b) Location of the 20 sites in Sweden. Locations marked with red have low plant species diversity road verges, and locations marked with blue have high plant species diversity road verges. Reproduced from Dániel-Ferreira et al. (2022).*

## 2.3 Moth survey

To investigate the effects of traffic intensity and road verge characteristics on moth mortality, ~1 km road segments in the study sites were selected and sampled via insect-vehicle collision rates. Four 33 x 22 cm sticky traps (Romax Mouse Glue Board, Barrettine Environmental Health, Bristol, England) were installed on a station wagon vehicle and driven back and forth on the road at a constant speed on each site. During the first sampling round in June 2019, the vehicle was driven back and forth only once (~2 km) at 70 km/h between sundown and sunrise in each site. During the second and third sampling rounds in July and August 2019, the sampling effort was increased by driving back and forth five times (~10 km) at 50 km/h. Each site had a minimum length of 1 km, with the shortest site being 1.1 km and the longest 1.5 km. This difference in sampling effort across the sampling rounds is accounted for in the statistical analysis to avoid bias in the significance of the second and third sampling rounds.

As moths tend to fly at different heights (Taylor et al. 1979; Ashton et al. 2015; De Smedt et al. 2019), two sticky traps were installed on the front grill of the vehicle and two on the windshields (Figure 2) . Also, given that moth abundance varies throughout the season (Neff et al. 2025), the sampling was conducted in three rounds, one in June, July and August. As this thesis focuses on nocturnal Lepidoptera, only the sticky traps used at night were used for further analysis.

After I received the sticky traps containing moths, I counted all individuals and, if possible, identified them to species level. However, due to the nature of the sampling method, some moths were too damaged or covered with glue and therefore were impossible to identify. The consistency of the glue and the fragility of the moths made it impossible to remove individuals from the traps without destroying them, which is why the moths could only be processed for identification while remaining on the sticky trap, making the examination of certain morphological traits needed for identification impossible. This issue was especially relevant with smaller moths (see smaller individuals in Figure 3). Moreover, 21 of the sticky traps containing moths were lost. Nonetheless, 59 % of the moths could be identified to the family level, and 24 % to the genus or species level.

To aid with the identification, I used three guides (Hydén et al. 2006; Sterling et al. 2012; Townsend et al. 2019) and the webpage vilkenart.se (*vilkenart.se* n.d.). I also tried to use the app ‘iNaturalist’ (iNaturalist n.d.) to provide additional support in the identification process. Due to the level of damage of the moth specimens, this did however not provide any helpful results. To get a detailed look at features helpful for identification – e.g., labial palps, ocelli, or antennae – I used a Nikon Alphaphot 2-YS2 microscope with a 4x objective. This was especially helpful for identifying micro-moths.

[redacted]

*Figure 2: Sampling vehicle with four sticky traps – two on the front grill and two on the windshield (Photograph by Juliana Dániel-Ferreira).*

*Figure 3: Example of a sticky trap installed on the grill of the vehicle during field sampling, showing captured insect specimens (Photograph by Juliana Dániel-Ferreira).*

To control for differences in moth abundance among sites, sweep-net sampling of the road verges was performed at night. The sweep-net survey was conducted to sample all active and resting moths present in the road verges. The surveyor walked 200 m on each side of the road while sweep-netting the vegetation and captured all insects in a jar for later processing. The different insect groups were categorized to order level in the laboratory. For this thesis, I focused only on the Lepidoptera caught in the sweep nets.

Moreover, the surveyors documented whether the road verges had been mown. All road verges that had been mown at least once during the summer season were categorised as mown, while those that had not been mown at all were categorised as unmown. Environmental variables like site temperature and wind speed and direction were measured to support possible further analysis. Temperature was taken at the site with a thermometer, while wind speed and direction were taken from the Swedish Meteorological and Hydrological Institute's (SMHI) mobile application.

## 2.4 Data analysis

The statistical analysis of the collected data was conducted in R version 4.4.2 (R Core Team 2024). All graphs were plotted with the package *'ggplot2'* (Wickham 2016) in a colour-blind-friendly palette following the recommendations of Wong (2011). For descriptive boxplots and data summarisation, traffic intensity (continuous) was factored into low and high traffic locations using a threshold of 1,000 vehicles/day. This threshold was justified by a natural gap in the data between 939 and 1,662 vehicles/day. However, in all statistical models, traffic intensity was included as a continuous variable.

### 2.4.1 Modelling moth abundance in road verges

To identify the factors influencing the abundance of moths in the road verges, the sweep net data was aggregated to round level, resulting in 60 data points (three per location). I fitted several generalized linear mixed effects models (GLMMs) with a negative binomial distribution. All models used moth abundance (continuous) as the response variable (n = 59, one data point was removed due to missing temperature data). Fixed predictors included traffic intensity (continuous), plant species diversity (factor: HD = high diversity, LD = low diversity) and sampling round (factor: rounds 1, 2, 3).

I tested models with different compositions and amounts of additional variables. These variables included verge width (continuous), temperature (continuous) and mowing (factor: Yes, No).

Traffic intensity, verge width and temperature were scaled in all models by subtracting the mean and dividing by the standard deviation to facilitate model convergence. Moreover, location was added as a random effect in all candidate models to account for the non-independence of observations, as three sampling rounds were conducted at each of the 20 locations. Models were run with and without interactions between traffic intensity and road verge plant diversity, and between mowing and traffic intensity. I tested the models for over- or underdispersion, and the residual diagnostics were checked visually for all models using the package *'DHARMa'* (Hartig 2024). The negative binomial distribution was chosen over a Poisson distribution due to issues with overdispersion using the command *glmer.nb* from the *'lme4'* package (Bates et al. 2015).

Model selection was conducted in two steps. First, I fitted a model with the baseline fixed predictors (traffic intensity, plant species diversity, sampling round). Sampling round was included in the baseline model to account for seasonal variation. Traffic intensity and plant species diversity are the main variables relevant for answering my hypotheses and are embedded in the original study design and thus were also included in the baseline model. The baseline model was then expanded by adding potential variables step by step with likelihood ratio tests (LRT). This included mowing, verge width and variable interactions. Variables were kept in the model if their removal significantly worsened model fit ($p < 0.05$). This approach was used due to the small sample size and to avoid convergence issues. Then, the resulting candidate models were compared using the Akaike Information Criterion corrected for smaller sample sizes (AICc) due to better performance compared to the AIC-criterion (Song et al. 2017). This was calculated with the *'MuMin'* package (Bartoń 2025). Models were ranked using Δ AICc, with models differing by less than 2 AICc units considered to have substantial support. AICc weights were calculated to assess the relative support for each candidate model.

Model effects were visualised with the packages *'ggeffects'* (Lüdecke 2018) and *'ggplot2'* (Wickham 2016).

Additionally, estimated marginal means (EMMs) for statistically significant categorical predictors were calculated using the *'emmeans'* package (Lenth et al. 2026). These provide model-based predicted values adjusted for the other variables included in the model. EMMs were computed on the link (log) scale and back-transformed to the response scale to obtain expected counts. Pairwise comparisons between factor levels were performed using Tukey-adjusted p-values to account for multiple comparisons.

### 2.4.2 Modelling moth road mortality

To identify the factors influencing the road mortality of moths, I built different generalized linear models (GLMs) using the *glm()* function. Due to differences in sampling effort across the three sampling rounds, the sticky trap dataset was aggregated to the location level. Therefore, seasonal differences in moth road mortality could not be analysed. Moreover, sampling time was also excluded from this analysis, as it varied across sampling rounds and could thus not be aggregated to the location level. Thus, mortality counts and their sampling times were only plotted against each other exploratively to identify possible patterns of peak activity. As mortality counts were aggregated to the location level, resulting in a single observation per location, a random effect for location was not included.

All candidate models had moth mortality (continuous, count data) as a response variable (n=20). Fixed predictors included traffic intensity (continuous, scaled) and plant species diversity (factor: HD and LD). Additional variables that were tested are road verge moth abundance (continuous) and verge width (continuous, scaled). Moreover, a model with an interaction between traffic intensity and plant species diversity was also tested.

Model dispersion was assessed using the *'DHARMa'* package (Hartig 2024). This showed that the Poisson models were overdispersed, so the models were fitted with a negative binomial distribution instead. The model selection process was done in two steps, consisting of Likelihood Ratio Comparison and AICc-criterion comparison as described in the previous section.

A community composition analysis was attempted, but due to the high proportion of unknown individuals (on the family and species level), it could not provide valuable results.

# 3. Results

## 3.1 Moth abundance in road verges

A total of 580 moths were caught in the sweep nets along the road verges, with about 10 moths on average per site and sampling round (mean ± SD = 9.78 ± 8.82; Table 1).

*Table 1: Descriptive statistics investigated for explaining road verge moth abundance. Plant species diversity is factored into high diversity (HD) and low diversity (LD) sites.*

| **Variables** | **Type + Unit** | **Mean ± SD** | **min** | **max** |
|---|---|---|---|---|
| Abundance | Continuous (count data) | 9.78 ± 1.15 | 1.00 | 36.00 |
| Traffic intensity | Continuous (vehicles/day) | 2054.40 ± 2222.80 | 125.00 | 6356.00 |
| Plant species diversity | Factor (HD/LD) | - | - | - |
| Sampling round | Factor (1,2,3) | - | - | - |
| Mowing | Factor (Yes/No) | - | - | - |
| Verge width | Continuous (meters) | 4.34 ± 0.68 | 2.88 | 5.41 |
| Temperature | Continuous (°C) | 14.99 ± 2.97 | 10.00 | 23.00 |

Moth abundance was higher at low traffic locations with under 1,000 vehicles/day (11.31 ± 9.72) compared to high traffic locations with more than 1,000 vehicles/day (7.54 ± 6.91; Fig. 4). Moth abundance showed little difference between low-diversity (9.53 ± 6.97) and high-diversity verges (10.03 ± 10.52; Figure 4B).

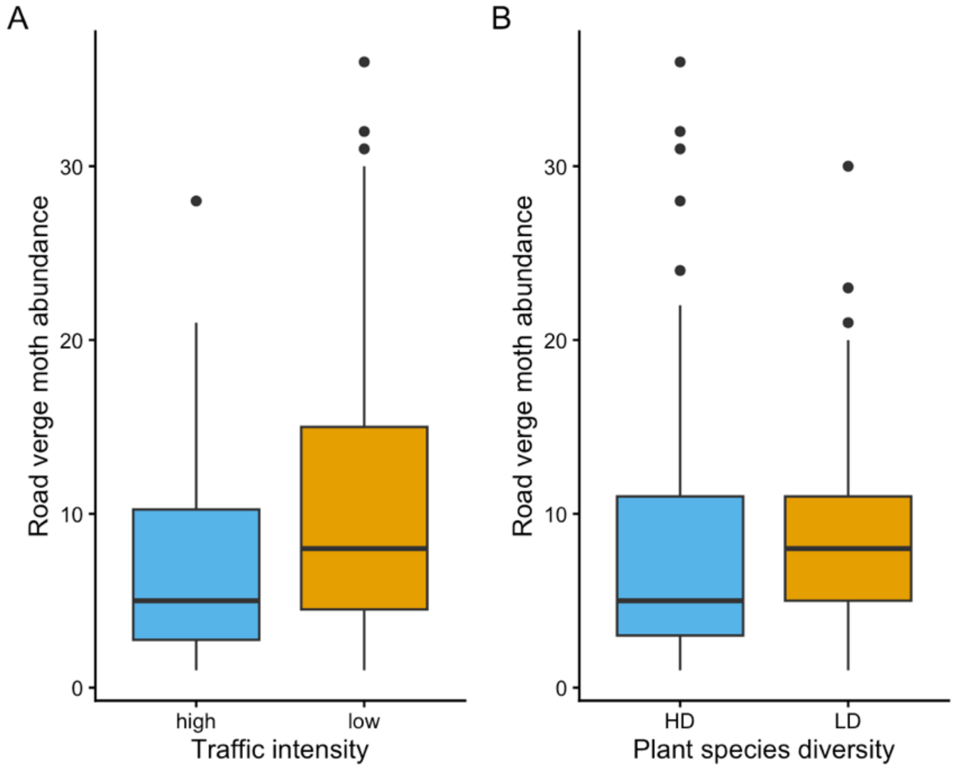

*Figure 4: Road verge moth abundance in relation to (A) traffic intensity (low: < 1000 vehicles/day; high: ≥ 1000 vehicles/day) and (B) plant species diversity (HD = high diversity; LD = low diversity). The box represents the interquartile range (IQR), the horizontal line the median, whiskers extend to 1.5× the IQR, and dots represent outliers.*

Moreover, moth abundance varied with the time of the night at which the sampling occurred. 21:30 to 22:30 and 23:30 to 00:30 (Table 2) were observed as the two hourly intervals with the highest moth abundance in the road verges (see Figure 5).

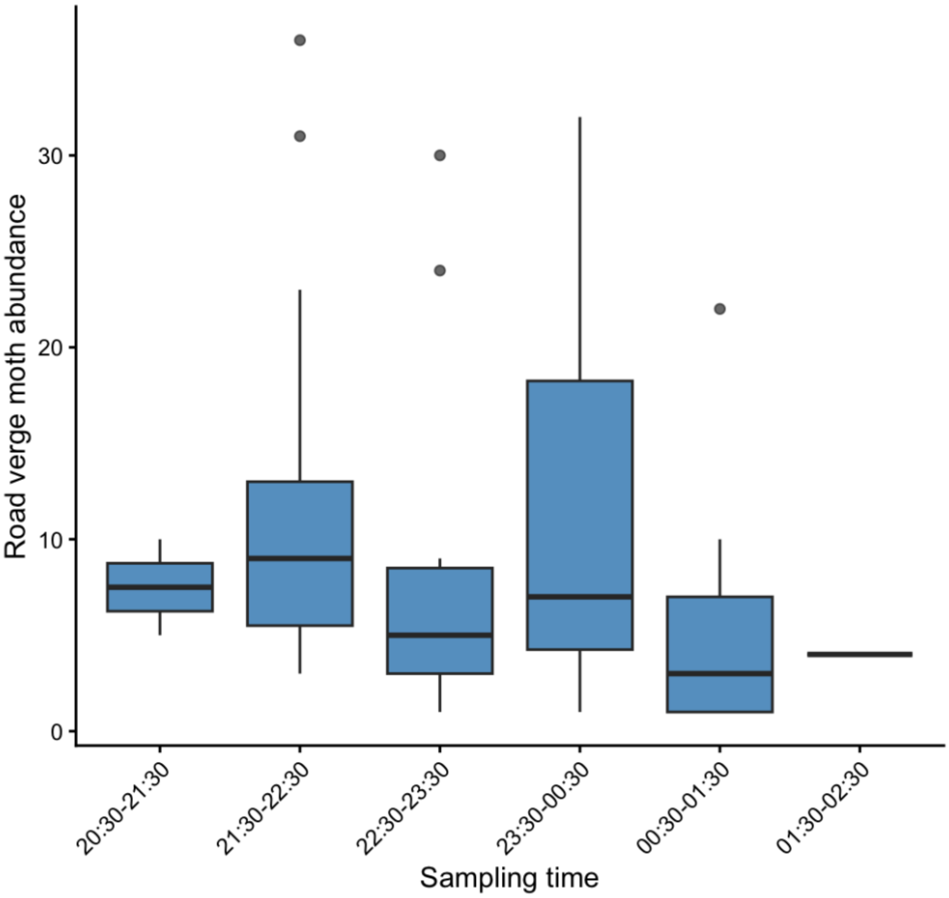

*Figure 5: Boxplots showing road verge moth abundance across six hourly sampling intervals. The box represents the interquartile range (IQR), the horizontal line the median, whiskers extend to 1.5× the IQR, and dots represent outliers.*

*Table 2: Number of moths in the road verges during hourly sampling intervals; the abundance of moths in the road verges describes the total amount of moths present in the road verges during the different timeframes; Mean ± SD (Standard deviation) shows the mean number of moths present per location and round.*

| **Sampling Time** | **Abundance of moths in the road verges** | **Mean ± SD** |
|---|---|---|
| 20:30-21:30 | 15 | 7.50 ± 3.54 |
| 21:30-22:30 | 258 | 11.22 ± 8.62 |
| 22:30-23:30 | 94 | 8.55 ± 9.55 |
| 23:30-00:30 | 159 | 11.36 ± 10.05 |
| 00:30-01:30 | 47 | 5.88 ± 7.30 |
| 01:30-02:30 | 4 | 4.00 ± 0.00 |

Road verge width ($\chi^2$ = 0.152, df = 1, p = 0.697) and temperature ($\chi^2$ = 1.664, df = 1, p = 0.197) did not significantly improve model fit. Adding mowing ($\chi^2$ = 10.696, df = 1, p = 0.001) did significantly improve model fit. Interactions between traffic intensity and plant species diversity ($\chi^2$ = 0.436, df = 1, p = 0.510) and between mowing and traffic intensity ($\chi^2$ = 1.878, df = 1, p = 0.171) were also tested, but they did not improve model fit.

Model selection based on AICc identified the model including traffic intensity, plant species diversity, sampling round and mowing as the most parsimonious model (ΔAICc = 0.00, weight = 0.556, Table 3). Models 4 (Table A1: 2) and 6 (Table A1: 1) also showed substantial support with a ΔAICc-value under 2. Their results can be found in Appendix 1. Models that included road verge width and the interaction between traffic intensity and plant species diversity received little support (Table 3), indicating that these variables did not substantially improve model fit. Thus, road verge width was not retained as an important predictor of moth abundance in road verges. Temperature was included in M4, which showed substantial support (ΔAICc = 1.13), but it did not show a statistically significant effect on the abundance of moths in road verges (z = 1.34, p = 0.181, Table A2). The interaction between mowing and traffic intensity was included in M6, which showed substantial support (ΔAICc = 0.92), but the interaction did not show statistical significance (z = -1.39, p = 0.165, Table A1).

*Table 3: Model Selection Table for the abundance model based on AICc. The best supported model (Model 5) is shown in bold. K = number of parameters; Log-Lik = log-likelihood; AICc = Akaike Information Criterion corrected for small sample size; ΔAICc = difference in AICc from the best model; diversity refers to plant species diversity.*

| **Model** | **Model Formula** | **K** | **Log-Lik** | **AICc** | **ΔAICc** | **AICc weight** |
|---|---|---|---|---|---|---|
| **M2** | abundance ~ traffic + diversity +round + mowing | 8 | -183.859 | 386.6 | 0.00 | 0.358 |
| M6 | abundance ~ diversity + round + mowing*traffic | 9 | -182.921 | 387.5 | 0.92 | 0.226 |
| M4 | abundance ~ traffic + diversity+ round + mowing + temperature | 9 | -183.028 | 387.7 | 1.13 | 0.203 |
| M5 | abundance ~ traffic*diversity + round + mowing | 9 | -183.641 | 389.0 | 2.36 | 0.110 |
| M3 | abundance ~ traffic + diversity + round + width | 9 | -183.028 | 387.7 | 6.90 | 0.018 |
| M1 | abundance ~ traffic + diversity + round | 7 | -189.208 | 394.6 | 8.01 | 0.007 |

The results of model 2 (Table 4) show significant seasonal variability in moth abundance in road verges with positive effects of sampling round 2 in July (z = 3.60, p = <0.001) and sampling round 3 in August (z = 4.02, p = <0.001). Post-hoc comparisons revealed that predicted moth abundance increased from approximately 3.81 individuals (95% confidence interval (CI): 2.48-5.86) in sampling round 1 to 9.89 (95 % CI: 7.11-13.77) in sampling round 2 and 14.17 (95 % CI: 9.71-20.68) in sampling round 3. Pairwise comparisons showed that abundance was significantly higher in sampling rounds 2 and 3 compared to sampling round 1 (round 1 vs. 2: ratio = 0.39, p < 0.001; round 1 vs. 3: ratio = 0.27, p < 0.001), while the difference between sampling rounds 2 and 3 was not statistically significant (p = 0.314). Thus, moth abundance increased across sampling rounds from early to late summer (Fig. 6).

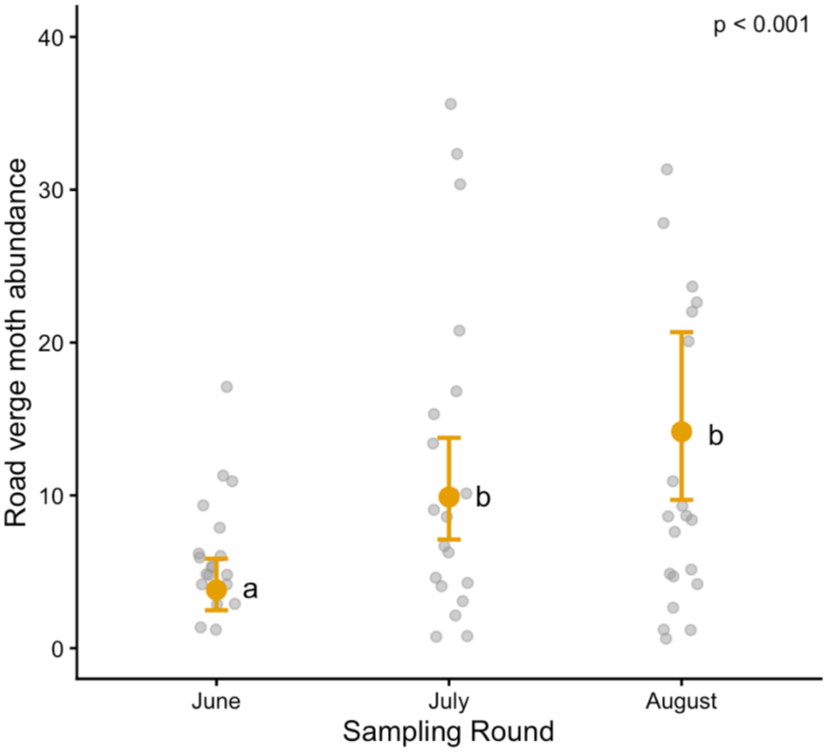

*Figure 6: Moth abundance in road verges across three sampling rounds. Sampling rounds 1, 2 and 3 correspond to June, July and August 2019. Grey points show raw observation, orange points indicate model-predicted means, and error bars represent 95% confidence intervals. Different letters indicate significant differences between sampling rounds based on post-hoc pairwise comparisons.*

Mowing of road verges had a significant negative effect on the abundance of moths (z = -3.49, p = <0.001, Figure 7). Post-hoc comparisons revealed that unmown road verges supported significantly higher predicted moth abundance than mown verges (ratio = 2.56, p = <0.001), with unmown verges having, on average, 2.56 times more moths than mown verges (unmown: 11.60, 95% CI: 8.59–15.70; mown: 4.54, 95% CI: 3.22–6.40).

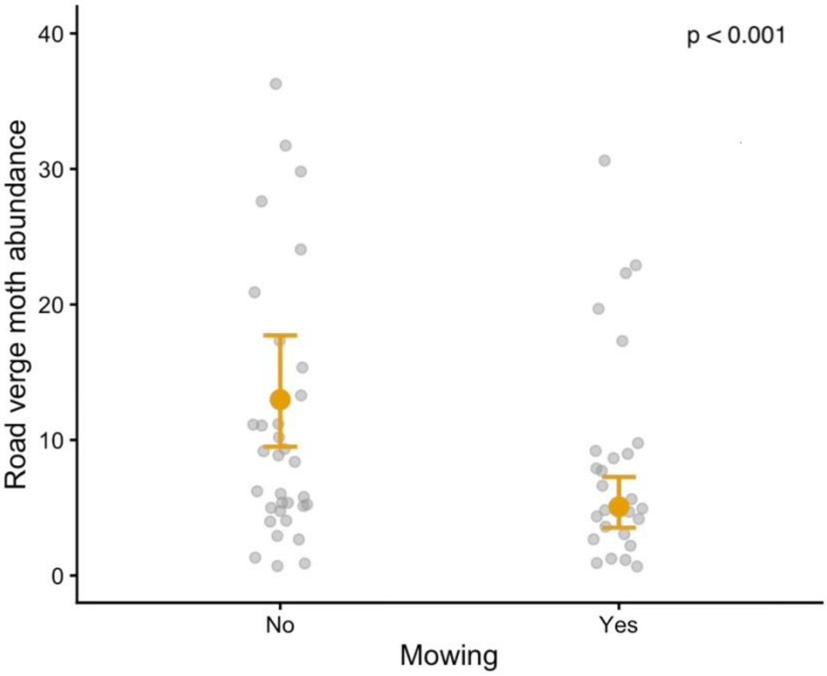

*Figure 7: Moth abundance in road verges in relation to mowing management. "Yes" corresponds to mown road verges, "No" to unmown road verges. Grey points show raw observations, orange points indicate model-predicted means, and error bars show 95% confidence intervals. Unmown road verges showed higher moth abundance compared to mown verges.*

The abundance of moths in road verges did differ significantly with high or low plant species diversity (z = 0.44, p = 0.662). Traffic intensity did not show statistical significance as well (z = -1.22, p = 0.223).

*Table 4: Results from the generalized linear mixed effects model with a negative binomial distribution exploring the relationship between moth abundance in road verges and traffic intensity, plant species diversity, mowing and sampling round. Shown are the estimates (e), standard error (s.e.), z-values and p-values. P-values in bold are significant at the 0.05 level or lower.*

| **Variables** | **e** | **s.e.** | **z-value** | **p-value** |
|---|---|---|---|---|
| Intercept | 1.765 | 0.206 | 8.55 | **<0.001** |
| Traffic intensity | -0.126 | 0.103 | -1.22 | 0.223 |
| Plant species diversity LD | 0.087 | 0.200 | 0.44 | 0.662 |
| Sampling round 2 | 0.953 | 0.265 | 3.60 | **<0.001** |
| Sampling round 3 | 1.312 | 0.326 | 4.02 | **<0.001** |
| Mowing Yes | -0.940 | 0.270 | -3.49 | **<0.001** |

## 3.2 Moth Road Mortality

In total, 137 moths were caught in the sticky traps and partially identified. The dead individuals were spread out over 69 of the total 240 sticky traps, with the two most successful traps containing seven individuals. A total of 15 different moth families were identified, comprising five macro-moth and ten micro-moth families. These groups accounted for 42 and 64 individual moths, respectively (Table 5). All moths that could not be identified due to the nature of the sampling method were micro-moths (n=56).

*Table 5: Macro- and micro-moth families caught in the sticky traps.*

| **Moth Family** | **Macro- / Micromoth** | **Individuals** |
|---|---|---|
| *Geometridae* | Macro | 13 |
| *Noctuidae* | Macro | 19 |
| *Erebidae* | Macro | 1 |
| *Nolidae* | Macro | 1 |
| *Hepialidae* | Macro | 8 |
| *Alucitidae* | Micro | 1 |
| *Choreutidae* | Micro | 1 |
| *Tortricidae* | Micro | 12 |
| *Pyralidae* | Micro | 7 |
| *Chimabachidae* | Micro | 1 |
| *Crambidae* | Micro | 4 |
| *Pterophoridae* | Micro | 8 |
| *Yponomeutidae* | Micro | 1 |
| *Gelechiidae* | Micro | 3 |
| *Tineidae* | Micro | 1 |
| unknown | Micro | 56 |
| **Total** | | **137** |

Within these families, I identified 19 moth species, and in four cases, identification was possible only to the genus level (Table 6). The families with the highest representation were *Noctuidae*, *Geometridae*, *Tortricidae*, *Pterophoridae* and *Pyralidae*. The most abundant taxa were *Hoplodrina spp.* and *Triodia sylina*.

*(A) Hoplodrina octogenaria*

*(B)Triodia Sylvina*

*Figure 8: (A) Hoplodrina octogenaria (Hoplodrina spp.), image by Ronny Lindman ;(B) Triodia Sylvina, image by Sven Johansson (vilkenart.se n.d.).*

*Table 6: Moth families and species/genus caught in the sticky traps.*

| Family | Species/Genus | Individuals/Species |
|---|---|---|
| *Geometridae* | *Eupithecia centaureata* | 1 |
| *Geometridae* | *Cabera pusaria* | 1 |
| *Geometridae* | *Eupithecia icterata* | 2 |
| *Geometridae* | *Camptogramma bilineata* | 1 |
| *Geometridae* | *Eupithecia millefoliata* | 1 |
| *Geometridae* | *Eulithis populata* | 1 |
| *Geometridae* | *Scotopteryx chenopodiata* | 1 |
| *Noctuidae* | *Macrochilo cribrumalis* | 1 |
| *Noctuidae* | *Hoplodrina spp.* | 7 |
| *Noctuidae* | *Mythimna spp.* | 2 |
| *Noctuidae* | *Mythimna conigera* | 1 |
| *Noctuidae* | *Lygephila pastinum* | 1 |
| *Hepialidae* | *Triodia sylvina* | 7 |
| *Hepialidae* | *Korscheltellus spp.* | 1 |
| *Erebidae (Arctiinae)* | *Eilema lurideolum* | 1 |
| *Alucitidae* | *Alucita hexadactyla* | 1 |
| *Tortricidae* | *Agapeta zoegana* | 1 |
| *Chimabachidae* | *Diurnea spp.* | 1 |
| *Tineidae* | *Oinophila v-flava* | 1 |
| **Total** | **19** | **33** |

On the location level, about seven moths were caught per site (Table 7).

*Table 7: Descriptive statistics investigated for explaining moth road mortality on the location level (n=20). Plant species diversity is factored into high diversity (HD) and low diversity (LD) sites.*

| Variable | Type + Unit | Mean ± SD | Min | Max |
|---|---|---|---|---|
| Mortality | Continuous (count data) | 6.85 ± 4.60 | 2.00 | 19.00 |
| Traffic intensity | Continuous (vehicles/day) | 2029.70 ± 2250.67 | 125.00 | 6356.00 |
| Plant species diversity | Factor (HD/LD) | - | - | - |
| Road verge abundance | Continuous (count data) | 29.00 ± 17.62 | 9.00 | 72.00 |
| Verge width | Continuous (meters) | 4.33 ± 0.69 | 2.88 | 5.41 |

Moth mortality counts were higher at low traffic locations (mean ± SD = 8.75 ± 4.88) compared to high traffic locations (4.00 ± 2.14; Figure 9). Moth mortality showed little difference between low diversity and high diversity verges, although low diversity verges showed slightly higher median mortality (SP: 7.10 ± 4.33, SR: 6.60 ± 5.08; Figure 9).

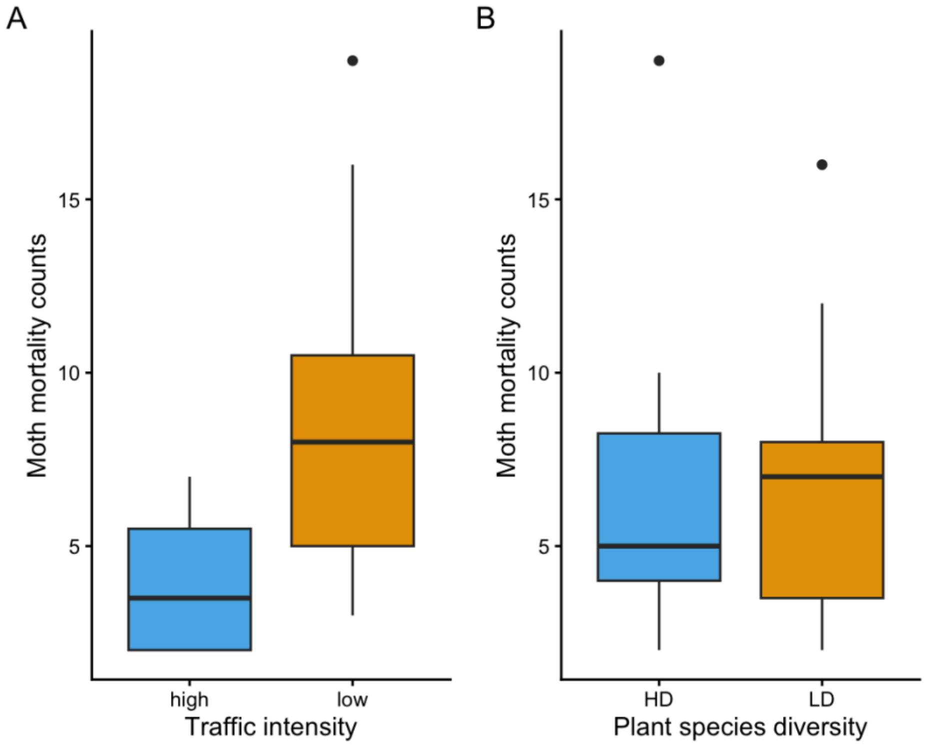

*Figure 9: Moth mortality counts in relation to (A) traffic intensity (low: <1000 vehicles/day; high: ≥1000 vehicles/day) and (B) plant species diversity (HD = high diversity; LD = low diversity). The box shows the interquartile range (IQR), the horizontal line the median, whiskers extend to 1.5× the IQR, and dots represent outliers.*

Moreover, moth mortality varied with the time of the night at which the sampling occurred. 21:30 to 22:30 and 22:30 to 23:30 (Table 8) were observed as the sampling times with the highest average numbers of moth mortality (Figure 10).

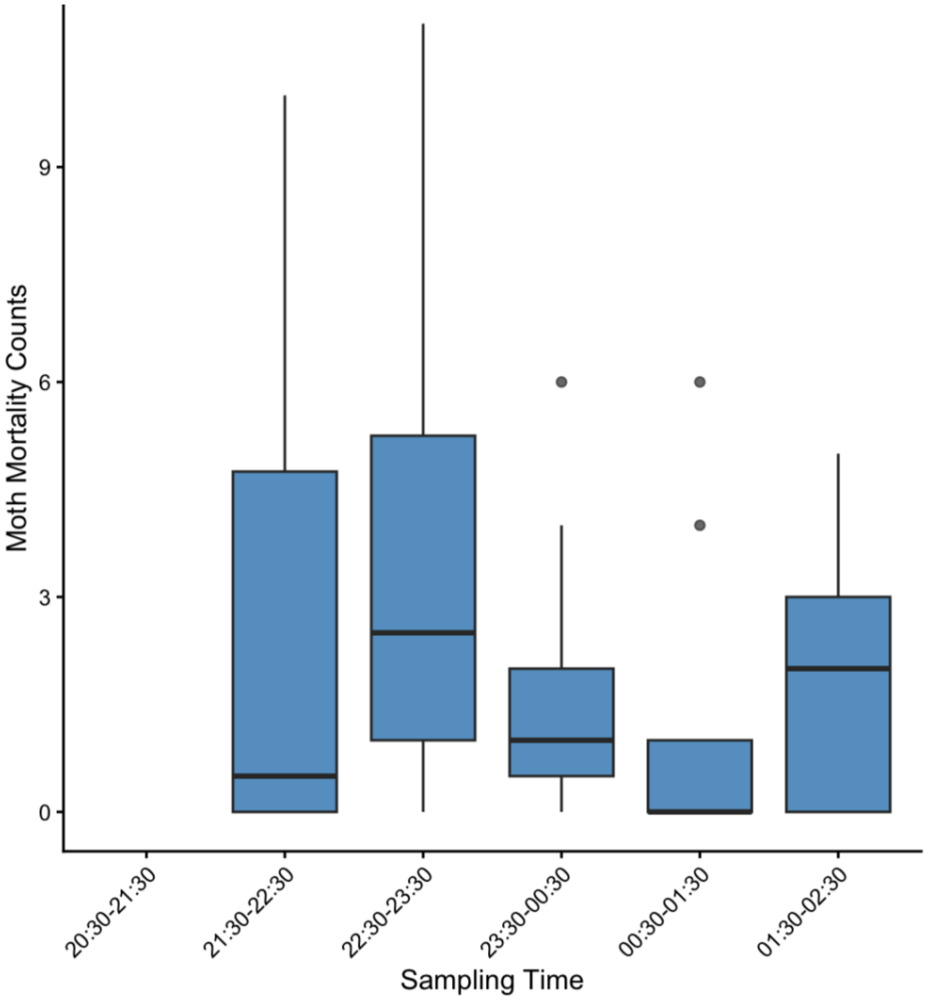

*Figure 10: Boxplots showing moth mortality across six hourly sampling intervals. The box represents the interquartile range (IQR), the horizontal line the median, whiskers extend to 1.5× the IQR, and dots represent outliers.*

*Table 8: Number of dead individuals during hourly sampling intervals; the number of dead individuals describes the total amount of moths caught in the different intervals; Mean ± SD (Standard deviation) shows the mean number of moths caught per location and round.*

| **Hourly Timeframe** | **Number of dead individuals** | **Mean ± SD** |
|---|---|---|
| 20:30-21:30 | 0 | NA |
| 21:30-22:30 | 28 | 2.80 ± 3.77 |
| 22:30-23:30 | 62 | 3.10 ± 2.86 |
| 23:30-00:30 | 25 | 1,67 ± 1.68 |
| 00:30-01:30 | 12 | 1.20 ± 2.10 |
| 01:30-02:30 | 10 | 2.00 ± 2.12 |

Including road verge width did not significantly improve model fit ($\chi^2 = 0{,}003$, p = 0,958). Interactions between traffic intensity and abundance ($\chi^2 = 1.073$, p = 0.300) and between traffic intensity and plant species diversity ($\chi^2 = 0.302$, p = 0.583) were also tested but did not improve model fit.

Model selection based on AICc identified the reduced model (M2), excluding verge width and interactions, as the most parsimonious (ΔAICc = 0.00, weight = 0.676, Table 9). The full model (M4) received little support (ΔAICc = 4.17, weight = 0.03, Table 9), confirming that the excluded variables and interactions did not meaningfully contribute to explaining moth road mortality. Thus, road verge width was not retained as an important predictor of moth road mortality.

*Table 9: Model Selection Table for the mortality model based on AICc. The best supported model (M2) is shown in bold. K = number of parameters; Log-Lik = log-likelihood; AICc = Akaike Information Criterion corrected for small sample size; ΔAICc = difference in AICc from the best model. Diversity refers to plant species diversity.*

| **Model** | **Model Formula** | **K** | **Log-Lik** | **AICc** | **ΔAICc** | **AICc weight** |
|---|---|---|---|---|---|---|
| **M2** | Mortality ~ traffic + diversity + abundance | 5 | -50.097 | 114.5 | 0.00 | **0.676** |
| M4 | Mortality ~ traffic*abundance + diversity | 6 | -49.56 | 117.6 | 3.10 | 0.143 |
| M3 | Mortality ~ traffic*diversity + abundance | 6 | -49.946 | 118.4 | 3.87 | 0.097 |
| M1 | Mortality ~ traffic + diversity + abundance + width | 6 | -50.095 | 118.7 | 4.17 | 0.084 |

The model results (Table 10) showed a significant positive effect of road verge moth abundance on moth mortality (z = 2.65, p = 0.008). Thus, with increasing moth abundance in the road verges, the road mortality of moths increased as well (Figure 11A). Moth mortality counts decreased with increasing traffic intensity (z = -2.00, p = 0.045; Figure 11B). Plant species diversity did not have a statistically significant effect on moth road mortality (z = -0.79, p = 0.432).

*Table 10: Results from the generalized linear model with a negative binomial distribution exploring the relationship between moth road mortality and traffic intensity, plant species diversity and moth abundance in road verges. Shown are the estimates (e), standard error (s.e.), z-values and p-values. P-values in bold are significant at the 0.05 level or lower.*

| **Variables** | **e** | **s.e.** | **z-value** | **p-value** |
|---|---|---|---|---|
| Intercept | 1.468 | 0,240 | 6.13 | <0.001 |
| **Traffic Intensity** | -0.253 | 0.126 | -2.00 | **0,045** |
| Plant species diversity HD | -0.176 | 0.224 | -0.79 | 0.432 |
| **Road verge abundance** | 0.016 | 0.006 | 2.65 | **0.008** |

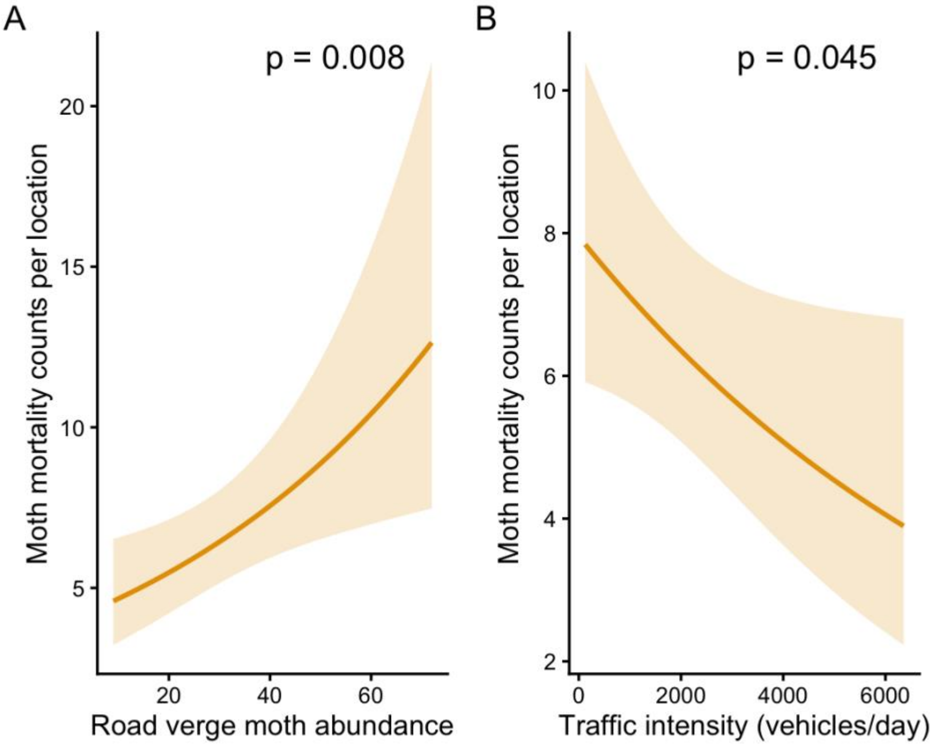

*Figure 11: Moth mortality in relation to (A) moth abundance on road verges and (B) traffic intensity. Shown are the fitted lines and the shaded areas represent the 95% confidence intervals.*

# 4. Discussion

This study investigated the factors influencing moth abundance in road verges and moth road mortality along Swedish roads, contributing to the limited body of research on the impacts of roads on nocturnal insects. The results partially supported the hypotheses, with mowing management emerging as the strongest driver of moth abundance in road verges (H2), while road verge plant species diversity and road verge width showed no significant effect, contrary to assumptions (H1). Road verge moth abundance was identified as the primary driver of road moth mortality (H3), while traffic intensity showed a counterintuitive negative effect, contradicting the initial assumption in H3.

## 4.1 Factors affecting moth abundance in road verges

As expected, mowing road verges negatively affected moth abundance (H2). Unmown verges had on average 2.56 times more moths than mown verges, indicating that moths can benefit from an absence of mowing. The potential of road verges to provide habitats for grassland species depends to a large extent on how they are managed (Horstmann et al. 2024). Mowing has been associated with a high direct mortality of moths, particularly larvae (Humbert et al. 2010; Sanetra et al. 2024). Humbert et al. (2010) found a 20-70 % reduction in butterfly caterpillars in meadows after mowing, depending on the method. Steidle et al. (2022) reported a 87 % loss of adult Lepidoptera when comparing unmown roadside grasslands with conventionally mown ones. Thus, the statistically significant effect of mowing on the abundance of moths in road verges may be partially explained by the direct killing of resting moths, particularly larvae.

Mowing furthermore decreases the availability of taller vegetation, which can provide resting sites and hiding places of particular importance for nocturnal moths and increased plant biomass for oviposition (Saarinen et al. 2005; Valtonen et al. 2006). Since a reduced mowing regime typically increases the richness and biomass of plant species over time (Sehrt et al. 2020; Piseddu et al. 2021), the availability and diversity of larval host plants are expected to be higher in unmown road verges than in mown ones. Thus, reduced resting places and larval feeding resources may be another indirect factor explaining the significant effect of mowing on moth abundance in road verges.

Moreover, unmown verges or those with reduced mowing frequency have been shown to facilitate a higher species richness of flowering plants (Halbritter et al. 2015; Horstmann et al. 2024). In agreement with this, higher flowering plant diversity has been associated with higher butterfly abundance in road verges (Skórka et al. 2013a). In a parallel study conducted at the same sites as those used in this thesis, a similar effect was also observed for bumblebees (Dániel-Ferreira et al. 2022). As bumblebees and butterflies, some nocturnal adult moths are nectarivores (Macgregor & Scott-Brown 2020). Due to this overlapping trait between moths and diurnal insects like bumblebees and butterflies, a higher flowering plant species richness may thus also indicate a higher abundance of moths in the road verges. Contrary to expectations (H1), flowering plant species diversity did not significantly affect moth abundance in road verges. Given that this study focused exclusively on flowering plants and did not include the diversity of grasses or sedges, the plant species diversity metric used here may have been too limited to detect effects on moth abundance (Table 4). Not all adult moths depend on flowering plants as they are neither nectarivores nor do they feed as adults at all (Saarinen et al. 2005; Townsend et al. 2019). Moths seem to be more favoured by the provision of tall, grassy vegetation as a shelter (Saarinen et al. 2005) than by a high flowering plant species diversity.

Nonetheless, some moths still are nectarivores and important nocturnal pollinators (Townsend et al. 2019; Macgregor & Scott-Brown 2020). These adult moths rely on flowering plants, but mechanisms necessary for nocturnal pollination, such as floral scent and night vision, might be disturbed, especially at night near traffic. The release of anthropogenic volatile pollutants (AVPs) from traffic disrupts to scent-based communication between flowers and pollinators (Macgregor & Scott-Brown 2020). They add background noise to floral signals by masking their detection by pollinators, and increase the degradation rate of floral volatiles (Fuentes et al. 2016; Jürgens & Bischoff 2017). Nitrogen enrichment of habitats may also influence floral scent by influencing the production and emission of a range of plant volatiles (e.g., Kivimäenpää et al. 2016). The effect of soil nitrogen availability on floral volatiles specifically, has however not been extensively studied (Macgregor & Scott-Brown 2020). Moreover, artificial light at night – in this case, pALAN caused by vehicle headlights – may impact both visual and floral scent cues for nocturnal pollination (Macgregor & Scott-Brown 2020). So, even though some adult moths are pollinators, the disturbances of nocturnal pollination caused by the proximity of road traffic might lower the significance of floral resources for pollinating individuals.

The results of this study contradict other findings regarding diurnal pollinators, such as butterflies or bumblebees, for which flowering plant diversity is an important factor in higher abundance (Skórka et al. 2013a; Dániel-Ferreira et al. 2022). These differences among insect groups underline the importance of studying nocturnal insects and highlight the need for dedicated research on moth communities in road verges.

Contrary to the assumptions made in H1, road verge width did not significantly increase moth abundance. Other studies showed that broader road verges had a positive effect on other insect groups (Skórka et al. 2013a; Horstmann et al. 2024). Moreover, Phillips et al. (2021a) found that pollinator densities were lower closer to the road edges, particularly within two meters (55 % lower than at seven to nine meters). For moths, this effect was however not statistically significant. Compared to my study (verge width range: 2.88 m to 5.41 m), the road verges in Phillips et al. (2021a) spanned a wider range, with all road verges measuring at least nine meters in width. Thus, verge width not having an impact on moth abundance in my study could be attributed to the need for a bigger range of verge width sizes. As road pollution and associated impacts decrease with distance from the road (Phillips et al. 2021a), future studies that include a wider range of road verge widths may yield more conclusive results.

Moth abundance also showed seasonal variability by increasing between June and July, with a similar rate of increase observed between July and August. This indicates that moths in the study area in Sweden are most abundant in July and August, which overall concurs with the seasonal abundance patterns of moths in other European countries (Gimesi et al. 2012; Jonason et al. 2014; Neff et al. 2025).

## 4.2 Factors affecting moth road mortality

As expected, moth mortality increased with moth abundance in the road verges (H3). This is consistent with findings on butterfly road mortality (Skórka et al. 2013a). Since insects usually have low or moderate dispersal abilities, most road-killed moths should be individuals living on road verges or in their proximity (Skórka et al. 2013a), and higher amounts of moths in the road verges may therefore lead to higher amounts of individuals available to fall victim to vehicle collisions.

One might assume that moth road mortality will also increase with higher levels of traffic intensity. However, the results of the best-fitting model showed that higher traffic intensity is associated with lower levels of moth road mortality (Figure 11B), contrary to expectations (H3). While this result first seems rather counterintuitive, and studies on other taxa have found that mortality increases with higher traffic intensity (McKenna et al. 2001; Skórka et al. 2013a; Dániel-Ferreira et al. 2022; Horstmann et al. 2024), there are several factors that might explain an association between lower moth road mortality and increasing traffic intensity. Martin et al. (2018) used a methodology similar to that of this thesis by installing sticky traps on a moving vehicle. They found that fewer insects were captured on high-traffic roads than on low-traffic roads, consistent with the results of this thesis. They suggest that this trend is caused by traffic itself negatively affecting insect abundance.

If busier roads lead to lower moth abundance in road verges, then fewer individuals are available to be killed. The literature contains a variety of evidence indicating that highly trafficked roads are associated with a lower insect abundance in their vicinity. In addition to the findings in Martin et al. (2018), Phillips et al. (2019) found that pollinator abundance in road verges decreased with increasing traffic. They propose this could be caused by turbulence from passing road traffic, which would make it difficult for moths to pollinate or rest on plants (Dargas et al. 2016; Phillips et al. 2019; Hennessy et al. 2020). In addition, there are other forms of pollution whose effects increase with higher traffic intensity, and that are potentially associated with a decreased abundance of moths in road verges adjacent to high-traffic roads. This may include noise, light, exhaust fumes, dust and metals (Forman et al. 2003; Phillips et al. 2021a). Roads and road traffic produce dust roughly the same size as pollen, which accumulates on vegetation, specifically flowers (Phillips et al. 2021a). Road dust can affect the pollination of flowers (Waser et al. 2017) and it contains metals from wear and tear of road vehicles and road surfaces, which accumulate in roadside soils and vegetation (Werkenthin et al. 2014). Many of these metals are toxic to insects at sufficiently high concentrations (Muñoz et al. 2015; Rothman et al. 2020). Moreover, Phillips et al. (2021a) observed that some pollinator taxa even avoided concentrations of metals found in flowers. In a recent study, avoidance behaviour towards high traffic was also observed in bumblebees (Blomqvist et al. 2025). In addition, the effects of light pollution, particularly pALAN, on moths are still not thoroughly researched. It is possible that vehicle headlights might not trigger a higher flight activity by causing erratic flight, as proposed in Fabusova et al. (2024), but more so reduce it. Light pollution is generally known to reduce moth activity (Boyes et al. 2020; Briolat et al. 2026), and sudden exposure to artificial light effectively blinds a moth until its eyes have readjusted, which can take up to 30 minutes (Bernhard & Ottoson 1960; Frank 1988; Boyes et al. 2020). The exposure to light may trigger the daytime response of ceasing activity and cause moths to become inactive (Frank et al. 2006).

Thus, higher traffic intensity and a more frequent exposure to vehicle headlights might cause lower flight activity and furthermore, lower mortality through vehicle collisions. Pollution forms like road dust and metals, which are particularly associated with high-traffic roads, may additionally reduce moth abundance in road verges by causing higher mortality or avoidance behaviour. Moth mortality in traffic seems mainly affected by the abundance of moths in road verges, which in turn may be reduced by higher vehicle traffic. Even though literature suggests lower numbers of moth abundance along high-trafficked roads and potential avoidant behaviour of moths towards high traffic, these mechanisms and their causes should be studied more thoroughly.

The number of individuals caught on the sticky traps varied with sampling time (Figure 10). Even though sampling time could not be included in the mortality model due to aggregation to the location level, the data plotted in Figure 10 can still provide suggestive patterns of moth activity. The highest number of individuals caught in the sticky traps occurred on average during 21:30 to 22:30

and 22:30 to 23:30, which concurs with a peak in moth activity during and right after sunset in the study area during summer. This pattern broadly aligns with the findings of Köhler et al. (2026) and is consistent with known patterns of moth nocturnal activity, where flight activity typically peaks shortly after sunset (Briolat et al. 2026). Even though the data illustrated in Figure 10 and Köhler et al. (2026) suggest a pattern of moth activity during the night with a potential peak around 22:30 to 23:30, there is still a lot of variability to be considered. Patterns of activity vary among species, with some having specified time windows of activity (Briolat et al. 2026; Köhler et al. 2026). Some species might be active in the darkest hours of the night; many also have prolonged activity into the mornings, sometimes showing higher activity at the beginning or end of the night or equal activity throughout (Briolat et al. 2026). Given the variety of moth families and species caught in the sticky traps, the difference in sampling effort and the limited sample size per timeframe, these patterns in moth activity should be considered exploratory rather than conclusive.

Another important factor to consider is the influence of species composition in road verges on the mortality of moths in traffic. Skórka et al. (2013a) found that road mortality in butterflies is, to some degree, a random process shaped predominantly by species composition and the abundance of butterflies on road verges. Due to similarities between moths and butterflies, this could also be the case for moth road mortality, especially given the positive effect of road verge abundance on mortality observed in the results. Even though a species composition analysis could not be conducted due to the limited number of identified species, some preliminary patterns can still be observed that might help contextualize the mortality results. Smaller butterflies have a tendency to be overrepresented in road-kills (Skórka et al. 2013a). Since smaller insects tend to fly over the asphalt at a lower altitude while crossing the road and therefore may be more at risk of colliding with a vehicle (Soluk et al. 2011; Skórka et al. 2013b; 2018), a similar pattern may apply to moths. Micro-moths (n = 64) were more frequently caught than macro-moths (n = 42), suggesting that smaller moths may be disproportionately vulnerable to vehicle collision.

None of the identified species were included in the Swedish Red List (SLU Artdatabanken 2026). Among the identified species, *Hoplodrina spp.* (n=7) and *Triodia sylvina* (n = 7) were the most frequently recorded in the sticky traps. Briolat et al. (2026) identified *Hoplodrina octogenaria (Hoplodrina spp.)* as one of the most active moths in their study, which investigated night-time activity patterns of nocturnal moths and the impacts of artificial light. This could also explain the higher abundance of *Hoplodrina spp.* in the sticky traps. During sampling, *Triodia sylvina* specimens appeared to be in mating season, exhibiting heightened flight activity. These observations suggest that moths with elevated activity levels are more likely to collide with passing vehicles, which could partially explain why road verge abundance was such a strong predictor of mortality. Thus, locations with more active moths would be expected to show higher mortality regardless of traffic intensity. To properly examine whether body size and activity had an impact on road mortality, a body size index and mobility index (see Skórka et al. 2013a) could be included in future research. As certain moth species are dependent on specific plant species or limited to specific habitats (Sterling et al. 2012; Townsend et al. 2019), an analysis of plant species in road verges may add additional value to a more comprehensive assessment of which moth species are most vulnerable to road mortality.

## 4.3 Implications for moth conservation and future research

As road verges are gaining attention as potential insect conservation sites (Meinzen et al. 2024; Horstmann et al. 2025), it is important to also consider management options that increase the habitat value of road verges for moths. The results of this thesis suggest that suspended or at least reduced mowing during the summer months has the biggest positive impact on the abundance of moths in road verges. A more comprehensive analysis of moth and plant species in road verges may provide more detailed suggestions for conservation and help identify potential beneficial measures for endangered moth species included in the Swedish Red List (SLU Artdatabanken 2026).

Improving the road verge quality in favour of moths is however, not without risk, as the results suggest that a higher abundance of moths in the road verges is associated with higher road mortality. This could imply that improving the quality of road verges for moths, and thus increasing moth abundance, will lead to higher rates of moth road mortality. So, the benefits of well-managed road verges could be outweighed by the negative impacts of traffic (Meinzen et al. 2024). Road verges could even act as an ecological trap – a sink habitat that is preferred rather than avoided (Battin 2004) - if they attract insects due to their habitat qualities and then trap them in a hostile environment next to road traffic. Ecological traps cause population sinks, which is an effect that has not yet been examined for any type of insect on any type of roadside (Meinzen et al. 2024).

However, there is evidence that adequate management of road verges can reduce insect mortality on roads and potentially offset the mortality risk associated with higher abundance. Skórka et al. (2013a) found that road verges with high diversity of flowering plants decreased the risk of butterfly mortality and suggested that the most suitable road verges for butterflies may suffer the least from road mortality. Even though they reported that the number of road-killed individuals increased with species richness and abundance in road verges, the proportion of road-killed individuals was not negatively affected. This indicates that the larger the butterfly population sizes in road verges, the lower the impact of road mortality on tose populations will be (Skórka et al. 2013a). Dániel-Ferreira et al. (2021) found that insects tend to stay longer in road verges with a high density of flowers. Moreover, mowing has been found to increase dispersal among butterflies and thus cause more frequent road crossings (Skórka et al. 2015). In addition to that, research shows that habitat patches with high resources can retain more moth individuals, and low host plant cover availability and poor resource conditions cause increased moth emigration (Harrison 1994; Menéndez et al. 2002; Karban et al. 2012). This may imply that road verges designed to benefit moths may act as environmental filters that stop them from emigrating and, furthermore, crossing a road, and minimize mortality caused by vehicle collisions (Skórka et al. 2013a).

To investigate fully whether high-quality road verges adapted to the habitat needs of moths can reduce the likelihood of road crossings and further decrease the mortality risks posed by passing vehicles, more comprehensive studies are necessary, especially since existing literature primarily focuses on diurnal insects. This may include investigating the direct effect of mowing on road moth mortality. I found that unmown road verges tend to support a higher abundance of moths and that, in turn, a higher abundance of moths increases moth road mortality. Therefore, it would be interesting to investigate whether unmown verges are associated with higher moth road mortality or whether their provision of tall vegetation as a suitable habitat hinders moths from crossing the road, indicating that road verges are valuable spots for moth conservation.

Another factor worth exploring might be the surrounding land cover. Skórka et al. (2013a) found that landscapes favouring butterflies, particularly grasslands, increased the number of road-killed butterflies but also increased their abundance and species richness. Moreover, the overall proportion of killed butterflies decreased, suggesting that grasslands may serve as a species pool, enabling butterflies to colonize road verges, and acting as a refuge during mowing (Skórka et al. 2013a). Thus, it would be of interest to investigate whether land cover types known to favour moths, such as grasslands or forests (Achury et al. 2025), in the vicinity of roads increase the moth conservation value of road verges. Due to the focus on local road verge characteristics, this was not done in this thesis.

As mentioned above, high traffic inherently increases exposure to threats such as pollutants or pALAN. Combining this with the lack of research regarding the potential risk of higher moth mortality rates along roads with high-quality verges, it is advisable to focus on road verges adjacent to low-traffic roads when designing conservation measures. This aligns with recent suggestions regarding other insect taxa (Dániel-Ferreira et al. 2022; Blomqvist et al. 2025; Horstmann et al. 2025). Further research could aid in establishing a threshold when traffic has such a large negative impact on moths that any effort to increase habitat quality might create an ecological trap.

# 5. Conclusion

This thesis investigated the factors influencing moth abundance in road verges and road moth mortality along Swedish road sites. The results highlight mowing management as the strongest driver of moth abundance in road verges, which emphasizes the importance of plant biomass as a resting and breeding place for moths. Contrary to expectations, the flowering plant species diversity of road verges did not significantly influence moth abundance, unlike findings for diurnal pollinators. This difference underscores the importance of studying diurnal and nocturnal insects separately, as the mechanisms driving their abundance in road verges appear to differ.

Moth road mortality was primarily driven by road verge abundance, with higher moth abundance associated with higher road mortality. Traffic intensity showed a negative effect on road mortality, which may be caused by a depletion mechanism where high traffic roads seem to support fewer moths in the adjacent road verges, resulting in fewer individuals available to be killed.

Together, these results raise an important conservation concern about whether road verges can serve as valuable conservation sites for moths. Even though results from other insect groups show that adequately managed road verges reduce the risk of road mortality and thereby offset the mortality risk associated with high road verge abundance, further research dedicated to moths is necessary. Extended research at the population level could clarify whether high-quality road verges act as ecological traps for moths and whether there is a traffic intensity threshold that triggers this population-sinking effect. Species-level analysis and detailed surveys of plant species in road verges would furthermore allow the development of more targeted conservation measures and the identification of especially vulnerable moth species. Additionally, incorporating surrounding land cover could provide a more complete picture of the conservation value of road verges for moths.

This thesis provided a first empirical assessment of the factors driving moth abundance in road verges and moth road mortality along Swedish roads. Given the significant negative impact of mowing on moth abundance in road verges, I suggest suspending mowing, particularly during July and August, as moth abundance peaks during these months. Since there is a gap in research regarding road verges potentially acting as ecological traps for moths, and high traffic intensity is associated with an increased exposure to different forms of pollution, moth conservation efforts in road verges should focus on low-traffic environments.

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# Popular science summary

Moths are one of the most species-rich insect groups on our planet, but have received considerably less attention from researchers and conservationists than their more colourful relatives, the butterflies. They remain largely understudied despite being crucial nocturnal pollinators and an important part of food webs across terrestrial ecosystems. Like many insects worldwide, moths are declining continuously, and roads are part of that problem. Their impact on insects extends beyond direct death through vehicle collisions. Roads also split the habitats of insects and expose them to pollutants, noise and artificial light. On the other hand, road verges could provide valuable habitats for insects in an otherwise increasingly developed landscape. Therefore, this thesis sets out to shed light on whether road verges are ultimately a boon or a bane for moths.

Over the course of three summer months in 2019, moths were sampled along 20 roads in Sweden. Sweep nets were used to catch resting and flying moths in the road verges, while sticky traps mounted on a car were used to collect moths killed through vehicle collision. The results revealed that the way road verges are managed matters enormously. Road verges that were not mown during the summer supported, on average, more than twice as many moths as mown verges. This suggests that simply suspending mowing of road verges could create big benefits for moths along roads. Moth abundance also increased over the summer, peaking in July and August. This serves as a reminder to suspend mowing, especially during these months. Interestingly, the diversity of flowering plants in road verges did not affect moth abundance, contrary to other findings on butterflies and bumblebees. This could be explained by an important difference between daytime and nighttime pollinators: Since not all moths are pollinators, they may rely more on tall, grassy vegetation for resting and egg-laying than on the diversity of flowers. When it comes to moth road mortality, more moths in the verges meant more moths killed by vehicles. But on busier roads moth mortality was lower, not higher. This counterintuitive finding may be explained by the fact that busy roads support fewer insects in the first place, leaving fewer individuals to be killed by vehicles. So, the damage caused by high-traffic roads may occur before the moths even reach the road.

If well-managed road verges attract moths into the danger zone next to roads, the benefits of good management could be offset by a high mortality risk. Research on other insects, however, suggests that a well-managed road verge reduces the likelihood that they will cross a road and thus reduces the mortality risk. Until this question gets clarified for moths specifically, I suggest focusing conservation efforts like reduced mowing on road verges adjacent to quieter, low-traffic roads. If done right, roads could become an unexpected ally in moth conservation.

# Appendix 1

*Table A1: 1: Results from the generalized linear mixed effects model with a negative binomial distribution exploring the relationship between moth abundance in road verges and traffic intensity, plant species diversity, mowing, sampling round and the interaction between mowing and traffic intensity (M6). Shown are the estimates (e), standard error (s.e.), z-values and p-values. P-values in bold are significant at the 0.05 level or lower.*

| **Variables** | **e** | **s.e.** | **z-value** | **p-value** |
|---|---|---|---|---|
| Intercept | 1.788 | 0.205 | 8.74 | **<0.001** |
| Plant species diversity LD | 0.024 | 0.202 | 0.12 | 0.905 |
| Sampling round 2 | 0.964 | 0.261 | 3.70 | **<0.001** |
| Sampling round 3 | 1.257 | 0.324 | 3.88 | **<0.001** |
| Mowing Yes | -0.963 | 0.263 | -3.66 | **<0.001** |
| Traffic intensity | -0.042 | 0.119 | -0.35 | 0.725 |
| Mowing Yes : traffic intensity | -0.324 | 0.233 | -1.39 | 0.165 |

*Table A1: 1: Results from the generalized linear mixed effects model with a negative binomial distribution exploring the relationship between moth abundance in road verges and traffic intensity, plant species diversity, mowing, sampling round temperature (M4). Shown are the estimates (e), standard error (s.e.), z-values and p-values. P-values in bold are significant at the 0.05 level or lower.*

| **Variables** | **e** | **s.e.** | **z-value** | **p-value** |
|---|---|---|---|---|
| Intercept | 1.648 | 0.221 | 7.46 | **<0.001** |
| Traffic intensity | -0.143 | 0.099 | -1.45 | 0.147 |
| Plant species diversity LD | 0.111 | 0.191 | 0.58 | 0.560 |
| Sampling round 2 | 1.123 | 0.282 | 3.99 | **<0.001** |
| Sampling round 3 | 1.525 | 0.340 | 4.49 | **<0.001** |
| Mowing Yes | -0.979 | 0.258 | -3.79 | **<0.001** |
| Temperature | 0.150 | 0.112 | 1.34 | 0.181 |

# Appendix 2

*Table A2: 1:Sticky trap data aggregated to location level (n = 20).*

| Location | Mortality | Road verge abundance | Plant species diversity | Traffic intensity | Verge width |
|---|---|---|---|---|---|
| Arlanda | 6 | 14 | HD | 829 | 5,41 |
| Aspö | 2 | 32 | HD | 5675 | 5,38 |
| Björklinge | 8 | 17 | LD | 247 | 2,88 |
| Enköping | 8 | 46 | LD | 841 | 4,29 |
| Gottröra | 3 | 9 | LD | 3718 | 4,4 |
| Häggeby | 2 | 18 | HD | 3312 | 4,665 |
| Hargshamn | 5 | 16 | HD | 1726 | 4,17 |
| Knutby | 9 | 12 | HD | 373 | 4,5 |
| Östhamnar | 2 | 16 | LD | 1662 | 3,55 |
| Rimbo | 3 | 16 | LD | 939 | 5,19 |
| Rovsättra | 4 | 23 | HD | 267 | 4,32 |
| Sigtuna | 4 | 15 | HD | 6356 | 5,231 |
| Skärplinge | 10 | 59 | HD | 570 | 3,8 |
| Skogstibble | 16 | 23 | LD | 158 | 3,98 |
| Skutskär | 19 | 72 | HD | 930 | 4,31 |
| Strängnäs | 12 | 29 | LD | 372 | 4,43 |
| Tierp | 5 | 33 | HD | 125 | 3,1 |
| Tosterön | 7 | 32 | LD | 5764 | 4,07 |
| Upplands Väsby | 7 | 43 | LD | 6168 | 4,76 |
| Vänge | 5 | 55 | LD | 562 | 4,15 |

*Table A2: 2: Sweep net data aggregated to round level (n = 59).*

| Location | Sampling round | Sampling time | Road verge abundance | Plant species diversity | Traffic intensity (vehicles/day) | Verge width (m) | Mowing | Temperature (°C) |
|---|---|---|---|---|---|---|---|---|
| Arlanda | 1 | 01:30-02:30 | 4 | HD | 829 | 5,41 | No | 15 |
| Arlanda | 2 | 23:30-00:30 | 6 | HD | 829 | 5,41 | Yes | 15 |
| Arlanda | 3 | 23:30-00:30 | 4 | HD | 829 | 5,41 | Yes | 12 |
| Aspö | 1 | 22:30-23:30 | 3 | HD | 5675 | 5,38 | No | 21,5 |
| Aspö | 2 | 00:30-01:30 | 1 | HD | 5675 | 5,38 | No | 12 |
| Aspö | 3 | 23:30-00:30 | 28 | HD | 5675 | 5,38 | No | 12 |
| Björklinge | 1 | 21:30-22:30 | 8 | LD | 247 | 2,88 | No | 14 |
| Björklinge | 2 | 21:30-22:30 | 4 | LD | 247 | 2,88 | Yes | 18 |
| Björklinge | 3 | 22:30-23:30 | 5 | LD | 247 | 2,88 | Yes | 15 |
| Enköping | 1 | 00:30-01:30 | 6 | LD | 841 | 4,29 | No | 18 |
| Enköping | 2 | 21:30-22:30 | 17 | LD | 841 | 4,29 | Yes | 12,5 |
| Enköping | 3 | 21:30-22:30 | 23 | LD | 841 | 4,29 | Yes | 15 |
| Gottröra | 1 | 23:30-00:30 | 3 | LD | 3718 | 4,40 | No | 10 |
| Gottröra | 2 | 00:30-01:30 | 5 | LD | 3718 | 4,40 | Yes | 13 |
| Gottröra | 3 | 22:30-23:30 | 1 | LD | 3718 | 4,40 | Yes | 14 |
| Häggeby | 1 | 21:30-22:30 | 11 | HD | 3312 | 4,67 | No | 15 |
| Häggeby | 2 | 23:30-00:30 | 2 | HD | 3312 | 4,67 | Yes | 12 |
| Häggeby | 3 | 22:30-23:30 | 5 | HD | 3312 | 4,67 | Yes | 14 |
| Hargshamn | 1 | 23:30-00:30 | 5 | HD | 1726 | 4,17 | No | 17 |
| Hargshamn | 2 | 20:30-21:30 | 10 | HD | 1726 | 4,17 | Yes | 20 |
| Hargshamn | 3 | 00:30-01:30 | 1 | HD | 1726 | 4,17 | Yes | 15 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Knutby | 1 | 21:30-22:30 | 6 | HD | 373 | 4,50 | No | 17,5 |
| Knutby | 2 | 21:30-22:30 | 3 | HD | 373 | 4,50 | Yes | 10 |
| Knutby | 3 | 22:30-23:30 | 3 | HD | 373 | 4,50 | Yes | 17 |
| Östhamnar | 1 | 00:30-01:30 | 1 | LD | 1662 | 3,55 | No | 15 |
| Östhamnar | 2 | 21:30-22:30 | 7 | LD | 1662 | 3,55 | Yes | 15 |
| Östhamnar | 3 | 23:30-00:30 | 8 | LD | 1662 | 3,55 | Yes | 15 |
| Rimbo | 1 | 21:30-22:30 | 4 | LD | 939 | 5,19 | No | 13 |
| Rimbo | 2 | 21:30-22:30 | 4 | LD | 939 | 5,19 | Yes | 11 |
| Rimbo | 3 | 22:30-23:30 | 8 | LD | 939 | 5,19 | Yes | 15 |
| Rovsättra | 1 | 21:30-22:30 | 9 | HD | 267 | 4,32 | No | 19 |
| Rovsättra | 2 | 23:30-00:30 | 13 | HD | 267 | 4,32 | No | 13 |
| Rovsättra | 3 | 22:30-23:30 | 1 | HD | 267 | 4,32 | Yes | 16 |
| Sigtuna | 1 | 23:30-00:30 | 5 | HD | 6356 | 5,23 | No | 13 |
| Sigtuna | 2 | 00:30-01:30 | 1 | HD | 6356 | 5,23 | Yes | 10,5 |
| Sigtuna | 3 | 21:30-22:30 | 9 | HD | 6356 | 5,23 | Yes | 15 |
| Skärplinge | 2 | 23:30-00:30 | 32 | HD | 570 | 3,80 | No | 17 |
| Skärplinge | 3 | 22:30-23:30 | 24 | HD | 570 | 3,80 | No | 12 |
| Skogstibble | 1 | 21:30-22:30 | 5 | LD | 158 | 3,98 | No | 17 |
| Skogstibble | 2 | 21:30-22:30 | 9 | LD | 158 | 3,98 | No | 12 |
| Skogstibble | 3 | 21:30-22:30 | 9 | LD | 158 | 3,98 | Yes | 14 |
| Skutskär | 1 | 21:30-22:30 | 5 | HD | 930 | 4,31 | No | 23 |
| Skutskär | 2 | 21:30-22:30 | 36 | HD | 930 | 4,31 | No | 18 |
| Skutskär | 3 | 21:30-22:30 | 31 | HD | 930 | 4,31 | Yes | 14 |
| Strängnäs | 1 | 23:30-00:30 | 11 | LD | 372 | 4,43 | No | 17 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Strängnäs | 2 | 21:30-22:30 | 9 | LD | 372 | 4,43 | No | 13 |
| Strängnäs | 3 | 22:30-23:30 | 9 | LD | 372 | 4,43 | Yes | 12 |
| Tierp | 1 | 23:30-00:30 | 1 | HD | 125 | 3,10 | No | 18,5 |
| Tierp | 2 | 00:30-01:30 | 10 | HD | 125 | 3,10 | No | 13 |
| Tierp | 3 | 00:30-01:30 | 22 | HD | 125 | 3,10 | Yes | 12 |
| Tosterön | 1 | 21:30-22:30 | 6 | LD | 5764 | 4,07 | No | 22 |
| Tosterön | 2 | 23:30-00:30 | 21 | LD | 5764 | 4,07 | No | 14 |
| Tosterön | 3 | 20:30-21:30 | 5 | LD | 5764 | 4,07 | No | 14 |
| Upplands Väsby | 1 | 21:30-22:30 | 17 | LD | 6168 | 4,76 | No | 20 |
| Upplands Väsby | 2 | 21:30-22:30 | 15 | LD | 6168 | 4,76 | No | 16 |
| Upplands Väsby | 3 | 21:30-22:30 | 11 | LD | 6168 | 4,76 | No | 17 |
| Vänge | 1 | 22:30-23:30 | 5 | LD | 562 | 4,15 | No | 18 |
| Vänge | 2 | 22:30-23:30 | 30 | LD | 562 | 4,15 | No | 11 |
| Vänge | 3 | 23:30-00:30 | 20 | LD | 562 | 4,15 | Yes | 15 |

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