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The impact of traffic, management and landscape on flower-visiting insects and plants in road verges

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Cover: Photograph of a road verge in Skåne that was partly mown in early summer, with Svenja Horstmann conducting a transect walk to inventory wild bees. Photo: Sophie Mueller.

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Abstract

Road verges can provide habitat for flower-visiting insects that depend on open grassland habitats for feeding and nesting resources. However, road verges can also be harmful or unattractive as habitat due to impacts from traffic or management. In this thesis, I contribute to understanding how traffic intensity, vegetation management and historical landscape context shape the diversity of wild bees, butterflies, plants and briefly solitary wasps in road verges. My results show that a considerable proportion of a region's wild bee and butterfly species can occur in road verges, including red-listed species. Older road verges exhibited a higher plant species richness than younger verges, and I detected a generally positive relationship between flower-visiting insect diversity and the availability of feeding resources. However, I show that high traffic can limit species abundance and richness of wild bees and butterflies, the attractiveness of potential nesting sites, as well as population growth and reproductive success of cavity-nesting insects. High traffic even limited the abundance of flower visitors in the surrounding landscape, although this did not influence pollination success of wild plants. Wide road verges buffered some of the negative effects of traffic on species abundance and richness. Vegetation management also played a significant role in determining habitat quality for insects. Road verges that were mown only once per year in late summer provided more floral resources and exhibited greater insect diversity, though this effect could vary depending on the specific conditions of the verge. Although road verges have the potential to support flower-visiting insects, I conclude that not all verges are equally suitable habitats. Furthermore, some species are particularly sensitive to the effects of traffic intensity, road verge width and management. Wide road verges along roads with little traffic offer the best opportunities for conservation actions. My findings can provide a roadmap for optimizing management to support the diversity of flower-visiting insects and plants along roads.

Keywords: Pollinator conservation, pollinating insects, roadside habitat, linear landscape elements, traffic volume, green infrastructure, mowing frequency, Lepidoptera, Hymenoptera, Aculeata

Effekter av trafik, skötsel och landskap på blombesökande insekter och växter i vägkanter

Abstract

Vägkanter kan utgöra livsmiljöer för blombesökande insekter som är beroende av öppna gräsmarker för föda och boplatser. Men vägkanter kan också vara skadliga eller oattraktiva som livsmiljöer på grund av påverkan från trafik eller skötsel. I den här avhandlingen bidrar jag till att förstå hur trafikintensitet, skötsel av vegetationen i vägkanterna, och den historiska landskapskontexten formar mångfalden av vilda bin, fjärilar, växter och solitära gaddsteklar i vägkanter. Mina resultat visar att en betydande andel av de vilda bi- och fjärilsarter som finns i en region också förekommer i vägkanter, inklusive rödlistade arter. Äldre vägkanter uppvisade en högre artrikedom av växter än nyare vägkanter. Generellt såg jag ett positivt samband mellan mångfalden av blombesökande insekter och tillgången på födoresurser. Jag visar dock att en tät trafik kan minska artrikedomen hos vilda bin och fjärilar, begränsa attraktionskraften hos potentiella boplatser, och populationstillväxten och reproduktionsframgången hos hållevande insekter. En tät trafik begränsade även antalet blombesökande insekter i det omgivande landskapet, även om detta inte påverkade pollineringen av vilda växter där. Breda vägkanter buffrar vissa av trafikens negativa effekter på artrikedomen. Vegetationsskötsel spelade också en viktig roll för att avgöra livsmiljöns kvalitet för blombesökande insekter. Vägkanter som klipptes endast en gång per år på sensommaren hade mer blommor och större mångfald av insekter, även om denna effekt kunde variera beroende på vegetationstyp. Även om vägkanter har potential att bidra till mångfalden av blombesökande insekter drar jag slutsatsen att alla vägkanter inte är lika lämpliga livsmiljöer. Vissa arter är dessutom särskilt känsliga för effekterna av trafikintensitet, vägkanternas bredd och skötsel. Breda vägkanter längs vägar med lite trafik erbjuder de bästa möjligheterna för naturvårdsåtgärder. Mina resultat kan ge en färdplan för att optimera skötseln för att bidra till mångfalden av blombesökande insekter och växter längs vägar.

Keywords: Bevarande av pollinatörer, pollinerande insekter, vägkanter, vägrenar, linjära landskapselement, trafikmängd, grön infrastruktur, slåtterfrekvens, fjärilar, steklar, gaddsteklar.

Die Auswirkungen von Verkehr, Vegetationsmanagement und Landschaft auf blütenbesuchende Insekten und Pflanzen in Straßenrändern

Abstract

Straßenränder können wertvolle Lebensräume für blütenbesuchende Insekten bieten, die für ihre Nahrungs- und Nistressourcen auf offene Graslandhabitate angewiesen sind. Gleichzeitig können Straßenränder jedoch durch den Einfluss von Verkehr und Vegetationsmanagement zu unattraktiven oder gar schädlichen Lebensräumen werden. In zeige in meiner Doktorarbeit, dass ein erheblicher Anteil der Wildbienen- und Schmetterlingsarten der Region in Straßenrändern vorkommt, darunter auch Rote Liste Arten. Ältere Straßenränder wiesen eine höhere Artenvielfalt an Pflanzen auf. Insgesamt konnte ich einen positiven Zusammenhang zwischen der Verfügbarkeit von Nahrungsressourcen und der Vielfalt blütenbesuchender Insekten feststellen. Allerdings konnte ich zeigen, dass stark befahrene Straßen die Artenvielfalt und die Abundanz von Wildbienen und Schmetterlingen, die Attraktivität potenzieller Nistplätze und das Populationswachstum sowie den Fortpflanzungserfolg von hohlraum-nistenden Insekten einschränken können. Sogar die Häufigkeit von Blütenbesuchern in der umgebenden Landschaft kann durch hohes Verkehrsaufkommen verringert werden. Breite Straßenränder können einige der negativen Auswirkungen des Verkehrs auf die Artenvielfalt und Abundanz reduzieren. Auch das Vegetationsmanagement, insbesondere die Häufigkeit und der Zeitpunkt der Mahd, spielt eine entscheidende Rolle für die Lebensraumqualität von Insekten. Straßenränder, die nur einmal jährlich und im Spätsommer gemäht wurden, wiesen mehr Blütenressourcen und eine größere Insektenvielfalt auf. Meine Ergebnisse zeigen, dass nicht alle Straßenränder gleichermaßen geeignete Lebensräume für Bestäuber darstellen. Breite Straßenränder an wenig befahrenen Straßen bieten die besten Möglichkeiten für Erhaltungsmaßnahmen. Die Ergebnisse meiner Studien können als Leitfaden zur Optimierung von Straßenrändern und somit zur Förderung der Diversität von blütenbesuchenden Insekten und Pflanzen dienen.

Keywords: Bestäuberschutz, bestäubende Insekten, Lebensraum am Straßenrand, lineare Landschaftselemente, Verkehrsaufkommen, grüne Infrastruktur, Mähfrequenz, Schmetterlinge, Hautflügler, Stechimmen

Dedication

To my family, and to my partner.

> “The greatest thing you'll ever learn
> is just to love and be loved in return”
> – in *Nature Boy*

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Svenja Horstmann, Alistair G. Auffret, Juliana Dániel-Ferreira, Erik Öckinger (2023). Species accumulation in novel grassland habitats is linked to land cover history. Ecography, 2023(8), e06704. https://doi.org/10.1111/ecog.06704

II. Svenja Horstmann, Alistair G. Auffret, Lina Herbertsson, Björn K. Klatt, Sophie Müller, Erik Öckinger (2024). Traffic intensity and vegetation management affect flower-visiting insects and their response to resources in road verges. Journal of Applied Ecology, 61(8), pp. 1955-1967. https://doi.org/10.1111/1365-2664.14692

III. Erik Öckinger, Svenja Horstmann, Lina Herbertsson, Björn K. Klatt, Alistair G. Auffret. Do species traits explain why certain wild bees and butterflies are not using road verges as habitat? (manuscript)

IV. Svenja Horstmann, Lina Herbertsson, Björn K. Klatt, Alistair G. Auffret, Erik Öckinger. Flower-rich road verges increase abundance of flower visitors in the surrounding landscape (under revision)

V. Svenja Horstmann, Sofia Blomqvist, Alistair G. Auffret, Lina Herbertsson, Björn K. Klatt, Matthew Low, Erik Öckinger. Abundance and reproductive success of cavity-nesting bees and wasps in road verges (manuscript)

All published papers are published open access.

The contribution of Svenja Horstmann to the papers included in this thesis was as follows:

I. Participated in the development of ideas and in the curation of the data, led the data analyses and the writing and revisions of the manuscript.

II. Participated in the development of the ideas and design of the study, performed the field work, led the data analyses and the writing and revisions of the manuscript.

III. Participated in the development of ideas, performed the field work, led the data analyses and participated in the writing of the manuscript.

IV. Participated in the development of the ideas and design of the study, performed the field work, led the data analyses and the writing of the manuscript.

V. Led the development of the ideas and design of the study, performed the field work, conceptualized the data analyses and led the writing of the manuscript.

1. Introduction

1.1 Flower-visiting insects in changing landscapes

1.1.1 Habitat loss as main driver of insect declines

Insect diversity is declining worldwide, with recent studies revealing declines in both abundance and species richness (Hallmann et al., 2017; Outhwaite et al., 2022; Sánchez-Bayo & Wyckhuys, 2019). Estimates suggest that even in protected areas, insect biomass has decreased by over 75% within three decades (Hallmann et al., 2017). Since 87% of all flowering plants are pollinated by animals and rely on animal pollination for genetic exchange among individuals (Ollerton et al., 2011; Winfree et al., 2011), this trend has sparked widespread concern about the future of biodiversity and ecosystem functioning. Indeed, there is evidence that flowering plant species that are pollinated by insects are declining disproportionally more than wind-pollinated plant species (Biesmeijer et al., 2006; Ehlers et al., 2021). There are multiple drivers of the insect decline, with land-use change and the accompanying habitat loss considered to be the main cause (Sánchez-Bayo & Wyckhuys, 2019; Zattara & Aizen, 2021).

Among the habitats severely affected by changes in land use in Europe are semi-natural grasslands, which are one of the most species-rich habitats in the world (Eriksson et al., 2002; Wilson et al., 2012), especially at small spatial scales. Over many centuries, semi-natural grasslands have been used for livestock farming as grazing land or to grow winter fodder, and the long continuity of low-intensity management through grazing or mowing has allowed the establishment of a diverse plant community (Cousins & Eriksson, 2002). Semi-natural grasslands support a diverse community of insects and contribute to the abundance and richness of flower-visiting insects even in the surrounding landscape (Öckinger & Smith, 2007b; WallisDeVries & Swaay, 2009). However, modern and more intensive farming methods have resulted in the abandonment of many semi-natural grasslands or to their conversion to arable fields or forest in northwestern Europe (Auffret et al., 2018; Cousins et al., 2015; Eriksson et al., 2002). Depending on the region, estimates of area losses of semi-natural grasslands range from 47-90% in the United Kingdom since the mid-1900s (Bullock et al., 2011; Ridding et al., 2015; Suggitt et al., 2023) and more than 90% during the last century in Sweden (Cousins et al., 2015; Eriksson et al., 2002).

As semi-natural grasslands are lost, so too is the biodiversity associated with them (Krauss et al., 2010; van Swaay et al., 2022). The past and ongoing loss of these flower-rich habitats severely impacts the diversity of flower-visiting insects due to the resulting loss of vital feeding and nesting resources (Dicks et al., 2021; IPBES, 2016; Potts et al., 2010). Flower-visiting insects such as wild bees, butterflies and solitary wasps feed on nectar as adults, but exhibit different life histories and reproductive strategies, which influence their habitat requirements and how they interact with the environment (Ekroos et al., 2010; Öckinger et al., 2010). Wild bee and solitary wasp species are central place foragers that need both feeding and nesting resources within their flight range (Greenleaf et al., 2007; Michener, 2007). Species that exhibit flower specialisation can be sensitive to environmental changes, as they rely on the availability of one plant species (monolecty) or several species within a genus or family (polylecty; Michener, 2007). However, even the more generalist polylectic species that forage on various plants face population declines (Michener, 2007; Winfree, 2010). Wild bees and solitary wasps nest above- or below-ground in pre-existing cavities or by excavating nests in soil, plant stems, or trees (Michener, 2007). In intensive agricultural landscapes with little natural or semi-natural habitats left, both woody plants and open, bare soil can be rare, which can limit nesting opportunities. Butterflies are not central-place foragers and are less specialised on flowers for adult feeding, yet many species are relatively specialised to a particular larval host plant, limiting the habitats in which they can reproduce (Settele et al., 2009). Furthermore, some butterfly species are more or less restricted to certain habitat types such as semi-natural grasslands, and less mobile and more specialised species are more susceptible to habitat change or loss than generalist species (Öckinger et al., 2010; Sekar, 2012).

1.1.2 Widening the focus for the conservation of insect diversity

Remaining fragments of semi-natural grasslands often still harbour a high plant and insect diversity (Cousins, 2006; Lindborg et al., 2014). However, these grassland remnants may be threatened by land-use changes that have already occurred. There is evidence that mainly plants but occasionally also flower-visiting insects can show delayed responses to land use change, and can still decline after several decades after landscape homogenization or habitat fragmentation (Bommarco et al., 2014; Kuussaari et al., 2009; Lindborg & Eriksson, 2004). Furthermore, despite ongoing conservation efforts, the area of semi-natural grasslands in Sweden is still decreasing by an estimated 0.8% every year (Wikberg et al., 2023). Hence, to support and conserve species associated with these open habitats, there is a need to include a broader range of habitats into conservation management. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) highlights in their pollinator report that the traditional focus on biodiversity conservation in core areas alone can contribute to meeting national and international biodiversity conservation goals (IPBES, 2016).

1.2 Novel grassland habitats along roads

1.2.1 A novel habitat for the conservation of flower-visiting insects

A less conventional conservation opportunity for flower-visiting insects that has been gaining attention are novel grassland habitats along linear infrastructure such as roads, railways and power lines (Figure 1). These habitats are managed regularly to maintain an open early-successional vegetation mainly for traffic safety reasons, but this has resulted in a vegetation that at least to some extent resembles that of traditionally managed semi-natural grasslands (Dániel-Ferreira et al., 2023; Gardiner et al., 2018). Indeed, road verges can harbour a species richness of plants and flower-visiting insects comparably to in semi-natural grasslands and support many endangered and grassland specialist species (Dániel-Ferreira et al., 2023; Gardiner et al., 2018; Helldin et al., 2015). They can offer feeding resources for flower-visiting insects (Halbritter et al., 2015; Noordijk et al., 2009), larval host plants for butterflies (Valtonen et al., 2006), and nesting and overwintering habitats for wild bees and other arthropods (Hopwood, 2008; Schaffers et al., 2012).

As well as providing suitable habitat conditions for grassland species, road verges also have the benefit that they already exist in most landscapes and might readily be used as tool for biodiversity conservation (Gardiner et al., 2018). Worldwide, the global road network now has an estimated length

Figure 1. Photos of two road verges in Skåne county, southernmost Sweden. Road verges can provide floral resources for flower-visiting insects, as well as resources for reproduction, such as larval host plants for butterflies or nesting opportunities for wild bees and solitary wasps in cavities in trees or plant stems or in bare open soil. Photos: Svenja Horstmann.

of almost 37 million kilometres, of which almost 7 million kilometres are found in across Europe (Central Intelligence Agency, 2024). Assuming that road verges have an average width of 4 metres on either side (cf. Phillips et al., 2020a) this would translate to 56,000 square kilometres of road verges in Europe, which is roughly the size of Croatia. In Sweden, the area covered by road verges is more than half the size of the area of traditionally managed semi-natural grasslands (Jordbruksverket, 2021; Stenmark, 2012).

Due to the combination of potentially attractive habitat and the large area they cover, novel grassland habitats along linear infrastructure have been discussed as potential replacement or supplementary habitats for species suffering from the loss of traditional semi-natural grasslands (Gardiner et al., 2018). Road verge management poses an immediate opportunity to enhance conditions for flower-visiting animals, including insects (IPBES, 2016). However, road verges do not support all species that can be found in semi-natural grasslands (Dániel-Ferreira et al., 2023) and can importantly also be potentially harmful habitats, involving risks from traffic mortality, pollution and disturbance via mowing (Muñoz et al., 2015; Phillips et al., 2020). With the growing focus on managing road verges to enhance grassland biodiversity, it is crucial that there is a thorough investigation of how the diversity of flower-visiting insects in road verges is affected by various anthropogenic and environmental impacts (Fig. 2).

1.2.2 Impacts and responses in road verges

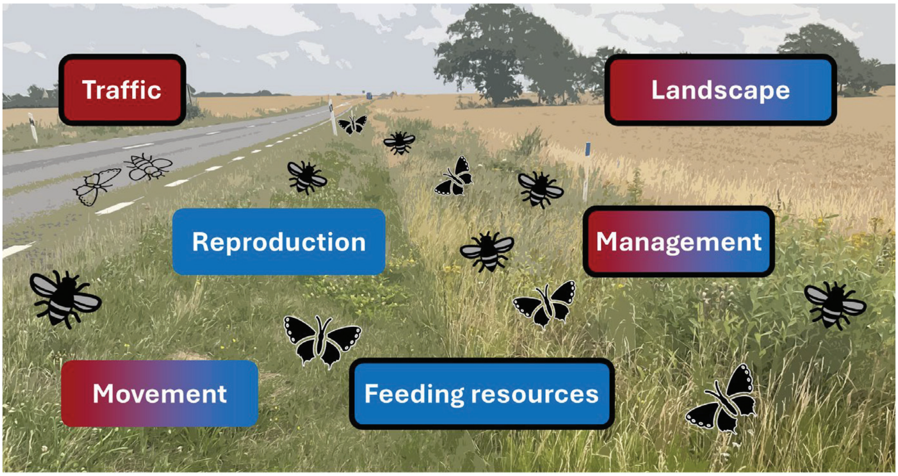


Figure 2. Simplified overview of different impacts (framed black) that can influence the diversity of flower-visiting insects and their movement and reproduction in road verges. Potential positive impacts are coloured blue, potential negative impacts red, and a colour combination indicates that both positive and negative impacts are possible. Photo in background: Svenja Horstmann.

Traffic

Traffic can impact flower-visiting insect populations and communities in road verges in several ways, including the direct mortality from collisions with vehicles (Dániel-Ferreira et al., 2022a; Muñoz et al., 2015; Skórka et al., 2013, 2015), but also by decreasing habitat quality by causing physical disturbance, vibrations, noise as well as dust and metal pollution (Meinzen et al., 2024; Mitchell et al., 2020; Phillips et al., 2021). Additionally, insects may avoid otherwise suitable habitats near roads for foraging if they perceive the environment as too hostile (Blomqvist et al., unpubl.), and may even avoid nesting in areas with a road in the proximity (Van der Meersch et al., 2022). With increasing traffic intensities, the abundance of flower-visiting insects in road verges has been shown to decline (Phillips et al., 2019), as well as the mortality of flower-visiting insects, as shown for butterflies and bumblebee queens (Dániel-Ferreira et al., 2022a; Skórka et al., 2013).

The impact of traffic can also vary depending on the road verge quality, and concerns have been raised that road verges with abundant floral resources are potential ecological traps, whereby individuals are attracted to seemingly high-quality habitats that then result in a lower fitness or higher mortality (Battin, 2004; Gardiner et al., 2018; Keilsohn et al., 2018). Furthermore, traffic does not appear to affect all species the same. In butterflies, traffic mortality was found to be higher for species that are smaller or more mobile (Halbritter et al., 2015; Munguira & Thomas, 1992; Remon et al., 2018; Skórka et al., 2013). Butterfly mortality may also be higher when there are fewer floral resources in a road verge, which may be explained by fewer butterflies leaving road verges with abundant resources (Ries et al., 2001; Skórka et al., 2013, 2015). However, less is known about road mortality in wild bees (Meinzen et al., 2024; Muñoz et al., 2015). Bee mortality may be higher when there are more floral resources available (Keilsohn et al., 2018), which is the opposite pattern of butterfly mortality (Skórka et al., 2015). However, in a Swedish study, flower diversity in road verges did not affect traffic mortality of bumblebee queens (Dániel-Ferreira et al., 2022a). It remains unclear if insect populations in road verges exhibit a positive net population growth, due to limited research on how traffic affects the reproductive success of flower-visiting insects in road verges (Meinzen et al., 2024) or how it may impact entire communities (Dániel-Ferreira et al., 2022b; Phillips et al., 2019).

Vegetation management

In many European countries and the United States, rural road verges are often mown once or twice per season for traffic safety reasons (Jakobsson et al., 2018). In Sweden, mowing twice per season is the norm, with the mowing frequency of road verges identified as having high biodiversity values reduced from to once per season, mainly targeting plant diversity (Lindqvist, 2018). However, depending on local habitat conditions in road verges of northern Europe, mowing only once per year may not be sufficient if the vegetation is dominated by competitive species, while mowing twice has been shown to keep the abundances of grasses at bay while increasing the abundance of forbs (Jakobsson et al., 2018). Providing general recommendations for plant diversity, the review by Jakobsson et al. (2018) showed that mowing once or twice only enhances plant diversity when combined with hay removal, because otherwise the cut hay increases nutrient deposition favourable for dominant species.

Changing the frequency of vegetation management also affects the timing of the disturbance and has a direct impact on flower-visiting insects in road verges. If road verges are mowed twice, they are usually mown both during and after the summer. Summer mowing can result in a subsequent decline of flower-visiting insects due to a removal or reduction of the pollen and nectar resources during peak flowering season (Halbritter et al., 2015; Phillips et al., 2019; Saarinen et al., 2005; Valtonen et al., 2006). However, subsequent regrowth following mowing can in turn offer feeding resources and host plants later in the season (Erhardt, 1985; Noordijk et al., 2009). For butterflies, mid-summer mowing may result in the damage of potential host plants at a critical time for many species (Valtonen et al., 2006) and even kill butterfly offspring in all developmental stages (Courtney & Duggan, 1983; Erhardt, 1985; Feber et al., 1996). Mowing may also have indirect but detrimental effects on butterflies, since it was shown to result in higher mortality rates through collisions with vehicles, likely by causing increased dispersal across the road (Skórka et al., 2013).

Recommendations to adapt the management for biodiversity conservation are often largely based on findings from other habitats such as semi-natural grasslands, and most studies about vegetation management in road verges have focussed on plants alone (Jakobsson et al., 2018). However, the response of plants and insects to management can differ (Berg et al., 2019) and it is not clear if a management beneficial for plant diversity is always beneficial for the diversity of flower-visiting insects.

Feeding resources

Road verges can offer abundant resources of flowering plants for flower-visiting insects (Gardiner et al., 2018; Meinzen et al., 2024; Phillips et al., 2019; 2020b) as well as host plants for butterfly larvae (Munguira & Thomas, 1992; Valtonen et al., 2006). There is a positive relationship between the general abundance of flowers and flower-visiting insects in road verges (Phillips et al., 2019). However, flower resources in road verges may be inaccessible to wild bees and other central-place foragers such as solitary wasps if there is no suitable nesting habitat nearby, or if the distance to nesting sites is too far. This may be particularly true for small species with limited foraging ranges (Greenleaf et al., 2007). Furthermore, feeding resources may be destroyed if the vegetation is managed at a crucial time for certain species, if the majority of the flowers that insects rely on are removed or larval host plants for specialist herbivores are destroyed.

Reproduction

Road verges can provide nesting sites for ground-nesting insects in bare, undisturbed soil (Hopwood, 2008) and cavity-nesting insects may find nesting opportunities in cavities in wood or plant stems. In a study about the effect of oilseed rape abundance on cavity-nesting bees and solitary wasps in experimental nest structures, the authors incidentally found that nest occupancy was lower in the vicinity of roads (Van der Meersch et al., 2022), indicating a deterring effect of roads on individuals searching for nesting sites. However, information about reproductive success in road verges is limited for butterflies and lacking for other flower-visiting insects such as wild bees and solitary wasps (Meinzen et al., 2024; Phillips et al., 2020b).

Movement

Road verges have been proposed to act as a part of a network of semi-natural grasslands, and that providing a broader network could enhance spatial and temporal dynamics of grassland ecosystems and buffer effects of habitat loss and fragmentation of semi-natural habitats on plant diversity (Auffret & Cousins, 2013; Lindborg et al., 2014). Road verges have also been shown to act as corridor for the movement flower-visiting insects, but at the same time, roads can serve as barriers for movement and may contribute to landscape fragmentation for insect populations (Andersson et al., 2017; Dániel-Ferreira et al., 2022b; Fitch & Vaidya, 2021).

So far, there is little knowledge about the contribution of road verges to insect abundance in the surrounding landscape. A study on the contribution of road verges to wild plant pollination planted within arable fields at a 30 m distance showed a positive relationship between the number of flower visitors and the flower abundance in the nearby road verge (Monasterolo et al., 2022). However, this study was conducted along small gravel roads with little traffic. Since traffic on the adjacent road can limit the abundance of potential pollinators (Phillips et al., 2019), it remains unclear if traffic can also limit the number of flower-visiting insects that move from the road verge to the surrounding landscape.

Landscape

Fragmented patches of semi-natural grasslands can be a source habitat for plants in homogenous landscapes, and road verges can be both habitats and dispersal corridors for plants (Lindborg et al., 2014; Tikka et al., 2001). Studies show that both past and present grassland land cover and connectivity can influence plant species richness in semi-natural grasslands and novel grassland habitats along linear infrastructure (Jakobsson et al., 2016; Lampinen et al., 2018; Lindborg et al., 2014). Legacy effects of historical land cover are more likely to occur in long-lived organisms such as plants, but have also been found for butterflies and hoverflies (Bommarco et al., 2014; Kuussaari et al., 2009; Sang et al., 2010). Furthermore, since insects depend on the sufficient availability of certain plants for feeding and reproduction, their colonisation in a new habitat may be indirectly delayed by the slow establishment of the local plant community (Krauss et al., 2010). Nonetheless, studies on landscape legacy effects in linear infrastructure habitats that include both plants and insects and how these interacting species groups are still limited.

Compared to old traditional semi-natural grasslands, many road verges are young habitats. Hence, while plant species in semi-natural grasslands that are affected by habitat fragmentation or degradation can exhibit a time-lagged local extinction (Auffret et al., 2018; Bommarco et al., 2014; Krauss et al., 2010), plant species richness in road verges may instead experience a time-lagged immigration of species and increase with road age (Auffret & Lindgren, 2020; Spooner & Smallbone, 2009). This ‘immigration credit’ (Jackson & Sax, 2010) seems to work slowly, as roads that are already older than 60 years are still not as species rich as historical roads that are at least twice as old (Auffret & Lindgren, 2020).

1.2.3 Disentangling drivers of insect diversity in road verges

Road and road verge characteristics, vegetation management and traffic intensity can all impact plant and insect communities in road verge habitats, positively or negatively (Angold, 1997; Lampinen et al., 2018; Meinzen et al., 2024; Phillips et al., 2019). The impact of traffic is especially important to understand, as it may interfere with otherwise beneficial habitat conditions such as the availability of feeding and nesting resources for insects. However, the limited number of experimental studies so far has made it challenging to clearly identify the specific traffic and non-traffic related factors influencing flower-visiting insects in road verges (Phillips et al., 2020b). To determine whether novel grassland habitats can effectively support flower-visiting insects, it is essential to further investigate different drivers of insect diversity in road verges, considering both a variety of different road verge characteristics, as well as different types of responses that insects can exhibit.

2. Aims and Objectives

The main aim of my thesis is to evaluate to what extent and under which conditions road verges can support flower-visiting insects. I address this by considering long-term effects of historical land cover and short-term effects of traffic and vegetation management on the diversity of vascular plants, wild bees and butterflies and briefly solitary wasps. Specifically, my research objectives are:

- To investigate if the landscape history in and around road verges influences present-day species richness of plants, butterflies and bumblebees (**Paper I**).
- To assess if management targeted to enhance plant diversity also benefits the diversity of flower-visiting insects, and if traffic moderates any potential positive effects of otherwise attractive habitats, both in terms of the abundance and species richness of wild bees and butterflies (**Paper II**), and how insect traits and road verge characteristics can explain which species are absent from road verges (**Paper III**).
- To test if flower-rich road verges enhance the abundance of flower-visiting insects in the surrounding landscape and hence contribute to wild plant pollination (**Paper IV**).
- To investigate how the abundance and reproductive success of cavity-nesting wild bees and solitary wasps in road verges is related to traffic intensity, and how road verges compare to semi-natural grasslands (**Paper V**).

3. Materials and Methods

3.1 Study sites and study design

All data for this thesis was collected in Sweden (Fig. 3). For **Paper I**, the data was collected across the counties of Uppsala, Stockholm, Södermanland and Västmanland. Data was collected in both road verges and power line corridors but in this thesis, only the road verges are discussed. For **Paper II-V**, the data was collected in and around road verges and in semi-natural grasslands (for **Paper V**) in Skåne county.

3.1.1 Paper I

To investigate the influence of more than 100 years of landscape history on present-day species richness of vascular plants and flower-visiting insects in road verges, biodiversity data was used that was collected in 2016 as part of a project that produced two other studies (Dániel-Ferreira et al., 2020, 2023). For these studies, 32 landscapes of 2 × 2 km were selected that currently have a similar cover of forest and arable land, but different amounts of semi-natural grasslands, and half of them to contain a power line corridor and half of them not (Dániel-Ferreira et al., 2020, 2023).

3.1.2 Paper II-V

To disentangle the effects of traffic intensity and road verge quality and management on flower-visiting insects, a crossed study design including originally 40 road verges across four different categories was set up in collaboration with the Swedish Transport Administration (Trafikverket). This study design was the basis of the biodiversity data collection for **Paper II-V** during 2021 and 2022 (Fig. 4).

The Swedish Transport Administration is continuously working on inventorying road verges to identify those road verges that are valuable for biodiversity (named species-rich road verges, artrik vägkant in Swedish), because they for example contain a high number of grassland indicator species or rare species (Lindqvist, 2018). These road verges, which are referred to as ‘valuable’ road verges in this thesis and included papers, are put under a biodiversity-targeted management regime of mowing only once per season, usually in August (‘late summer’ mowing; category (i) in Fig. 4).

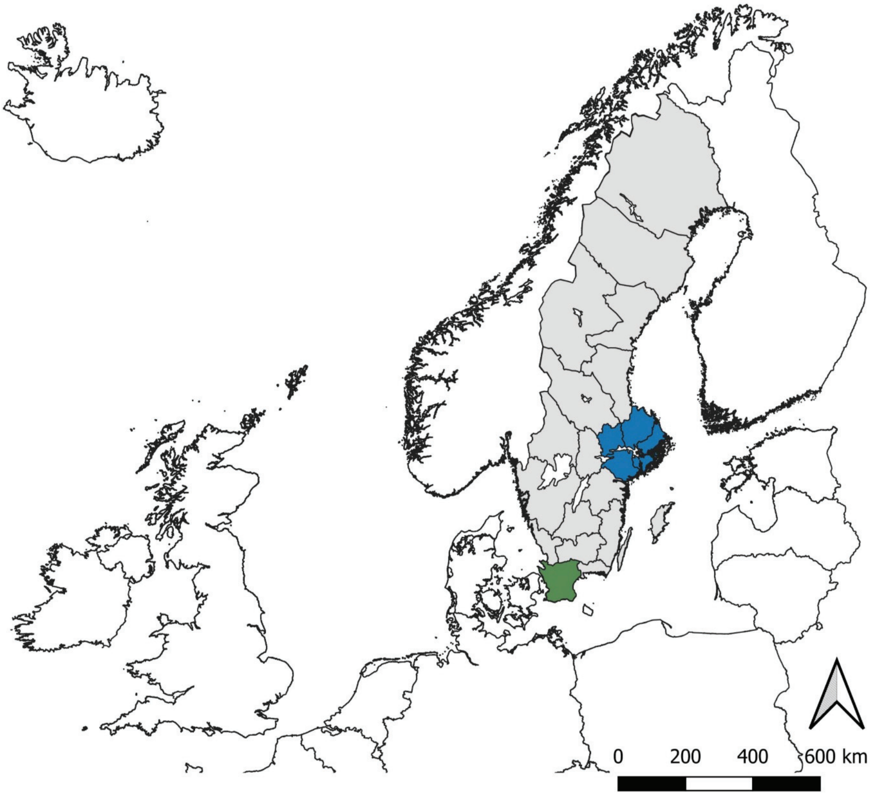


Figure 3. A map of parts of northwestern Europe, with Sweden highlighted in grey and colours, with blue and green showing the study areas of this thesis. For **Paper I**, data was collected in the counties of Uppsala, Stockholm, Södermanland and Västmanland (all shown in blue). For **Paper II-V**, data was collected in Skåne (shown in green).

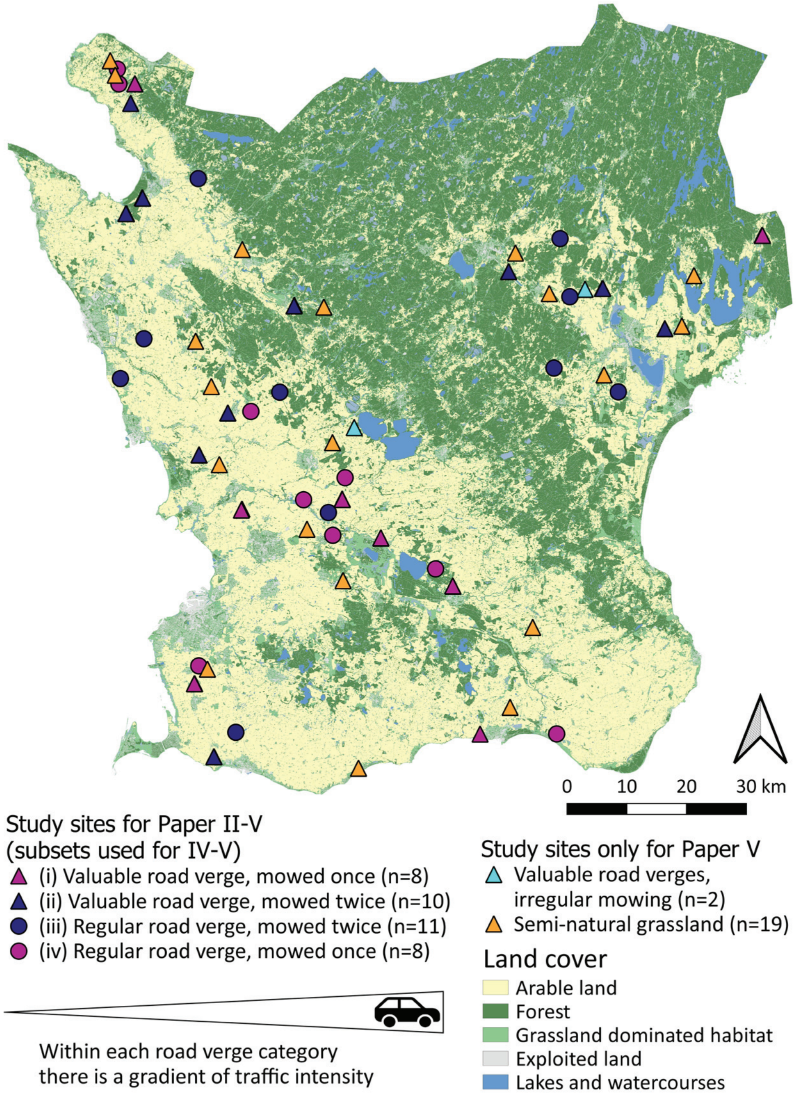


Figure 4. A map of Skåne county in southernmost Sweden, indicating the locations of all final 58 study sites across **Paper II-V**. Road verges were selected to achieve a crossed study design, separating effects of habitat quality (shapes) and mowing regime (colours). Within each road verge category (combination of shape and colour), a similar gradient of traffic intensity was ensured. For **Paper II** and **III**, the same 37 study sites were used, all of them road verges, indicated by pink and dark blue shapes. For **Paper IV**, a subset of 19 road verges across all categories was used (not indicated in the map). For **Paper V**, 19 semi-natural grasslands were used (yellow triangles), as well as all except one valuable road verge from **Paper II** and **III** and two other road verges (light blue triangles), resulting in 38 study sites (all triangles except the bottom pink one).

During the late summer mowing, the complete road verge is mown. For road verges that have just recently been classified as valuable, it usually takes one or two years until the mowing regime is adapted. Therefore, these road verges form a temporary third category of valuable road verges that are mown twice (category (ii) in Fig. 4). Mowing twice is the ‘regular’ management regime for road verges in Sweden, which entails mowing once before mid-June and once in late September (referred to as ‘early summer’ and ‘autumn’ mowing in **Paper II**; category (iii) in Fig. 4). During the first mowing, only the first approximately 1.5 m adjacent to the road are mowed, whereas during the second mowing the whole road verge is mowed (see Fig. 5 for a photo). To complete the crossed study design, some regular road verges that are usually mown twice were put under the biodiversity-targeted management of mowing only once, only for the duration of the field inventories conducted for this thesis (category (iv) in Fig. 4). This was achieved in collaboration with the Swedish Transport Administration and their contractors. The mowing regimes, regardless of regular or biodiversity-targeted, usually do not involve the subsequent removal of the hay material from the road verge.

Figure 5. Photos of two road verges in Skåne county in southernmost Sweden. The road verge on the left is under the ‘regular’ management and is mown twice per year, in early summer and autumn. The early summer mowing is only conducted along the first approximately 1.5 m along the road, which can be seen in the photo, whereas the second mowing is conducted across the whole road verge width. The photo on the right shows a ‘valuable’ road verge, which is under biodiversity-targeted management, i.e. it is only mown once per year, in late summer, and then across the whole road verge width. Photos: Svenja Horstmann.

To select the road verges used in **Paper II-V**, environmental and infrastructure data from the National Road Database was used (Trafikverket, 2021), which contains among others information about valuable road verges and their mowing regime. Road verges in rural landscapes that are classified as valuable and are longer than 200 m, along roads with speed limits of 50 km/h or above were selected. Traffic intensity data, measured as the average number of vehicles per day, was extracted from the same database. The selection of potential study sites was filtered for roads surrounded by up to 50% forest and at least 30% arable land within a 2 km buffer and excluding areas with valuable grassland habitat within 350 m using QGIS (QGIS.org, 2020) and data from the National Land Cover Database and the TUVA database of meadows and pastures of high-nature value in Sweden (Jordbruksverket, 2021; Naturvårdsverket, 2020). 20 valuable road verges were selected that were at least 2 km apart, half of which mown once, i.e. in late summer, and half twice, i.e. in early summer and autumn, ensuring a gradient of traffic intensity between the adjacent roads. For comparison in the crossed study design, 20 regular road verges were selected to be within 2–20 km distance of the paired species rich road verges, with matching traffic and landscape criteria of the paired valuable road verges. For half of these regular road verges, a change in mowing regime from twice to once was organized in collaboration with the Swedish Transport Administration. Within each road verge category ((i) valuable, mowed once; (ii) valuable, mowed twice; (iii) regular, mowed twice; (iv) regular, mowed once), there is a gradient of traffic intensity from 92 to 5661 vehicles per day (Fig. 4). The mean width of selected road verges varied between 1.9 m and 13.9 m, but was independent from road verge classification and mowing regime. Thus, with this study design, it is possible to separate the effects of habitat quality and mowing regime along a gradient of traffic intensity on plants and flower-visiting insects in road verges.

For some of the original 40 road verges the category had to be changed afterwards due to changes in mowing regime and one was excluded completely. From the 39 remaining road verges, different combinations were used within the different paper (Fig. 4). For **Paper II** and **III**, the complete data set from the 39 road verge sites described above was used, but two sites had to be excluded due to an irregular mowing regime, resulting in 37 road verges (8 from category (i), 10 from (ii), 11 from (iii) and 8 from (iv); see Fig. 4). For **Paper IV**, the focus was put on floral resources in the road verges, and mowing regime or road verge quality were not investigated. Hence, a subset of 20 road verges across all categories was used, still ensuring a gradient in traffic intensity. The road verges were selected for having a linear landscape element diverging approximately orthogonal from road verge. These elements were either field borders between two fields or between a field and a small private road. One study site had to be excluded, resulting in 19 road verges included in **Paper IV** (7 from category (i), 1 from (ii), 7 from (iii) and 4 from (iv) For **Paper V**, all except one of the18 valuable road verge that were included in **Paper II** and **III** were used, as well as two additional road verges (Fig. 4). Furthermore, 20 semi-natural grasslands were selected, each as close to one paired road verge as possible, but not closer than 2 km (resulting in distances between 2.9 and 24.3 km, with a median of 7.7 km). Only semi-natural grasslands that were larger than 0.5 ha, not classified as wet habitats (Jordbruksverket, 2021) and managed by either grazing or mowing were selected. One semi-natural grassland had to be excluded, resulting in 19 semi-natural grasslands and 19 road verges used in **Paper V**.

3.2 Data collection

3.2.1 Field inventories of plants and flower-visiting insects

Paper I

Within each of the 32 2 × 2 km landscapes, biodiversity surveys were conducted in each one road verge of a gravel and a paved road. Within these study sites, one 200 m transect was created, within which transect walks were conducted to survey butterflies and burnet moths (hereafter included in 'butterflies') and bumblebees four times between June and August 2016. Butterflies were counted and identified within 2.5 m of the observer ('Pollard Walk'; Pollard, 1977), and bumblebees were observed within 1 m of the observer. If the road verges were narrower than the transect width, the whole road verge width was inventoried, but the area adjacent to it was not included. To sample vascular plants, four 1 × 1 m plots were placed within each transect, and species' presences within each plot were noted.

Paper II-V

For **Paper II-V**, the biodiversity data was collected together as part of one big study design. In each of the in total 39 road verge sites, a 200 m transect was selected on one side of the road, within which transect walks to survey butterflies (including burnet moths) and wild bees were conducted between May and July 2021. Butterflies were counted and identified during a Pollard Walk, i.e. within 2.5 m of the observer during four separate surveys (Pollard, 1977). Wild bees were surveyed three times during the study period, observed within 1.5 m of the observer, during which bumblebees were counted and identified in the field and solitary bees were collected for later identification in the lab. The transect walks were always conducted so that the outer observation range was adjacent to the road, and for road verges narrower than the planned transect width the whole road verge width was surveyed. Within the same 200 m transects and on the same day as the wild bee surveys, all currently flowering plants were identified and their abundance estimated across the whole width of each road verge. Furthermore, all vascular plants were identified once per road verge in either 2021 or 2022, in 10 1 × 1 m plots that were placed within the same 200 m transect that was used for the butterfly, wild bee and flowering plant inventories. In addition to the plot surveys, the presence of important larval host plants or nectar plants outside of the plots was checked by walking once along the middle of the 200 m transect (list of plants in Supplementary Material of Paper **III**).

For **Paper V**, the data of currently flowering plants in road verges was only used for the outer edge of the road verge, i.e. the area that was not mown during the field inventories, regardless of mowing regime. Additionally, currently flowering plants were inventoried in 19 semi-natural grasslands, three times between May and July 2022. To match the method used in the road verges, a 200 m transect was used. The width reflected the mean width of the outer edge of all road verges included in this study (4.2 m). To reflect the edge conditions in the road verges, the transects were either placed as a continuous line close to the edge of the semi-natural grassland, or if this was not possible, split and placed within a 100 m semi-circle. Within each transect, the abundance of all currently flowering plants was estimated.

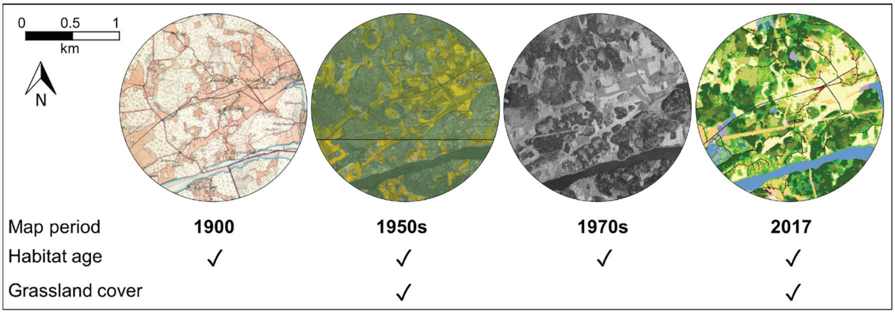
3.2.2 Analyses of historical and contemporary maps

Historical and current land cover

For **Paper I**, historical and current land cover in the surroundings of surveyed road verges was calculated in a 2 km buffer around the study sites using maps from two time periods (Fig. 6). For historical land cover, published digitisations of the 1940s–1960s Swedish Economic Map (*Ekonomiska kartan*, hereafter '1950s map') were used (Auffret et al., 2017a, 2017b). The digitisations give information about land cover of surface water, arable, forest and grassland. The grassland category mostly consists of semi-natural grassland habitat, but can also include other open land, such as wetlands and urban land (cf. Auffret et al. 2018). For current land cover, Sweden's National Land Cover Database (*Nationella marktäckedata*) based on data from 2017-2019 was used (hereafter '2017 map'; Naturvårdsverket, 2020). The 25 land cover categories from the 2017 map were reclassified to match the four broader land cover types of the 1950s map (Supporting information of **Paper I**), and the proportion of grassland within each buffer at each time period was calculated. Because there is no differentiation of species-rich semi-natural grassland from other grassland types in the 2017 map, the proportion of pixels within each buffer that was classified as grassland both in the 1950s and in the 2017 maps was calculated additionally (referred to as 'continuous grasslands' in **Paper I**). All land cover calculations were conducted using R (R Core Team, 2021).

Habitat age

To identify the age of the studied road verges in **Paper I**, four maps from different time periods were used (Fig. 6). In addition to the 1950s and 2017 maps that were used for the land cover calculations, two other non-digitised sources were used: historical maps created between 1859-1911 for our landscapes (*Häradsekonomiska kartan*, hereafter '1900 map'), and geo-referenced aerial photographs that were taken between 1970 and 1976 (hereafter '1970s map'). First, it was examined in which map each studied road verge appeared for the first time, then all habitats were grouped into four categories corresponding to the four points in time (Supporting information of **Paper I**). Knowledge about the exact management history of the road verges is not available, but it is assumed that the vegetation has always been kept relatively open. All maps except the 1900 map are geo-referenced and the habitats were visually assessed using QGIS (QGIS.org, 2020). For the 1900 map, the habitats were located manually using unaltered landmarks.



Map period	1900	1950s	1970s	2017
Habitat age	✓	✓	✓	✓
Grassland cover		✓		✓

Figure 6. Overview of maps from four different time periods that were used to assess habitat age and historical and current grassland cover around linear infrastructure habitats (within a 2 km buffer, as shown). The 1950s map was digitised (Auffret et al., 2017a, 2017b), other pictures show the original. The figure is reprinted from **Paper I** under the Creative Commons CC BY license (https://creativecommons.org/licenses/by/4.0/).

3.2.3 Species traits from published sources

In **Paper III**, data on the regional species pools and species traits was compiled to investigate if all wild bee and butterfly species occurring in the study region can take advantage of resources provided in road verges, or if some species are affected by traffic and road verge characteristics more than others. The list of all bee and butterfly species observed during 2000-2023 in Skåne was downloaded from the Swedish Species Gateway (Artportalen, 2024). To exclude potentially misidentified species and those not regularly breeding in the region, any species with fewer than five records were excluded. For butterflies, three wetland specialist species and two migrant species were excluded (van Swaay et al., 2006). Furthermore, honeybees were excluded. Wild bees were split into four groups, differentiating between non-parasitic and kleptoparasitic solitary bees and bumblebees (Table 1). Trait data relating to body size, feeding specialization and nesting habitat or overwintering stage was collected for all five groups, i.e. one butterfly and four wild bee groups (see Table 1 for details on traits). Using the vascular plant data gained in the inventories described in section 3.2.1 for Paper **II-V**, it was determined if respective larval host plants or preferred pollen plants were available in each road verge and for each butterfly and solitary bee species from the regional species pool. The presence of host species for kleptoparasitic solitary bees and bumblebees was determined using the transect walk data as also described in section 3.2.1 for Paper **II-V.** Furthermore, the status of each wild bee and butterfly species in the national

Swedish Red list was compiled as a binary categorical variable, i.e. either “Least concern” (LC) or “Red-listed” (including categories CR = Critically endangered, EN = Endangered, VU = Vulnerable and NT = Near threatened; SLU Artdatabanken, 2024).

Table 1. A list of all group-specific species traits or trait-related factors (grey-shaded) that were included in the analyses for **Paper III**. Data was compiled from [1]Eliasson et al. (2005), [2]the Swedish species information database Artfakta (SLU Artdatabanken, 2024), [3]following Öckinger et al. (2010) and [4]determined using species data from the biodiversity inventories conducted on the respective road verges.

Group	Traits/ trait-related factors	Type
Butterflies	Wingspan[1,2]	Numeric (mm)
	Host plant specialization[3]	Factor (oligo-/polyphagous)
	Overwintering stage[1]	Factor (adult/pupa/larva/egg)
	Host plant presence[4]	Factor (presence/absence)
Solitary bees	Body length[2]	Numeric (mm)
	Lecty[2]	Factor (oligo-/polyphagous)
	Nesting type[2]	Factor (cavity/soil)
	Pollen plant presence[4]	Factor (presence/absence)
Kleptoparasitic[2] solitary bees	Body length[2]	Numeric (mm)
	Host species presence[4]	Factor (presence/absence)
Bumblebees	Nesting type[2]	Factor (above-/below-ground)
Kleptoparasitic[2] bumblebees	Nesting type of host species[2]	Factor (above-/below-ground)
	Host species presence	Factor (presence/absence)

3.2.4 Flower visitation and pollination success of phytometers

Standardised experimental plants, so called ‘phytometers’, can be used to assess differences in environmental conditions on selected plant development measures such as pollination success (Dietrich et al., 2013). In **Paper IV**, a cultivated variety of the wild strawberry plant (Fragaria vesca 'Ruegen') was used as phytometer. In the surrounding area of each of the originally 20 road verges included in **Paper IV**, one set of phytometers was placed in a linear landscape element diverging from the road verge at a 20 m and an 80-100 m distance from the road verge (Fig. 7A). Each set consisted of three pots with three individual plants per pot. All pots contained the same peat-free soil to standardise growth conditions. The pots in each set were placed close together and buried to prevent dehydration (Fig. 7B). Prior to placing the plants in the field between June 7-11 2021, open flowers were removed to ensure that pollination occurred only at the designated sites. The plants were collected after approximately five weeks, between July 12-17, 2021. One site was excluded due to plant destruction.

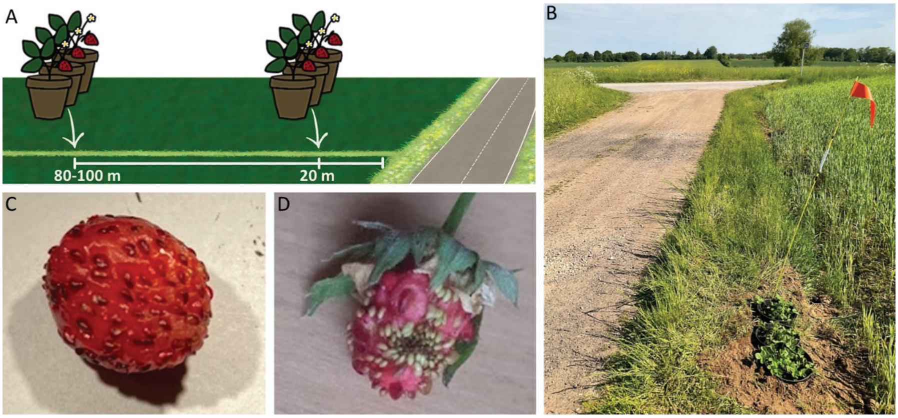


Figure 7. Graphical illustration of the study design of **Paper IV**. A) At a linear landscape element (a field border between two fields or one field and a small private road) diverging from a road verge, sets of potted strawberry plants were placed at 20 m and 80-100 m distance. B) Photo of one of the study sites, with three pots (i.e. one set) of strawberry plants with the road verge in the background. C) A strawberry harvested from the experimental plants with many developed achenes (large and separated), versus D) many undeveloped achenes (small and close together). Photos and illustrations in A, B, D: Svenja Horstmann. Photo in C: Annika Swensson Källén.

Each study site was visited five times, approximately once per week. During each visit, flower visitors were observed for 15 minutes at each set of phytometers, ripe strawberries were harvested, and plants were watered if necessary. Flower visitor observations were conducted between 10.00 and 17.00, but only if vegetation was dry, wind was at most moderate, and air temperature was at least 13 °C if cloud cover was low, or 17 °C if cloud cover was high. The timing of visits was alternated across sites to cover different parts of the day at each site. Wild bees and butterflies were identified to the species level, while other insect visitors such as hoverflies, ants, and mosquitoes were identified to family level. As a measure of pollination success, the number of developed (and undeveloped) achenes was recorded (cf. Herbertsson et al., 2017a; Klatt et al., 2014) for each harvested strawberry at the end of the day or latest the following day (Figure 7C, 7D). After the fifth and final observation round, the strawberry plants were moved to a mesh-covered area to protect them from birds. Flowers and buds were removed, leaving only developing strawberries pollinated at the sites. Between July 19-29, ripe strawberries were collected daily, and the number of developed and undeveloped achenes was recorded for each harvested strawberry.

3.2.5 Trap nests to measure reproductive success of cavity-nesting insects

To record abundance and diversity of cavity-nesting insects, such as wild bees and solitary wasps, standardized nest structures can be used, so called ‘trap nests’ (Staab et al., 2018; Tscharntke et al., 1998). Trap nests can provide information about reproduction, including mortality, success and parasitism rate (Holzschuh et al., 2010; Tscharntke et al., 1998; Zaragoza-Trello et al., 2021). They can also be used to measure population growth, if they are installed over two or more years (Dainese et al., 2018; Steffan-Dewenter & Schiele, 2008). Hence, trap nests can be used to draw conclusions about the habitat quality for the nesting insects (Beyer et al., 2023; Holzschuh et al., 2010; Prendergast, 2023; Staab et al., 2018). Trap nests were installed in originally 20 road verges and 20 semi-natural grasslands in two consecutive years (2021 and 2022). Due to destruction of the trap nests, each one study site per habitat had to be excluded, resulting in 38 study sites with trap nests. Each trap nest consisted of a plastic tube filled with 15 cardboard straws (14 cm long) of each 4, 6 and 8 mm to attract insects of different sizes diameter (resulting in 45 straws per trap nest). On every study site, two trap nests were attached horizontally to the top end of a 1.5 m wooden pole, set up facing south (sun-facing aspect). In the road verges, trap nests were placed near the outer edge of the road verge and within the 200 m transect used in **Paper II-IV** (Fig. 8A). In semi-natural grasslands, trap nests were placed along habitat edges to reflect edge conditions in the road verges (Fig. 8B). Adjacent habitats were primarily arable fields, with some production forests.

In year one, the trap nests were installed from early May to August 2021. Afterwards, trap nests were checked for for occupied straws, which were stored outside but sheltered from rain from August 2021 to March 2022. In year two, trap nests were equipped with new straws and installed from mid-March to August 2022, at the same positions as in year one. Additionally, ‘emergence tubes’ (cf. Steffan-Dewenter & Schiele, 2008) were used in which all occupied straws from year one were returned to their site of origin

Figure 8. Photos of trap nests in A) a road verge in year one and B) at the border of a semi-natural grassland in year two. Each trap nest, i.e. each green plastic tube, was filled with empty cardboard straws, which are used by cavity-nesting insects to build nests inside (as in C). In year two, straws that have been occupied in year one were returned to the study site they originated from, and placed in emergence tubes (the grey tube with blue lids in B). C) Occupied cardboard straws that were opened after year two, to identify the number of cells and differentiate between successful cells and those that failed. In the straws in the photos, all cells failed, which can in this case be determined by finding individuals that were interrupted in their development in the leaf cells of a leafcutter bee (*Megachile* sp.; green cells on the left half, built from leaves) or by finding 'pollen cakes' that were not eaten, potentially with eggs on them, from a mason bee (*Osmia* sp.; yellow balls in cells built with mud, on the right half). Photos: Svenja Horstmann.

in the second year (Fig. 8B). Emergence tubes were attached to the same pole as the two trap nests but positioned facing north (with holes in the respective lid) and close to the ground, but above the surrounding vegetation, and with the occupied straws loose within the tube. Doing so allowed the nesting individuals to hatch and leave the tube but making it unappealing for new nesting. Trap nests and emergence tubes were collected in August 2022 (all straws were left inside) and stored at outside temperature until October 2022 and in a fridge thereafter (4-6 °C). In early April 2023, all trap nests and emergence tubes were moved to a room with ambient temperature. For every trap nest or emergence tube, a net was attached to the open front as a trap for the hatching individuals. The nets were checked daily until the end of July 2023, and hatched individuals were immediately terminated by freezing. All wild bees were identified to species level and solitary wasps and non-bee parasitoids to family level. Afterwards, trap nests and emergence tubes were stored in a freezer until all occupied straws from each trap nest and emergence tube were dissected in early 2024. Within each straw, the number of all cells was counted, differentiating in successful and failed cells due to parasitism or terminated individuals in different developmental stages (hereafter referred to as 'developmental interruption'; Fig. 8C). It was also noted if a cell was unfinished.

3.3 Data handling and analyses

All statistical analyses were conducted using R (R Core Team, 2021). (Generalised) Linear models and generalised linear mixed models are the most common tool used for the data analyses. **Paper II-V** are based on the same study design, but use different subsets of study sites and investigate different impacts. Table 2 shows an overview of which impacts, i.e. variables, were included in which paper (including **Paper I**).

In **Paper I**, generalised linear mixed models were used to separately analyse species richness of (grassland specialist) plants, bumblebees and butterflies in road verges. Single-predictor generalised linear models were used to identify which of the correlated grassland covers (from the 1950s, 2017, or the continuous grassland) should be included as predictor variable in each model.

Table 2. Variables that were included in **Paper I-V**. Hooks (✓) indicate that a variable was considered in the respective paper, grey cells indicate that the variable was not assessed; one asterisk (*) indicates that a variable was accounted for by including it as covariate; and two asterisk (**) indicate that the subset study sites were selected based on the variable. Road verge quality refers to regular and valuable road verges, as determined by the Swedish Transport Administration.

Paper	Feeding resources	Traffic intensity	Mowing regime	Landscape (history)	Road verge quality
I	✓	▨	▨	✓	▨
II	✓	✓	✓	*	✓
III	✓	✓	✓	*	
IV	✓	✓		*	
V	✓	✓		*	**

In **Paper II**, generalised linear models were used to analyse abundance, species richness and Shannon evenness for wild bees and butterflies, as well as plant richness and flower density in road verges. The Shannon evenness index was calculated by dividing the Shannon diversity (Oksanen et al., 2020) by the natural logarithm of the species richness. As a result, Shannon evenness indicates the relative abundance of species in a community with values ranging between 0 and 1, where higher values represent more even communities. Furthermore, to analyse differences between plant communities in different road verge categories, a non-metric multidimensional scaling analysis was conducted to visualize the degree of overlap and a permutational analysis of variance analysis was used to statistically test the differences between communities of different road verge categories (Oksanen et al., 2020).

In **Paper III**, generalised linear mixed models were used to analyse the probability of different wild bee and butterfly species being absent, i.e. missing, from a road verge, considering group-specific species traits (Table 1). For this, three filters were used across the five species groups (butterflies, solitary bees, kleptoparasitic solitary bees, bumblebees and kleptoparasitic bumblebees). The ‘Regional trait filter’ considers which traits determine the general absence of species from the regional species pool from all studied road verges, regardless of road verge characteristics (traffic intensity, mowing regime, road verge width). In the ‘Regional habitat and trait filter’, it is analysed whether certain road verge characteristics determine if species with certain traits are absent from a road verge. Here, again all species from the regional species pool are included. The ‘Specific habitat and trait filter’ considers if species that have feeding or breeding resources available in a specific road verges are still absent depending on traits and road verge characteristics. Here, only species that were generally found in road verges are included, and of those only species that can find larval host plants (for butterflies), pollen plants (solitary bees) or host species (kleptoparasitic solitary bees and bumblebees) in a road verge (referred to as the ‘road verge (species) pool’). Furthermore, it was analysed if nationally red-listed species were more likely to be absent from a road verge than species of least concern. For this, the same model approach as in the Regional habitat and trait filter and Specific habitat and trait filter were used, but now only considering red list status and road verge characteristics, but no species traits.

In **Paper IV**, generalised linear mixed models were used to analyse the number of strawberry flower visitors and the number of developed achenes on harvested strawberries at two distances from each road verge. Furthermore, a linear mixed effect model was used to explore if one or more groups of flower visitors are particularly important for strawberry pollination success.

In **Paper V**, a Bayesian modelling framework was used to analyse occupancy rate of trap nests by cavity-nesting insects in road verges and grasslands, as well as population growth (measured as the change in occupancy from year one to year two), hatching success rate and the rate of failed cells and reasons for failure. Models were implemented with minimally informative priors in JAGS (Plummer, 2003) called from R (R Core Team, 2021). For occupancy rate, hatching success rate and failed cells rate, a binomial likelihood was used, whereas for population growth a Gaussian likelihood was used. For each of the four response variables, two levels of analysis were conducted: first comparing semi-natural grasslands and road verges, and second, specifically analysing road verges and the impact of traffic intensity.

4. Results and Discussion

In this thesis, I have gained valuable insights about how traffic, vegetation management and landscape impact wild bees, butterflies, plants and briefly solitary wasps in road verges (Fig. 9). In the following sections, I will synthesise my findings from the five chapters and disentangle these different impacts, while also considering how they act together in shaping the local diversity of flower-visiting insects. Traffic emerged as particularly disruptive factor, limiting the potential of otherwise attractive road verge habitats.

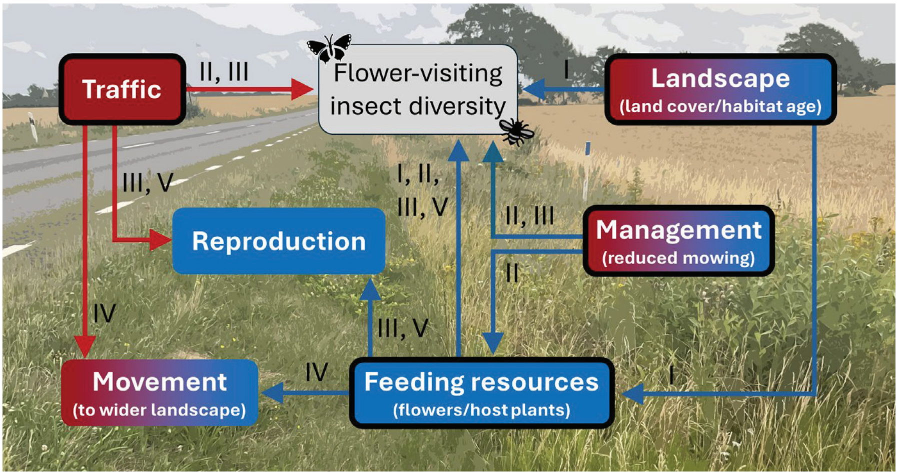


Figure 9. Simplified overview of different impacts (framed black) that can influence the diversity of wild bees and butterflies (grey box) and their movement and reproduction (here including solitary wasps) in road verges. Potential positive impacts are coloured blue, potential negative impacts red, and a colour combination indicates that both positive and negative impacts are possible. Arrows indicate direction of effects. Roman numerals indicate the relevant chapter of my thesis. Photo in the background: Svenja Horstmann.

4.1 Traffic

4.1.1 Negative effects of high traffic in narrow but not wide road verges

With increasing traffic intensity, I identified a decline in the abundance of butterflies and wild bees, and a decline in wild bee species richness in road verges (**Paper II**). However, this was only the case in narrower road verges

(Fig. 10A), while wide road verges seemed to buffer negative effects of traffic, which may be caused by noise, pollution, turbulence or direct mortality through collision with vehicles (reviews by Meinzen et al., 2024; Phillips et al., 2020b). The proximity to traffic may cause the area adjacent to the road to be especially unattractive for flower-visiting insects, and narrow road verges might thus be unattractive as a whole. Indeed, turbulence from passing vehicles has been observed to interrupt the majority of insects foraging on a flower species (Dargas et al., 2016), and the abundance of flower-visiting insects has been shown to increase with distance to the road (Phillips et al., 2019). In **Paper IV**, I further found that narrow road verges along high traffic roads can even limit the number of flower visitors to experimental plants (i.e. phytometers) in the surrounding landscape (Fig. 10B), likely because these road verges support a much smaller community of flower visitors that can move into wider road verges (as found in **Paper II**). This is discussed in further detail in section 4.3.2.

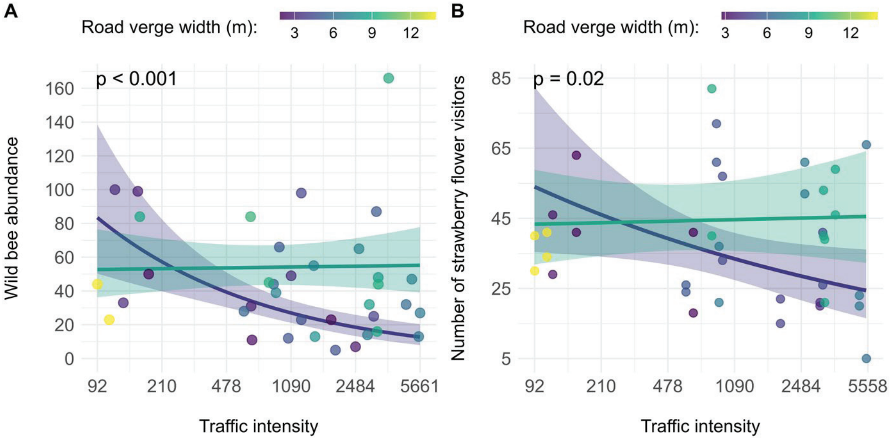


Figure 10. A) The relationship between wild bee abundance and traffic intensity depending on road verge width (**Paper II**). I found similar patterns for butterfly abundance and wild bee species richness. B) The relationship between the number of strawberry flower visitors to in the surrounding landscape of road verges and traffic intensity on the nearby road changes, depending on the width of the road verge (**Paper IV**). In A) and B), traffic intensity was log-transformed for the analyses, and the colour gradient illustrates the width of the road verge for samples (represented as circles), model predictions (lines) for 4.7 and 9.3 m width respectively, and 95% confidence intervals (shaded areas). Figure A) is modified from **Paper II**, which is published under the Creative Commons CC BY NC license (https://creativecommons.org/licenses/by-nc/4.0/).

Wider road verges provide more habitat than narrow verges, both through an increased area of habitat, but also providing a more suitable environment further away from the disturbing traffic. Indeed, I found a higher abundance of butterflies and wild bees, as well as a higher wild bee species richness in wider road verges, despite high traffic. Furthermore, road verge width also had a positive effect on butterfly species richness, regardless of traffic intensity (**Paper II**), as shown by others (Munguira & Thomas, 1992; Skórka et al., 2013). However, I found no relationship between road verge width and trap nest occupancy of cavity-nesting insects (**Paper V**). A study on trap-nesting insects in field boundaries found that occupancy was generally lower with roads in the proximity (Van der Meersch et al., 2022). When combined with my findings, this indicates that roads possibly have a wide zone of influence, reducing the attractiveness of nesting possibilities even beyond the road verge itself.

4.1.2 Traffic can limit butterfly species richness despite high amounts of resources

A high diversity of plants generally correlates with a high diversity of flower-visiting insects (Biesmeijer et al., 2006; Fründ et al., 2010), and as I discuss in section 4.2.2, I also found the same relationship in road verge habitats (**Paper I**). However, I observed in **Paper II** that this positive relationship can be moderated by traffic intensity. Butterfly species richness increased with plant species richness only along roads with lower traffic intensities, but not along roads with higher traffic intensities (Fig. 11; **Paper II**). There are two potential explanations. First, the conditions along roads with high traffic might not be tolerable for some butterfly species, which avoid adjacent road verges for foraging or reproduction. Second, the high mortality risk associated with higher traffic results in these road verges becoming sink habitats, i.e. a habitat where local mortality succeeds local reproduction. To shed light on this, I analysed a number of species traits in **Paper III**, to see if they, in interaction with local road verge conditions, drive the absence of certain species more than others. Other studies found that traffic mortality was higher for species that are either smaller (Skórka et al., 2013) or more mobile (Halbritter et al., 2015; Munguira & Thomas, 1992; Remon et al., 2018). I used wingspan as measure for body size and mobility (Sekar, 2012) and found no evidence that traffic influenced the occurrence of some butterfly species more than others (**Paper III**). It is however important to note that I used species absences as response variable, hence my findings are likely to be more conservative and cannot show if species with certain traits are still present but in lower abundances. On the other hand, I also found no effect of traffic on the community evenness of butterflies in **Paper II**, indicating that the relative abundance of those species that are present is similar across traffic intensities (but generally, species richness still declined with increasing traffic). In other words, traffic does not seem to disproportionately affect individuals from certain species or those with certain traits (**Paper II & III**), at least in my study setup.

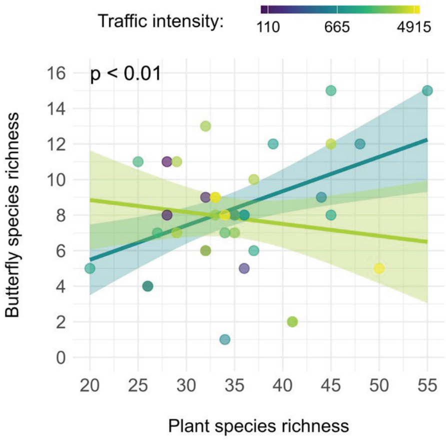


Figure 11. The relationship between butterfly species richness and plant species richness, depending on traffic intensity. Traffic intensity was log-transformed for the analyses. The colour gradient illustrates the traffic intensity next to road verges for samples (represented as circles), model predictions (lines) for 665 and 3294 vehicles per day, respectively (selected to reflect the median of the lower and higher half of all traffic intensities along road verges), and 95% confidence intervals (shaded areas). The figure is modified from **Paper II**, which is published under the Creative Commons CC BY NC license (https://creativecommons.org/licenses/by-nc/4.0/).

4.1.3 Traffic can impact road verges as nesting habitat

Higher traffic intensities increase the probability that below-ground nesting bumblebee species are absent from road verges (**Paper III**, Fig.12A). In fact, a previous study showed that the highest proportions of bumblebee queens killed by traffic were held by two below-ground nesting species (Dániel-Ferreira et al., 2022a). However, it is likely that species nesting below-ground are generally more susceptible to vibrations or pollution caused by traffic and road management than species nesting above-ground (Phillips et al., 2021). There is evidence that vibrations may disturb bumblebees (Jandt et al., 2012), and heavy metals and salts can accumulate in road verge soils, potentially causing negative physiological effects on certain insect species (Mitchell et al., 2020).

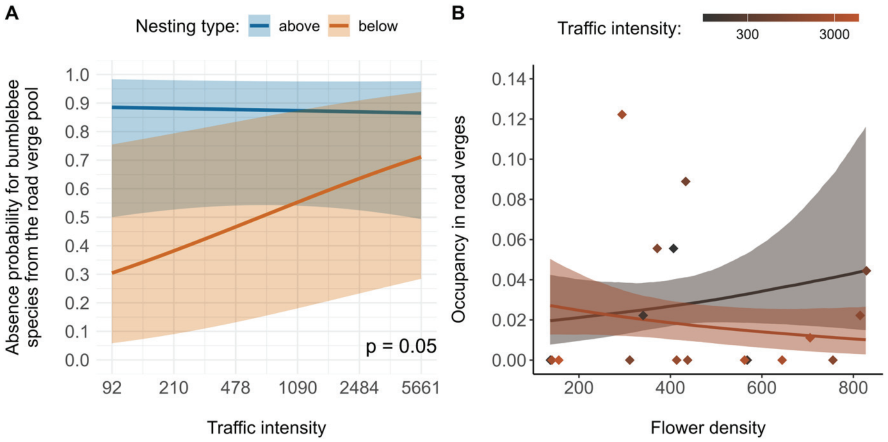


Figure 12. A) The absence probability for bumblebee species of the road verge species pool relating to an interaction between traffic intensity and nesting type (**Paper III**). Lines and bands represent model predictions and 95% confidence intervals. B) The relationship between occupancy (%) in road verges and flower density, depending on traffic intensity (**Paper V**). Traffic intensity was log-transformed for both analyses. The colour gradient in B) illustrates the traffic intensity next to road verges for samples (represented as diamonds), model predictions (lines) for 300 and 3000 vehicles per day, respectively, and 95% credible intervals (shaded areas).

In **Paper V**, I observed that traffic also affects insects nesting in cavities above-ground. While there was a positive relationship between flower density and trap nest occupancy in semi-natural grasslands, this was not the case in road verges, where flower density only had a positive effect on occupancy when traffic intensity was low, but not high (Fig. 12B). In line with **Paper II**, this suggests that traffic limits the positive influence of floral resource availability on flower-visiting insects in road verges. While we know that wild bees and butterflies can reproduce in road verges (e.g. Hopwood, 2008; Munguira & Thomas, 1992), little is known about how successful this reproduction is, especially in the case of wild bees (Meinzen et al., 2024). I observed that high traffic intensity not only limited trap nest occupancy, but further limited population growth, measured as the change in occupancy between two subsequent years (**Paper V**). At a low traffic intensity of 300 vehicles per day, occupancy was estimated to increase 4.5-fold between subsequent years, while at a higher traffic intensity of 3000 vehicles per day, occupancy decreased by about one third. A portion of the emerging females are expected to return to the trap nest to construct their own nests (Jayasingh & Freeman, 1980; Klein et al., 2004). However, it is possible that this proportion was lower at higher traffic intensities, either because emerged females were killed by passing vehicles (cf. Dániel-Ferreira et al., 2022a; Keilsohn et al., 2018), or because they found the habitat unattractive (cf. Blomqvist et al., unpubl.). It is also possible that pollution influences the fitness of nest building females (Moroń et al., 2014). In fact, I observed a positive relationship between traffic intensity and the number of unfinished cells in the trap nests, which suggests that more nest-building females were either killed or deterred at higher traffic intensities (**Paper V**; Fig. 13A).

Traffic intensity further also showed a positive relationship with parasitism rate of trap nests. Studies on trap nest communities in other habitats have found that parasitism rate is higher when floral resources are scarce, probably because foraging females were forced to spend more time away from the nest, leaving it more vulnerable for parasitoids (Ganser et al., 2021; Goodell, 2003). Foraging females in road verges can be disturbed by traffic (cf. Dargas et al., 2016) and hence may spend more time away from the nest. Interestingly however, I also found in **Paper III** that the probability that parasitic solitary bee species are absent from road verges is lower at higher traffic intensities (Fig. 13A). In other words, the species richness of kleptoparasitic bees increases with traffic intensity, which likely contributes to an increase of parasitism with increasing traffic intensity.

Despite the impacts of traffic on occupancy and population growth in trap nests, I detected that hatching success was generally higher in road verges than semi-natural grasslands and not affected by traffic intensity. This finding was unexpected but offers valuable insights into local interactions and environmental pressures: the higher survival of cavity-nesting insects in road verges is likely due to lower mortality from parasitism and developmental interruption compared to in semi-natural grasslands (Fig. 13B), where older and more stable populations may have facilitated parasite establishment and disease spread. Importantly, since we stored the trap nests in a protected environment between autumn and spring, we cannot exclude that traffic may still affect larval development during this time.

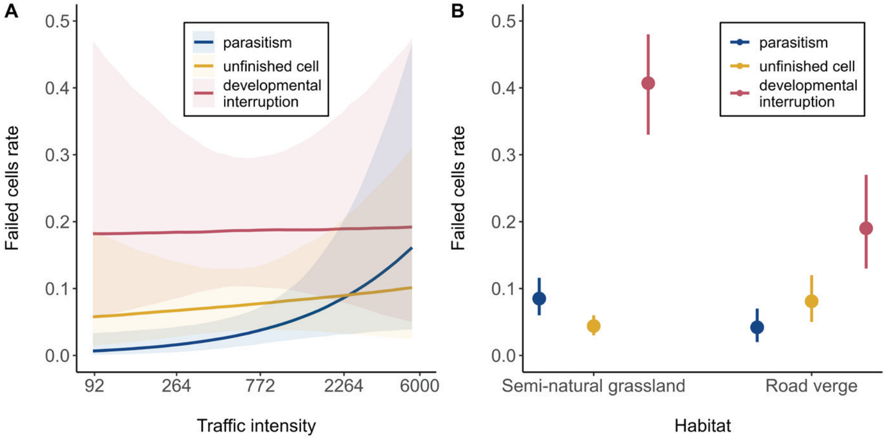


Figure 13. A) The relationship between traffic intensity and the rates of failed cells in road verges (due to parasitism, unfinished cell building or developmental interruption with colours as indicated in the legend; **Paper V**). Traffic intensity was log-transformed for analysis. Lines and shaded areas indicate model predictions and 95% credible intervals. B) The rates of failed cells depending on the habitat (**Paper V**). Dots indicate model predictions, lines the 95% credible intervals.

4.2 Management

4.2.1 Short-term effects of current vegetation management

Altering the mowing regime to a reduced frequency can have short-term effects on plants and thus flower-visiting insects (**Paper II**). I found that road verges that were mown only once in late summer had a higher flower density than those mown twice, in early summer and autumn (**Paper II**). This can be explained by the fact that only the early summer mowing took place during our field study, and that the observed patterns are most likely due to the immediate reduction of flower cover after mowing. However, it also highlights that mowing flower-rich habitats during peak season for flower-visiting insects can reduce their feeding resources, resulting in subsequent declines in their abundance (Phillips et al., 2019). Indeed, I observed that wild bee abundance and species richness was strongly associated with flower density (**Paper II**; Fig. 14A), and that the probability that solitary wild bee species were absent was lower in road verges that were mown during the field inventories (in other words, species richness was lower; **Paper III**). However, mowing did not disproportionately affect some species more than others based on their body size or food plant specialisation (**Paper III**).

Butterfly diversity in road verges has previously been shown to benefit from reduced mowing (Halbritter et al., 2015; Saarinen et al., 2005; Valtonen et al., 2006). I observed this only in road verges classified as valuable for plant diversity, but not in regular road verges (**Paper II**; Fig. 14B). I found no clear differences in plant community composition between road verge categories that could explain this finding (**Paper II**). Furthermore, the results also indicate that a higher mowing frequency makes butterfly abundance and species richness more similar across road verge categories (**Paper II**), but I found no evidence that mowing affects some species more than others depending on their wingspan or host plant specialisation (**Paper V**). While I am uncertain about underlying causes for these findings, they reveal that the effect of a reduced mowing regime varies between different road verge types. Hence, the Swedish Transport Administration, which is responsible for classifying and managing the road verges, likely uses adequate plant-diversity based criteria to select valuable road verges that also have benefits for butterflies under a reduced mowing regime.

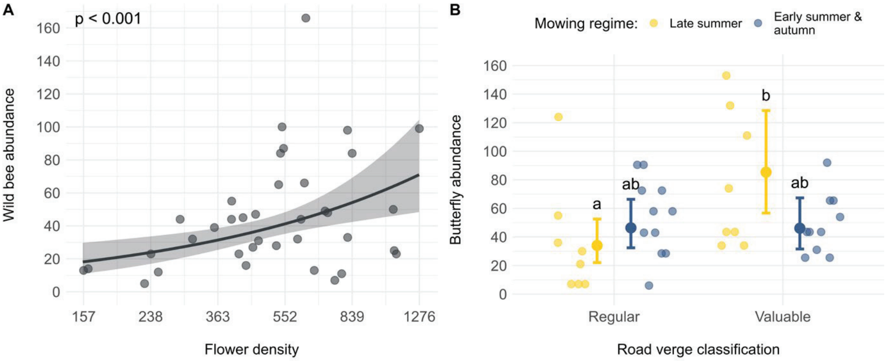


Figure 14. A) The relationship between wild bee abundance and flower density (**Paper II**). I found similar patterns for wild bee species richness. Dots indicate raw data, line model predictions and shaded area 95% confidence intervals. B) The relationship between butterfly abundance and road verge classification, depending on the mowing regime (**Paper II**). I found similar patterns for butterfly species richness. Dots indicate raw data, dots with lines model predictions and 95% confidence intervals. Both figures are reprinted from **Paper II**, which is published under the Creative Commons CC BY NC license (https://creativecommons.org/licenses/by-nc/4.0/).

The positive relationships between plant species richness and butterfly diversity and between flower density and wild bee diversity highlight the critical role of diverse plant communities and abundant flower resources for flower-visiting insects in road verges. However, reducing the mowing frequency and mowing later in the season does not seem to be a universally successful approach for a biodiversity-targeted management with regards to flower-visiting insects. Instead, I show that the effectiveness might depend on local habitat conditions (also see Jakobsson et al., 2018; Noordijk et al., 2009).

4.2.2 Long-term management continuity

Vascular plants

The long-term continuous and low intensity management of semi-natural grasslands has positive effects on the plant diversity (Cousins & Eriksson, 2002; Eriksson, 2013; Gustavsson et al., 2007). In **Paper I**, I found that this can be true for linear infrastructure habitats as well. Although we have no exact knowledge on the management history of surveyed road verges, it can be assumed that the vegetation has always been kept relatively open and that this benefitted plant richness over time. Plant species richness marginally increased with age of a road and was on average 47.3% higher along historical roads that already existed around 1900 than along newer roads that were established before 2017 (Fig. 15). However, I found no effect of habitat age on species richness of grassland specialist plants (in contrast to the findings of Auffret & Lindgren, 2020). Based on the results from **Paper I** and findings from other studies including open habitats in both road verges and power line corridors (Auffret & Lindgren, 2020; Jakobsson et al., 2016; Lampinen et al., 2015, 2018), I infer that novel grassland habitats along linear infrastructure can exhibit an immigration credit (Jackson & Sax, 2010).That is, that plant species richness can further increase with advancing time since habitat establishment, if current conditions remain (Jakobsson et al., 2016). However, it may take over a century to see the immigration credit being paid (**Paper I**).

In the study design for **Paper II**, we changed the mowing regime for one of the four road verge categories only for the year of our study (i.e. for some regular road verges that were usually mown twice, but were then mown once). Furthermore, in valuable road verges that are mown once, it is likely that the biodiversity-targeted management of mowing once in late summer was only implemented within the last few years. However, plant communities take several decades to respond to a change in management (Ladouceur et al., 2023). It is therefore not possible to draw conclusions about the long-term effect of the mowing regimes on vascular plant communities in the studied road verges. Indeed, between the four road verge categories there was no difference in plant species richness or the relative occurrence of grasses and mostly overlapping plant community compositions. Furthermore, a review showed that the removal of hay has a larger positive effect on plant diversity in road verges than the mowing frequency alone (Jakobsson et al., 2018).

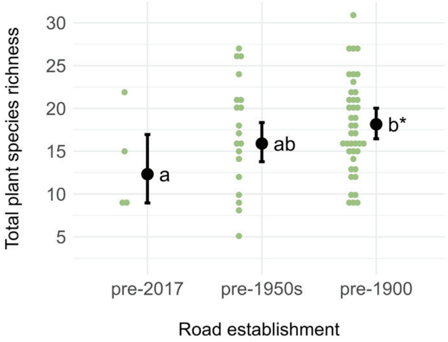


Figure 15. The relationship of plant species richness and the time period in which a road was established, i.e. road age (**Paper I**). Green dots indicate raw data, black dots with lines model predictions and 95% confidence intervals. Means sharing a letter are not statistically different ($p < 0.05$), and asterisk letters show marginal statistical differences ($p < 0.07$; using tukey-adjusted pairwise comparisons). The figure is modified from **Paper I**, which is published under the Creative Commons CC BY license (https://creativecommons.org/licenses/by/4.0/).

Flower-visiting insects

Mobile species with short generation times, such as flower-visiting insects, can react quickly to habitat change (Kuussaari et al., 2009). However, they depend on the sufficient availability of certain plants, and therefore their colonisation in a new habitat can be indirectly delayed by the local plant community (Krauss et al., 2010). Considering of my finding of a positive relationship between habitat age and plant species richness (**Paper I**), and those of Auffret & Lindgren (2020) and Lampinen et al. (2015, 2018), it is therefore likely that habitat age and surrounding source habitats are also important drivers for the species accumulation of more mobile species in novel grassland habitats, especially for grassland specialists. However, studies directly addressing landscape legacy effects on both plants and insects in infrastructure habitats are limited. In **Paper I**, I show that although butterfly and bumblebee species richness are not directly affected by habitat age of road verges (or power line corridors), there was a positive relationship between their respective species richness and plant species richness (cf. **Paper II**). Bumblebees responded positively to overall plant richness, probably because they are generalists and respond to the availability of various forb species (Fig. 16A; Steinert et al., 2020), while butterflies, whether grassland specialists or not, responded positively to the species richness of grassland specialist plants, which likely reflects the availability of a range of important nectar and host plants in the road verge (Fig. 16B; Ekroos et al., 2013). Habitat age, and with it the long continuity of low intensity vegetation management, may therefore play an indirect role in determining habitat quality for bumblebees and butterflies, through enhancing the plant community.

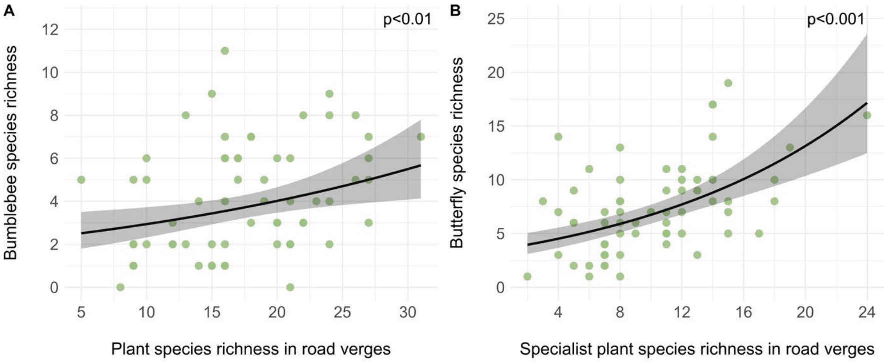


Figure 16. The relationships between A) bumblebee species richness and plant species richness and B) butterfly species richness and grassland specialist plant richness in road verges (**Paper I**). Green dots represent raw data. Lines indicate model predictions, shaded areas the 95% confidence interval. The figure is modified from **Paper I**, which is published under the Creative Commons CC BY license (https://creativecommons.org/licenses/by/4.0/).

4.3 Landscape

4.3.1 From the landscape to the road verge

Both past and present grassland land cover and connectivity can influence plant species richness in semi-natural grasslands and novel grassland habitats along linear infrastructure (Jakobsson et al., 2016; Lampinen et al., 2018; Lindborg et al., 2014). However, I found no effect of past or present grassland area within a 2 km buffer of road verges on total or grassland plant species richness (**Paper I**), and similar results were also found by Auffret & Lindgren (2020). Low amounts of potential source habitat in the surrounding landscape may have hindered the colonisation of plant species, especially of grassland specialist species which often exhibit slow colonisation rates (Auffret et al., 2017c; Helsen et al., 2013; Jakobsson et al., 2016; Lindborg et al., 2014). Indeed, less than 3% of the land within 2 km around the road verges was covered by continuous semi-natural grasslands that existed since at least the 1950s and might be expected to be potential source habitats (Cousins & Eriksson, 2002). Furthermore, while communities of plants and butterflies in road verges (and power line corridors) share a large proportion of species with semi-natural grasslands, they are not the same, indicating that linear infrastructure habitats cannot fully act as replacement habitat (Dániel-Ferreira et al., 2023).

Regarding the influence of landscape history on flower-visiting insects in linear infrastructure habitats, I found that species richness of bumblebees was higher in road verges that had a higher cover of grasslands in the 1950s in the surrounding landscape (Fig. 17; **Paper I**). In Sweden, landscapes that were historically dominated by grassland habitat have undergone a large-scale increase in forest cover and abandonment of grasslands during the last century (Auffret et al., 2018; Cousins et al., 2015). As a result, these landscapes may now be composed of a mosaic of forest and different-aged or abandoned grasslands in fact, and the resulting landscape heterogeneity may in turn promote diversity of bumblebees and other taxa (Rundlöf et al., 2008; Senapathi et al., 2015).

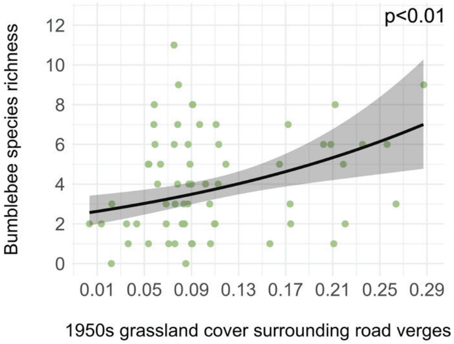


Figure 17. The relationship between bumblebee species richness and the proportion of grassland cover in the 1950s in landscapes surrounding road verges (2 km buffer). Green dots represent raw data, the black line model predictions, and shaded areas the 95% confidence interval. The figure is modified from **Paper I**, which is published under the Creative Commons CC BY license (https://creativecommons.org/licenses/by/4.0/).

4.3.2 From the road verge to the landscape

I have shown that road verges with a high density of feeding resources can enhance the abundance and species richness of flower-visiting insects locally (**Paper I & II**). Hence, the question arises if road verges can also contribute to the diversity of flower-visiting insects and pollination services in their surrounding landscape. A previous study showed that flower-rich road verges along rural dirt roads with little traffic increased the number of flower-visitors on experimental wild plants located 30 m away in an adjacent arable field (Monasterolo et al., 2022). I found evidence that flower-rich road verges enhance the number of flower visitors even up to 100 m away, since the number of flower visitors was independent of the distance to the road verge at 20 m and 80-100 m (Fig. 18). This is likely due to flower-rich road verges supporting a larger community of flower-visiting insects, especially when traffic is low (as found in **Paper II**), that can move into the wider landscape exceeding 100 m. However, high traffic limited the number of flower visitors in the surrounding landscape if road verges were narrow (see section 4.1.1; **Paper IV**).

I did not find the same positive effect of flower-rich road verges pollination services, estimated as the number of visitors per strawberry flower and developed achenes per strawberry. Hence, although flower-rich road verges enhance the number of flower visitors in general, the effect may be too weak to in turn enhance pollination services. Instead, I even found that pollination success tended to be lower closer to the road than further away, with an expected mean of 5.8% more developed achenes on the strawberries harvested further away from the road verge. However, since there was no difference in the number of flower visitors and none of the coarse visitor groups (ants, wild bees, beetles, non-syrphid flies, hoverflies and mosquitos) significantly impacted pollination success, I argue that a difference in pollinator behaviour or the pollen they carry may explain this finding (Chagnon et al., 1993; Herbertsson et al., 2017b; Villa-Galaviz et al., 2023). To conclude, the findings of **Paper IV** together with those from **Paper II** show that flower-rich road verges can benefit pollinator populations in the surrounding landscape, but that traffic can limit this effect.

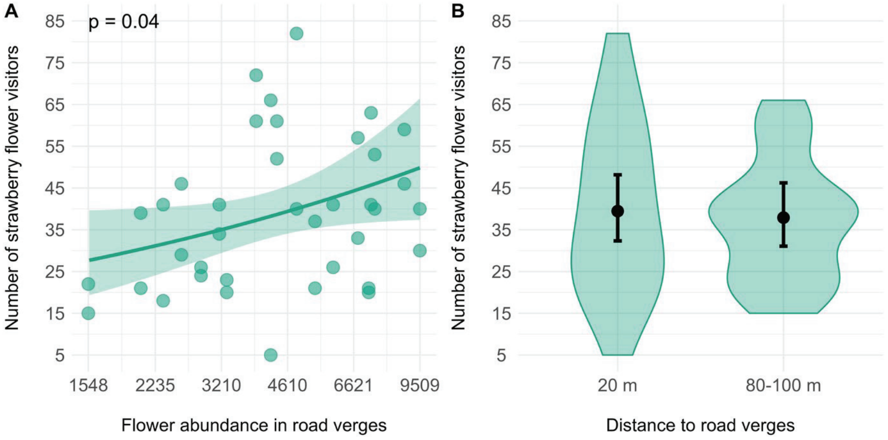


Figure 18. A) The relationship between flower abundance in the road verges and the number of flower visitors to experimental strawberry plants in the surrounding landscape. Flower abundance was log-transformed for the analyses. Dots indicate raw data, the line and shaded area indicate the model predictions and 95% confidence intervals. B) The number of strawberry flower visitors was similar between the two distances to the road verge (i.e. not statistically different). Violin shapes represent spread of raw data, with wider parts indicating more data points. Black dots with error bars indicate model predictions and 95% confidence intervals.

4.4 Road verges – a habitat for all?

Road verges can support a high species richness and abundance of flower-visiting insects, as found by my own studies (**Paper I** and **II**) as well as by others (Dániel-Ferreira et al., 2023; Phillips et al., 2019). However, road verges only partially support similar community compositions compared to semi-natural grasslands (Dániel-Ferreira et al., 2023). Furthermore, most studies have so far mainly focussed on the availability of food resources to infer if road verges are attractive for flower-visiting insects (Meinzen et al., 2024). To support a flower visiting insect throughout their life cycle, a habitat should also offer resources for reproduction. In other linear habitat elements like uncultivated field margins, wild bee and butterfly populations seem to be partly dependent on the spill-over of individuals from nearby semi-grassland habitats (Öckinger & Smith, 2007a, 2007b). Thus, to generate informed strategies for biodiversity conservation, it is important to understand if certain species groups are less likely to use road verges as habitat, or more likely to suffer from negative effects of traffic or management. I investigated this in **Paper III**, by testing if species traits such as wingspan or host plant specialisation for butterflies, and body size or nesting type for wild bees, in combination with habitat conditions such as traffic intensity and mowing regime explain why some species are absent from road verges.

4.4.1 Butterflies

Among butterflies, neither wingspan nor host-plant specialisation explained why some species were absent from road verges as a whole, regardless of the characteristics of the road or the road verge (traffic intensity, mowing regime, road verge width). Instead, species occurrence was linked to the presence of their respective larval host plants, such that butterfly species were generally more likely to be absent in road verges where their host plants were unavailable, irrespective of their wingspan (Fig. 19A). Since wingspan can partly indicate mobility (Sekar, 2012), this suggests that even the most mobile species are unlikely to use road verges only for foraging. Combined with the finding that butterfly species richness in these verges is closely linked to the species richness of the plant community (**Paper I & II**), this suggests that a significant proportion of the butterfly species that I observed in road verges may also have reproducing populations there. To understand the extent to which these populations are self-sustaining or are sink populations that rely on immigration for long-term persistence requires further investigation (Gardiner et al., 2018; Meinzen et al., 2024).

Besides the relationship with host plant availability, I found that butterfly species absence was explained by the types of habitat conditions that are likely to explain species absence in any habitat. Species that are oligophagous at the larval stage, i.e. that are more specialised, were more likely to be absent from road verges than species with polyphagous larvae. Both species groups were less likely to be absent in wider road verges than in narrow road verges, and I previously showed that wider road verges are generally more likely to support a larger community of butterflies (**Paper II**). Furthermore, an increased habitat area enhances the probability of a larger plant community and offers more habitat further away from the hazards associated with the road (Phillips et al., 2019).

4.4.2 Wild bees

Wild bees are central place foragers, and thus require both feeding and nesting resources within their flight range (Greenleaf et al., 2007; Michener, 2007). I observed that solitary bees nesting in cavities were more likely to be absent from road verges than soil-nesting species (Fig. 19B). This finding indicates that most solitary bees observed in road verges also reproduce there, especially since many species have foraging ranges of a few hundred metres from their nests (Greenleaf et al., 2007). Considering body size, I found that small oligolectic bees were more likely to be absent from road verges than small polylectic species (**Paper III**). Small-bodied bees usually have shorter foraging ranges (Greenleaf et al., 2007), and for species that also feed only on a limited number of plant species, it is likely that they have very localised distributions, explaining why they rarely occur in road verges. On the contrary, bumblebees are larger-bodied generalists (SLU Artdatabanken, 2024), and indeed all except one bumblebee species (which is locally rare) from the regional species pool occurred in at least one of our road verges, regardless of their nesting type. However, high traffic reduces species richness of below-ground nesting bumblebees (i.e. increasing the probability these species are absent; **Paper III**), which I discussed in section 4.1.3.

For cavity-nesting solitary bee species occurring in road verges, I found a marginally lower probability for their absence in wider than narrower road verges, while the absence probability of soil nesting species tended to be not affected by road verge width (**Paper III**). Road verges in the study region were dominated by open, herbaceous vegetation with generally few trees, woody plants or other structures such as stone walls that could provide nest sites for cavity nesters (personal observation). On the other hand, wider road verges more often had woody plants at the outer road verge edge adjacent to the neighbouring habitat (in most cases arable fields), probably because the mowing is often conducted incompletely towards the outer edge (personal observation).

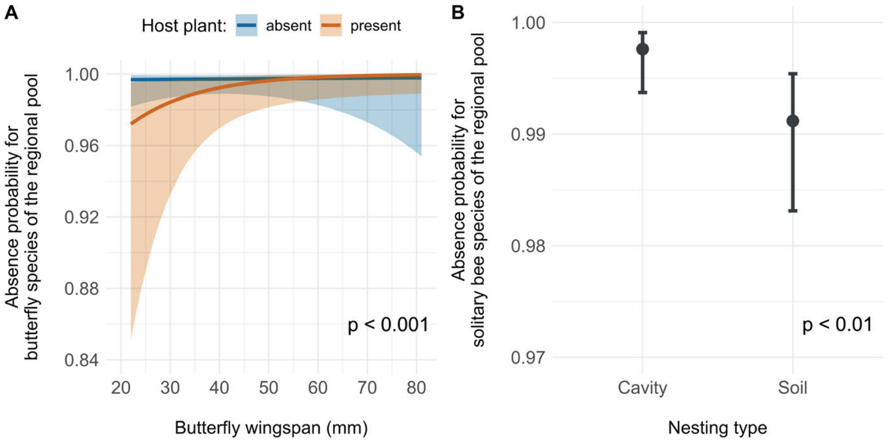


Figure 19. A) The relationship between the absence probabilities for butterfly species of the regional species pool and butterfly wingspan, depending on host plant availability in a road verge. Lines with shaded areas represent model predictions and 95% confidence intervals. B) The relationship between the absence probability for solitary bee species of the regional species pool and their nesting type. Dots with error represent model predictions and 95% confidence intervals.

4.4.3 Red-listed wild bees and butterflies

I observed 15 % of the regionally occurring, nationally red-listed bee species and 33% of red-listed butterfly species in the road verges. Red-listed butterfly species were equally unlikely to be absent as not red-listed species, but solitary bee species showed a trend for higher absence probabilities when red-listed. Previous studies have shown that some insect species may even have their total or a large proportion of their population in road verges and other infrastructure habitats (Helldin et al., 2015; Noordijk et al., 2011). This highlights the possibility that road verges can indeed act as habitat for many species, including those that are rare and threatened. Biodiversity-targeted management (i.e. mowing only once per year) did not increase the probability that red-listed species would occur in road verges.

5. Conclusions and management recommendations

Synthesising the insights I have gained across the chapters in this thesis allows me to draw sound conclusions about how the specific impacts of traffic, vegetation management and landscape affect species diversity in road verges and to evaluate under which conditions road verges can or cannot support flower-visiting insects. My findings can provide a roadmap for optimising management to support the diversity of flower-visiting insects and plants along roads.

As fixed structures, road verges can offer permanent feeding, nesting and overwintering resources for flower-visiting insects. Indeed, I detected 39% of all regionally occurring wild bee species and 43% of all regionally occurring butterfly species (except wetland specialists) in road verges (**Paper III**). Considering that I only surveyed a small fraction of all road verges and only 0.4% of the land area of the study region overall, this is an impressively high proportion of species. Moreover, I found 15 % of the regionally occurring nationally red-listed bee species and 33% of the red-listed butterfly species in the road verges (**Paper III**). The positive relationships between plant resource availabilities and the abundance and species richness of wild bees and butterflies (**Paper I & II**) as well as the abundance of flower visitors in the wider landscape (**Paper IV**) highlight the critical role of abundant floral resources and diverse plant communities for the communities of flower-visiting insects in road verges and beyond. However, I conclude that the management targeted on enhancing plant diversity by mowing only once and in late summer compared to twice, in late summer and autumn, does not appear to be a universally successful approach to support flower-visiting insects (**Paper II**). Instead, local road verge conditions should be considered for targeted management actions whenever possible.

Considering the landscape history in and around road verges in **Paper I**, I found that plant species richness increased with road age, indicating that species establishment in these habitats occur with a time lag. Potential time lags in the (future) establishment of local diversity should be considered when making management decisions (see Watts et al., 2020). The slow assembly of plant communities might have direct impact on pollinator diversity by limiting resources for foraging and reproduction.

A key takeaway from my research is that that high traffic intensity can have severe impacts on flower-visiting insects in road verges, limiting species abundance and richness, the attractiveness of potential nesting sites, population growth and reproductive success (**Paper II**, **III** and **V**), and even abundance of flower visitors in the surrounding landscape (**Paper IV**). Furthermore, high traffic intensities increased the probability that fewer below-ground nesting bumblebee species were present in a road verge. While I found that traffic does not limit the overall occurrence of solitary bee and butterfly species depending on certain traits such as nesting type, body size, mobility or (larval) feeding preferences (**Paper III**), it is still possible that traffic affects species abundances depending on these traits (Halbritter et al., 2015; Munguira & Thomas, 1992; Remon et al., 2018; Skórka et al., 2013). Although I cannot clearly determine the exact mechanisms through which traffic affects flower-visiting insects, whether by decreasing habitat attractiveness through vibrations, pollution or noise, or increasing mortality from collisions with vehicles, my findings highlight that higher traffic intensities consistently result in negative impacts on insect communities, regardless of the mechanism. This is particularly concerning, because with an average maximum of less than 6000 vehicles per day, the traffic intensity along the road verges that I studied is still fairly fairly moderate in comparison to that in studies conducted in other countries (Keilsohn et al., 2018; Phillips et al., 2019).

To conclude, although road verges have the potential to support flower-visiting insects, not all road verges are equally suitable habitats, and not all road verges can become equally suitable habitats when reducing the mowing regime. Management efforts should be focused on road verges along low-traffic roads. Wide road verges in particular have a high potential as habitat for flower-visiting insects and should be considered for enhancing habitat quality if needed (also found by Phillips et al., 2019). Wide road verges may also be considered for management actions despite higher traffic, but this should be considered with caution, since it is not yet clear whether road verges with abundant resources for feeding and reproduction may attract flower-visiting insects despite resulting in lower fitness or higher mortality (Keilsohn et al., 2018; Meinzen et al., 2024). Vegetation management should be adapted to local conditions including different vegetation types to ensure its effectiveness. Since many species have the potential to reproduce in road verges (**Paper III** and **V**), adequate management of road verges should be adapted to not only provide abundant flower resources, but also ensure that there is a high diversity of plants including larval host plants for butterflies and other specialised plant-feeding insects. Furthermore, an addition of woody plants and dead wood near road verges could increase the quality of road verges for cavity-nesting insects.

6. Future perspectives

While my thesis has provided important insights into the role of road verges in supporting flower-visiting insects, several knowledge gaps remain, and there are key areas that future research should address.

One important task for future research is to identify under which conditions road verges are sink habitats by causing a higher local mortality than reproduction. My findings highlight that even moderate traffic levels can reduce the abundance and species richness of flower-visiting insects. However, it is likely that the impact of traffic interacts with other conditions such resource availability and species traits. Indeed, another area of concern is whether road verges near high-traffic roads could act as ecological traps, where flower-visiting insects are attracted to the habitat e.g. through a high floral resource availability, although they eventually experience higher mortality rates or reduced reproductive success due to collisions with vehicles or exposure to pollution. I show that indeed many species that I observed in road verges are likely to reproduce there, but I also show that pressures on insects nesting in road verges can differ to semi-natural grasslands. Moreover, traffic decreases the attractiveness of nesting habitats and may also contribute to a higher mortality of nest-constructing females. To date, there is little research about the effects of traffic on flower-visiting insects in winter, but this could be relevant since pollution could affect overwintering or developing individuals in road verges. Future research should work on identifying if insect populations in road verges exhibit a positive net population growth, or if there is a threshold at which traffic contributes to more losses than gains of flower-visiting insects.

Regarding the vegetation management, studies considering the long-term effect of different mowing frequencies in road verges could contribute valuable information about the effectiveness of biodiversity-targeted management. Furthermore, knowledge on the effect of mowing timing and frequency on the diversity of flower-visiting insects that are active in late summer would be valuable to infer if mowing during early summer can enhance floral resources later in the season by allowing the vegetation to regrow. This might be particularly relevant for landscapes that are otherwise scarce in resources later in the season, such as landscapes dominated by arable fields.

Considering the future of transportation, the ongoing transition to electric cars could potentially reduce some of the negative impacts of traffic on flower-visiting insects in road verges. Electric vehicles produce less noise and fewer emissions compared to engines running with fossil fuels, which may decrease the disturbances from pollution and vibrations. However, the risk of collisions with vehicles would remain, emphasising the need for continued research on the overall impact of traffic.

By addressing these questions, the effectiveness of management strategies can be maximised to enhance the conservation potential of road verges, in Sweden and elsewhere.

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Popular science summary

Insects are declining globally at an alarming rate, raising serious concerns about the future of biodiversity and the functioning of ecosystems. The decline of pollinating insects is particularly concerning, as 87% of flowering plants rely on animal pollinators, including insects, to reproduce. One of the main drivers of insect decline is the loss of habitats that provide vital resources for feeding and reproduction.

Semi-natural grasslands have historically supported a diverse range of plants and insects and are among the most species rich habitats worldwide. However, due to changes in land use in large parts of Europe, these habitats have largely been afforested, abandoned or replaced by intensive agriculture. In Sweden alone, over 90% of semi-natural grasslands have disappeared during the last century. This dramatic transformation has left pollinators with fewer places to forage and nest. As these vital habitats continue to disappear or degrade in their quality, road verges may offer an alternative to help compensate for this habitat loss. Road verges cover more than 56,000 square kilometres across Europe, an area comparable in size to Croatia, and represent a significant yet often overlooked resource that could play an essential role in supporting pollinator populations. For pollinators such as wild bees, butterflies, and solitary wasps, road verges can provide permanent feeding, nesting, and overwintering resources. However, the effectiveness of road verges as habitats for pollinators depends on several factors, including the surrounding landscape history, vegetation management, and the risks posed by nearby traffic.

Landscape history might not be the first thing that comes to mind when considering what affects present-day insect diversity. Yet my research found that both habitat age and historical grassland cover have a significant impact on the diversity of plants and pollinators in road verges. Older road verges had higher plant species richness, likely due to the continuous establishment of species in newly created habitats. Additionally, the number of bumblebee species in road verges was linked to the amount of semi-natural grassland present in the 1950s. This relationship likely arises because landscapes that were historically dominated by open grassland habitats have experienced an abandonment and afforestation of grasslands over time, and the resulting heterogenous landscapes today may support a higher diversity of species.

These findings emphasise the importance of considering both historical and current landscape context when making management decisions.

Vegetation management is a crucial factor in determining the suitability of road verges as habitats for insects. In Sweden, road verges are typically mown twice a year to maintain low vegetation for traffic safety reasons. However, road verges with high plant species richness or specific valuable species are often mown only once a year, with the aim of enhancing the local plant diversity. In my research, I explored whether pollinator communities could also benefit, comparing their diversity and abundance in road verges mowed once per year with those mowed twice. The results showed that verges mowed only once had a higher density of flowers and supported more pollinators. Late-season mowing, which allows vegetation to grow and flower throughout the summer, provides essential resources for insects during their active months. Therefore, the timing and frequency of mowing are critical aspects of road verge management, with the potential to either support or limit pollinator populations. However, the benefits of reducing mowing frequency were not universal, and varied depending on local habitat conditions. This suggests that road verge management should be adapted to the specific context of each site, and that applying the same approach across all verges might not be effective everywhere.

Traffic represents another major challenge for pollinators in road verges. Vibrations, noise, and pollution from passing vehicles can create a hostile environment, and insects are also at risk of being killed by collisions with vehicles on the road. A key takeaway from my research is that high traffic intensities can have severe negative effects on pollinators. It limits the number of species and individuals in road verges, reduces the attractiveness of nesting sites, hinders population growth and reproductive success, and even diminishes the abundance of flower visitors to wild plants in the surrounding landscape. Interestingly, I found that wider road verges can mitigate some of the negative impacts of traffic, likely by creating more room for pollinators to avoid the direct effects of traffic. However, even wide verges seem to be less attractive as nesting sites for pollinating insects. Overall, I showed that high traffic makes road verges less suitable or even dangerous for pollinators. As a result, conservation efforts should be concentrated in wide road verges in low-traffic areas, where the benefits of increasing habitat quality for pollinator diversity are more likely to be realised.

There are also concerns about road verges potentially acting as ecological traps. This happens when a habitat appears to be of high quality but actually poses risks to the individuals that use it. For instance, wide road verges next to busy roads may attract pollinators with their abundance of flowers, but the proximity to traffic could increase mortality rates due to collisions. Future research is needed to investigate whether road verges in high-traffic areas act as ecological traps, and if so, how management strategies can be adapted to reduce this risk. Looking ahead, there are also broader changes that could influence how traffic affects pollinators, such as the transition to electric vehicles. But while a reduced pollution and noise could create a more favourable environment for insects in road verges, the risk of direct collisions will remain.

Based on my findings, it is clear that road verges have the potential to support pollinators, but their effectiveness depends on several factors. Management practices should be adapted to the specific conditions of each site. In low-traffic areas, road verges can be optimised for biodiversity by reducing mowing frequency and promoting diverse plant communities. In high-traffic areas, a more cautious approach is needed to ensure that road verges do not become ecological traps. In conclusion, road verges can represent an underutilised resource for biodiversity conservation, particularly for pollinators. With the right management practices in place, these habitats can support the diversity of pollinators in our rapidly changing landscapes.

Populärvetenskaplig sammanfattning

Insekter minskar globalt i en alarmerande takt, vilket väcker allvarliga farhågor om framtiden för den biologiska mångfalden och ekosystemens funktion. Minskningen av pollinerande insekter är särskilt oroande, eftersom 87% av blommande växter är beroende av pollinering med hjälp av djur, inklusive insekter, för att reproducera sig. En av de viktigaste orsakerna till insekternas tillbakagång är förlusten av livsmiljöer som ger viktiga resurser för föda och reproduktion.

Ängs- och hagmarker har historiskt sett gett näring åt en mängd olika växter och insekter och är bland de mest artrika livsmiljöerna i världen. På grund av förändrad markanvändning har dessa livsmiljöer till stor del beskogats, övergivits eller ersatts av intensivt jordbruk i stora delar av Europa. Bara i Sverige har över 90 procent av ängs- och hagmarkerna försvunnit under det senaste århundradet. Denna dramatiska omvandling har lett till att pollinatörerna har färre platser att söka föda och bygga bo på. Eftersom dessa viktiga livsmiljöer fortsätter att försvinna eller försämras i kvalitet kan vägkanter erbjuda ett alternativ för att kompensera för denna förlust av livsmiljöer. Vägkanter täcker mer än 56 000 kvadratkilometer i Europa, ett område som i storlek är jämförbart med Kroatien, och utgör en betydande men ofta förbisedd resurs som kan spela en viktig roll för att stödja pollinatörernas populationer. För pollinerande insekter som vilda bin, fjärilar och solitära steklar kan vägkanter erbjuda permanenta resurser för föda, reproduktion och övervintring. Hur bra vägkanter är som livsmiljöer för pollinerande insekter beror dock på flera faktorer, bland annat det omgivande landskapets historia, hur vegetationen sköts, och de risker som trafiken i närheten utgör.

Landskapshistoria är kanske inte det första man tänker på när man funderar på vad som påverkar dagens mångfald av insekter. Men min forskning visade att både vägens ålder hur mycket gräsmarker det historiskt funnits i det omgivande landskapet påverkar mångfalden av växter och pollinatörer i vägkanter. Äldre vägkanter hade högre artrikedom av växter, sannolikt på grund av ett ny växtarter kontinuerligt tillkommer i nyskapade livsmiljöer. Dessutom var antalet humlearter i vägkanter kopplade till mängden ängs- och hagmarker som fanns i landskapet på 1950-talet. Detta samband beror sannolikt på att landskap som historiskt dominerades av öppna gräsmarker har övergivits och beskogats med tiden, och de heterogena landskap som uppstår i dag kan ha en högre artrikedom. Dessa resultat understryker vikten av att beakta både historiska och nuvarande landskapssammanhang när man fattar beslut om skötsel.

Hur man sköter vegetationen är en avgörande faktor för att avgöra hur lämpliga vägkanter är som livsmiljöer för insekter. I Sverige klipps vägkanter vanligtvis två gånger per år för att hålla vegetationen låg av säkerhetsskäl. Vägkanter med hög artrikedom eller specifika värdefulla arter klipps dock ofta bara en gång om året, i syfte att öka mångfalden av växter. Det är dock inte helt klart om detta också gynnar pollinerande insekter. I min forskning jämförde jag mångfalden och förekomsten av pollinerande insekter i vägkanter som klipptes en gång per år med vägkanter som klipptes två gånger. Resultaten visade att vägkanter som klipptes endast en gång hade en högre täthet av blommor fler pollinatörer. Att klippa sent på säsongen, vilket gör att vegetationen kan växa och blomma under hela sommaren, ger viktiga resurser för insekter under deras aktiva månader. Tidpunkten för och frekvensen av klippning är därför viktiga aspekter av skötseln av vägkanter, med potential att antingen stödja eller begränsa populationer av pollinerande insekter. Fördelarna med att minska klippfrekvensen var dock inte universella utan varierade beroende på lokala miljöförhållanden. Detta tyder på att skötseln av vägkanter bör anpassas till de specifika förhållandena på varje plats och att en standardiserad metod som tillämpas på alla vägkanter inte nödvändigtvis kommer att vara effektiv överallt.

Trafiken utgör en annan stor utmaning för pollinerande insekter i vägkanter. Vibrationer, buller och föroreningar från passerande fordon kan skapa en ogästvänlig miljö, och insekterna riskerar också att dödas av kollisioner med passerande fordon. En viktig slutsats från min forskning är att tät trafik kan ha allvarliga negativa effekter på pollinerande insekter. En alltför tät trafik begränsar antalet arter och individer i vägkanter, gör boplatserna mindre attraktiva, begränsar populationstillväxten och reproduktionsframgången och minskar till och med antalet blombesökare på vilda växter i det omgivande landskapet. Intressant nog fann jag att bredare vägkanter kan mildra vissa av de negativa effekterna av trafiken, sannolikt genom att skapa mer utrymme där insekterna kan undvika de direkta effekterna av trafiken. Men även breda vägrenar verkar vara mindre attraktiva som boplatser för vilda bin. Sammantaget visar jag att hög trafik gör vägkanter mindre lämpliga eller till och med farliga för pollinerande insekter. Därför bör naturvårdsinsatser prioritera breda vägkanter i lågtrafikerade områden, där det är mer sannolikt att fördelarna med att öka habitatkvaliteten för insekternas mångfald kan realiseras.

Det finns också farhågor om att vägkanter kan fungera som ekologiska fällor. Detta inträffar när en livsmiljö verkar vara av hög kvalitet men i själva verket utgör en risk för de individer som använder den. Breda vägkanter intill trafikerade vägar kan t.ex. locka pollinerande insekter med sitt överflöd av blommor, men närheten till trafiken kan öka dödligheten på grund av kollisioner. Framtida forskning behövs för att undersöka om vägkanter i högtrafikerade områden fungerar som ekologiska fällor, och hur skötselstrategier i så fall kan anpassas för att minska denna risk. Om vi blickar framåt finns det också bredare förändringar som kan påverka hur trafiken påverkar pollinerande insekter, t.ex. övergången till elfordon. Men även om minskade föroreningar och minskat buller kan skapa en mer gynnsam miljö för insekter i vägkanter, kommer risken för direkta kollisioner att kvarstå.

Baserat på mina resultat är det tydligt att vägkanter har potential att stödja populationer av pollinerande insekter, men att deras effektivitet beror på flera faktorer. Skötselmetoderna bör anpassas till de specifika förhållandena på varje plats. Längs lågtrafikerade vägar kan vägkanter optimeras för biologisk mångfald genom att minska klippfrekvensen och främja en hög mångfald av blommande växter. Längs högtrafikerade vägar krävs en mer försiktig strategi för att säkerställa att vägkanterna inte blir ekologiska fällor. Sammanfattningsvis kan vägkanter utgöra en underutnyttjad resurs för att bevara den biologiska mångfalden, särskilt för pollinerande insekter. Med rätt skötselmetoder på plats kan dessa livsmiljöer stödja mångfalden av pollinerare i våra snabbt föränderliga landskap.

Populärwissenschaftliche Zusammenfassung

Der weltweite Rückgang der Insektendiversität ist alarmierend und gibt Anlass zu ernster Sorge über die Zukunft der biologischen Vielfalt und das Funktionieren der Ökosysteme. Der Rückgang von bestäubenden Insekten ist besonders besorgniserregend, da 87% der Blütenpflanzen zur Fortpflanzung auf tierische Bestäuber, einschließlich Insekten, angewiesen sind. Einer der Hauptgründe für den Rückgang der Insekten ist der Verlust von Lebensräumen, die lebenswichtige Ressourcen für die Ernährung und Fortpflanzung bieten.

Naturnahe Graslandschaften haben in der Vergangenheit eine große Vielfalt an Pflanzen und Insekten beherbergt und gehören zu den artenreichsten Lebensräumen weltweit. Aufgrund der veränderten Landnutzung in weiten Teilen Europas wurden diese Lebensräume jedoch weitgehend aufgeforstet, aufgegeben oder durch intensive Landwirtschaft ersetzt. Allein in Schweden sind im letzten Jahrhundert über 90% der naturnahen Graslandschaften zurückgegangen. Dieser dramatische Wandel hat dazu geführt, dass Bestäuber immer weniger Platz zur Nahrungssuche und zum Nisten haben. Da diese lebenswichtigen Lebensräume weiterhin verschwinden oder ihre Qualität abnimmt, können Straßenränder eine potentielle Alternative bieten, um diesen Lebensraumverlust zu kompensieren. Straßenränder bedecken mehr als 56.000 Quadratkilometer in ganz Europa, eine Fläche vergleichbar mit der Größe Kroatiens, und stellen eine bedeutende, aber oft übersehene Ressource dar, die eine wesentliche Rolle bei der Unterstützung von Bestäuberpopulationen spielen könnte. Für Bestäuber wie Wildbienen, Schmetterlinge und solitäre Wespen können Straßenränder dauerhafte Nahrungs-, Nist- und Überwinterungsmöglichkeiten bieten. Die Qualität von Straßenrändern als Lebensraum für Bestäuber hängt jedoch von mehreren Faktoren ab, wie zum Beispiel die Landschaftsgeschichte, das Management der Vegetation und die Gefahren, die vom Straßenverkehr ausgehen.

Die Landschaftsgeschichte ist vielleicht nicht das Erste, was einem in den Sinn kommt, wenn man über Einflüsse auf die heutige Insektenvielfalt nachdenkt. Meine Untersuchungen ergaben jedoch, dass sowohl das Alter der Straße als auch die historische Fläche von Graslandschaften in der

Umgebung einen Einfluss auf die Vielfalt der Pflanzen und Bestäuber in Straßenrändern haben können. Straßenränder entlang über 100 Jahre alter Straßen wiesen einen höheren Pflanzenartenreichtum auf als neue Straßenränder, was wahrscheinlich auf die kontinuierliche Einwanderung von Arten in neu geschaffenen Lebensräumen zurückzuführen ist. Darüber hinaus war die Anzahl der Hummelarten in Straßenrändern mit der Menge an Graslandschaften in den 1950er Jahren verknüpft. Dieser erstaunliche Zusammenhang ist wahrscheinlich darauf zurückzuführen, dass in Landschaften, die in der Vergangenheit von Graslandschaften dominiert wurden, im Laufe der Zeit eine starke Aufforstung und Aufgabe dieser Flächen geschah, so dass die daraus resultierenden heterogenen Landschaften heute eine höhere Artenvielfalt aufweisen. Diese Ergebnisse machen deutlich, wie wichtig es ist, bei Entscheidungen zum Management von Straßenrändern sowohl den historischen als auch den aktuellen Landschaftskontext zu berücksichtigen.

Das Management der Vegetation ist ein entscheidender Faktor bei der Bestimmung zur Eignung von Straßenrändern als Lebensraum für Insekten. In Schweden werden Straßenränder in der Regel zweimal im Jahr gemäht, um aus Gründen der Verkehrssicherheit eine niedrige Vegetation zu erhalten. Straßenränder mit einer hohen Pflanzenvielfalt oder bestimmten wertvollen Arten werden jedoch oft nur einmal im Jahr gemäht, um die lokale Pflanzenvielfalt zu erhöhen. In meiner Forschungsarbeit untersuchte ich, ob auch Bestäuberpopulationen von der reduzierten Mahd profitieren könnten. Die Ergebnisse zeigten, dass nur einmal gemähte Straßenränder eine höhere Blütendichte aufwiesen und dadurch mehr Bestäuber vorwiesen. Die späte Mahd, die es der Vegetation ermöglicht, den ganzen Sommer über zu wachsen und zu blühen, bietet den Insekten während ihrer aktiven Monate wichtige Nahrungsressourcen. Daher sind der Zeitpunkt und die Häufigkeit des Mähens entscheidende Aspekte der Pflege von Straßenrändern, die die Bestäuberpopulationen entweder fördern oder einschränken können. Die Vorteile einer Verringerung der Mähhäufigkeit waren jedoch nicht universell, sondern variierten je nach den örtlichen Bedingungen. Dies deutet darauf hin, dass das Management von Straßenrändern an die spezifischen Gegebenheiten des jeweiligen Standorts angepasst werden sollte und dass die Anwendung des gleichen Management-Ansatzes auf allen Straßenrändern nicht überall gleich effektiv ist.

Der Verkehr stellt eine weitere große Herausforderung für Bestäuber an Straßenrändern dar. Erschütterungen, Lärm und Verschmutzung durch vorbeifahrende Fahrzeuge können ein unattraktives und schädliches Umfeld schaffen. Zudem sind die Insekten dem Risiko ausgesetzt, durch Kollisionen mit Fahrzeugen auf der Straße getötet zu werden. Eine wichtige Erkenntnis aus meiner Forschung ist, dass eine hohe Verkehrsintensität schwerwiegende negative Auswirkungen auf Bestäuber haben kann. Es schränkt die Zahl der Arten und Individuen in Straßenrändern ein, verringert die Attraktivität von Nistplätzen in Straßenrändern, behindert das Populationswachstum und den Fortpflanzungserfolg und verringert sogar die Zahl der Blütenbesucher von Wildpflanzen in der umgebenden Landschaft. Interessanterweise habe ich festgestellt, dass breitere Straßenränder einen Teil der negativen Auswirkungen des Verkehrs abmildern können, wahrscheinlich weil sie den Bestäubern mehr Platz bieten, um den direkten Auswirkungen des Verkehrs auszuweichen. Allerdings scheinen auch breite Straßenränder als Nistplätze für bestäubende Insekten nicht attraktiv zu sein. Insgesamt habe ich gezeigt, dass ein hohes Verkehrsaufkommen Straßenränder weniger geeignet oder sogar gefährlich für Bestäuber macht. Daher sollten sich die Erhaltungsmaßnahmen auf breite Straßenränder in verkehrsarmen Gebieten konzentrieren, wo die Vorteile einer verbesserten Lebensraumqualität für die Bestäubervielfalt am ehesten zum Tragen kommen.

Es gibt zudem Bedenken, dass Straßenränder als ökologische Fallen wirken könnten. Dies ist dann der Fall, wenn ein Lebensraum von hoher Qualität zu sein scheint, aber in Wirklichkeit Risiken für die Individuen birgt, die ihn nutzen. So können beispielsweise breite Straßenränder neben stark befahrenen Straßen mit ihrem Blütenreichtum Bestäuber anlocken, aber die Nähe zum Verkehr könnte die Mortalitätsrate durch Kollisionen erhöhen. Künftige Forschungsarbeiten sind erforderlich, um zu untersuchen, ob Straßenränder in stark befahrenen Gebieten als ökologische Fallen wirken, und wenn ja, wie Managementstrategien angepasst werden können, um dieses Risiko zu verringern. Mit Blick auf die Zukunft gibt es auch umfassendere Veränderungen, die sich auf die Auswirkungen des Verkehrs auf Bestäuber auswirken könnten, wie zum Beispiel der Übergang zu Elektrofahrzeugen. Auch wenn eine geringere Umweltverschmutzung und ein geringerer Lärmpegel ein günstigeres Umfeld für Insekten an Straßenrändern schaffen könnten, wird das Risiko direkter Kollisionen bestehen bleiben.

Auf Grundlage meiner Ergebnisse ist klar, dass Straßenränder das Potenzial haben, Bestäuber zu unterstützen, ihre Wirksamkeit hängt jedoch von mehreren Faktoren ab. Das Vegetationsmanagement sollte an die spezifischen Bedingungen des jeweiligen Standorts angepasst werden. In verkehrsarmen Gebieten können Straßenränder für die Diversität von Bestäubern optimiert werden, indem die Mähhäufigkeit reduziert und vielfältige und blütenreiche Pflanzenpopulation gefördert werden. In Gebieten mit hohem Verkehrsaufkommen ist ein vorsichtigerer Ansatz erforderlich, um sicherzustellen, dass Straßenränder nicht zu ökologischen Fallen werden. Zusammenfassend lässt sich sagen, dass Straßenränder eine unzureichend genutzte Ressource für die Erhaltung der Diversität von Bestäubern darstellen können. Mit den richtigen Strategien des Vegetationsmanagements können diese Lebensräume die Vielfalt der Bestäuber in unseren sich rasch verändernden Landschaften unterstützen.

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ECOGRAPHY

Research article

Species accumulation in novel grassland habitats is linked to land cover history

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Novel grassland habitats along linear infrastructure have gained attention as potential supplementary or replacement habitats for species suffering from the widespread loss of traditionally managed semi-natural grasslands. However, it can take time for species to colonise new habitats, and both the historical and the current landscape composition can affect colonisation rates, particularly for grassland specialist species. We investigated the influence of more than 100 years of landscape history on present-day species richness of plants, butterflies and bumblebees in two types of linear infrastructure habitats: road verges and power line corridors. We analysed the effects of time since habitat establishment and the amount of surrounding grassland cover in different time periods on species richness of the three taxa. Our results suggest a long time lag in the establishment of plant species in novel grassland habitats, with richness of butterflies and bumblebees largely dependent on the richness of plant species. There was no direct relationship between habitat age and the richness of butterflies or bumblebees, but we found unexpected legacy effects of grassland area on present-day species richness. Higher richness of bumblebee species in road verges located in landscapes with larger surrounding grassland cover in the past is most likely a consequence of those landscapes containing a mosaic of afforested and abandoned grassland habitats today. Furthermore, we found that power line corridors might be important replacement habitats for butterflies in landscapes with little other grassland area left. Provided that road verges and power-line corridors are managed appropriately, our results show that their species richness can be expected to increase in the future.

Keywords: landscape history, linear infrastructure, pollinator, power line, road verge, vascular plants

Introduction

Semi-natural grasslands that have been managed through low-intensity grazing or mowing for centuries host diverse plant and insect communities and are one of the most species rich habitats in Europe (Cousins and Eriksson 2002, Wilson et al. 2012).

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However, starting around the turn of the 20th century, intensive agriculture displaced traditional management across the continent (Eriksson et al. 2002). Improved farming methods including artificial fertilizers and the increased production of ley and grain on fields led mainly to the abandonment of many semi-natural grasslands or to their conversion to forest (Eriksson et al. 2002, Cousins et al. 2015, Auffret et al. 2018). Yet at the same time as historical grasslands have been lost, new grassland habitats are emerging along linear infrastructure. These managed, open areas along roads, railways and power line corridors have gained attention as potential replacement habitats for species suffering from the loss of traditionally managed semi-natural grasslands (Berg et al. 2016, Phillips et al. 2020, Vanneste et al. 2020). Such habitats are largely kept open for safety reasons, but the resulting open vegetation provides grassland habitats that at least to some extent resemble traditionally managed semi-natural grasslands (Gardiner et al. 2018). Road verges provide habitat for grassland specialist plants (Vanneste et al. 2020) and act as hotspots of pollinator diversity (Phillips et al. 2020). Both road verges and power line corridors can sustain a richness and abundance of bumblebees comparable to semi-natural grasslands (Hill and Bartomeus 2016), and power line corridors can even be a source habitat for butterflies (Berg et al. 2016). As these habitats cover large areas, they provide an opportunity to preserve grassland biodiversity in human-dominated landscapes (Wojcik and Buchmann 2012, Gardiner et al. 2018). However, it is unclear whether these novel grassland habitats have had the time to accumulate a diversity similar to that in their older counterparts, and whether this accumulation depends on the amount of core habitat in the surrounding landscape, particularly with regard to interactions between plants and pollinators.

Changes in local land use, management, or connectivity to other habitat patches in the landscape can alter diversity accumulation and structure in both the short and long term. Although some changes such as habitat loss or degradation can immediately affect local diversity, the full response to change is often apparent after a delay, resulting in an extinction debt (Kuussaari et al. 2009). This can be either because individuals and local populations persist for some time even after local conditions have become unsuitable, or because metapopulations can survive long after the balance between local extinctions and (re)colonisations is altered (Hanski and Ovaskainen 2002, Hylander and Ehrlén 2013). This landscape legacy effect has for example been observed for plants and butterflies, where current diversity was better explained by historical than by present cover and connectivity of semi-natural grasslands (Bommarco et al. 2014). The time lag in local extinction of species that are not in equilibrium with their environment implies a future decline of diversity even if current environmental conditions remain stable (Jackson and Sax 2010, Bommarco et al. 2014). Time lags can also occur in the assembly of target communities following habitat creation or restoration, such that there is a colonisation credit (Watts et al. 2020). The successful (re-)colonisation by target species is broadly determined by the ability of species to disperse to, and establish in, new habitat patches (Hanski 1999). This in turn is often limited by landscape factors, because the amount and configuration of nearby habitat can determine how easy a species can move in space (Tischendorf and Fahrig 2000). As such, species diversity can be expected to increase when connectivity between habitats increases (Damschen et al. 2019), and this has broadly been shown in novel habitats such as road verges and power line corridors (Lampinen et al. 2018, Auffret and Lindgren 2020).

Responses to landscape composition and configuration vary across taxonomic groups – grassland specialist plants – whose effective dispersal relies almost entirely on external factors such as landscape connectivity and presence of dispersal vectors – often exhibit very slow colonization rates, especially in fragmented landscapes with little suitable habitat (Helsen et al. 2013, Auffret et al. 2017c, Damschen et al. 2019). Mobile species with short generation times, such as flying insects, are often able to react more rapidly to habitat changes (Kuussaari et al. 2009), and hence their diversity is more likely to already be in balance with the current landscape connectivity (Krauss et al. 2010). Nonetheless, herbivorous and pollinating insects depend on the sufficient availability of certain plants. This dependence on plant community responses means that pollinator arrival to a new habitat may be indirectly delayed (Krauss et al. 2010). Hence, time since habitat establishment and the amount of surrounding source habitat are likely to be important drivers for the species accumulation in novel grassland habitats, especially for grassland specialists. However, studies on landscape legacy effects on plant and insect diversity in linear infrastructure habitats are limited and conflicting. Auffret and Lindgren (2020) found no effect of either historical or current surrounding grassland cover on plant richness in road verges. In power line corridors, historical connectivity to grassland habitats was shown to increase the richness of plant species, but there is less evidence of a relationship between historical or current connectivity and butterfly richness (Lampinen et al. 2018).

In this study, we investigated the effects of historical land cover and habitat age on species accumulation of vascular plants, butterflies and bumblebees in novel grassland habitats along roads and power line corridors. We ask 1) if increasing habitat age leads to a local species accumulation of vascular plants overall and grassland specialist plants especially, and 2) if habitat age affects faster dispersing taxa such as butterflies and bumblebees. Considering present and historical land cover, we also ask 3) how the surrounding grassland cover from the past or the present affects local species richness. Since we lack sufficient knowledge on how historical or current land cover affects species accumulation, we used a combination of ecological model formulation approaches and statistical optimization methods to find the most relevant predictor variables for each taxon. Also, by investigating plants and flower-visiting insects in the same study design, we were able to assess how these interacting species groups react to the establishment of novel infrastructure habitat.

Material and methods

Study area

To select study landscapes, we first created 2 × 2 km landscape grids over the counties of Uppsala, Stockholm, Södermanland and Västmanland in Sweden and selected landscapes that were dominated by forest (45.2–81.2%) and had a gradient in the cover of semi-natural grasslands (0.8–9.9%) (Supporting information). Additionally, we filtered for contrasting road densities (low density: average of 4.9 km, high density: average of 16.3 km), and presence (n = 16) or absence (n = 16) of a power line corridor of at least 1 km length and surrounded by forest. This allowed us to select 32 landscapes (i.e. grids of 2 × 2 km) with contrasting road density, presence versus absence of power line corridors, and a gradient in the area of semi-natural grasslands (Dániel-Ferreira et al. 2020). We previously used this study design to describe effects of the presence or absence of power line corridors and road density on landscape scale diversity of plants, butterflies and bumblebees (Dániel-Ferreira et al. 2020), and on the differences of alpha and beta diversity of the species groups between the different habitats (Dániel-Ferreira et al. 2023). For the current study, we used a subset of this data, i.e. from one road verge along a small gravel road, one road verge along a larger paved road and one power-line corridor (in the 16 landscapes with power line corridors present) within the 32 landscape grids. We did not include road density, since this information was only calculable for the present but not the historical landscapes. From each of these habitats, we used data on the diversity of plants, butterflies and bumblebees, collected in in 2016.

In the study region, power line corridors are managed by clearing shrubs and young trees every eight years, hence maintaining an early-successional vegetation. The power line corridors in our study had been cleared between 0 and 6 years prior to the biodiversity surveys, with a median of 2.5 years for all power line corridors. The power line corridors were between 28 and 95 m wide, with an average width of 39.9 m. Road verges in Sweden are typically mown once or twice per year and cuttings are usually not removed. All road verges were at least 1.5 m wide. Verges along gravel roads had a maximum width of 5 m and an average width of 2.8 m, and verges along paved roads had a maximum width of 5.5 m and an average width of 2.9 m.

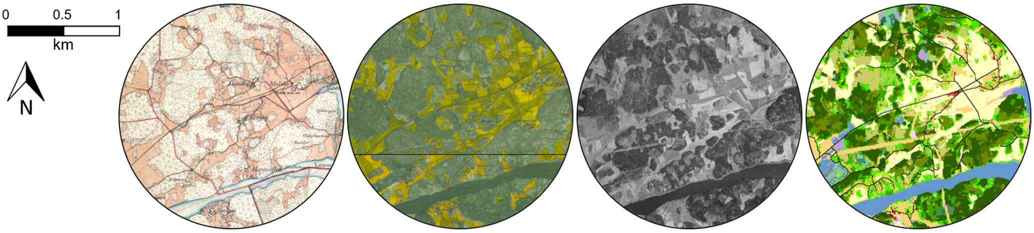
Plant and insect surveys

In each study site, we separately surveyed plants, butterflies and bumblebees along a 200 m long transect. For the plants, we placed four 1 × 1 m plots along each transect, separated by a distance of 50 m. In every plot, we recorded the presence or absence of all plant species from a pre-defined list of 169 species, all of which are frequently occurring in various types of grassland habitat in the study region. The list contained the absolute majority of the species present across all sites. The plant inventory was carried out once per site between 13 July and August 24 in 2016. Walking slowly along the same transects, we identified and counted all butterflies and burnet moths (Zygaenidae; from here on included in 'butterflies') within 2.5 m to each side and 5 m to the front of the observer. For narrower road verges, we counted all individuals along the transects. Burnet moths are diurnal and were included among butterflies because they have similar habitat requirements. We surveyed bumblebees along the same transects but within 1 m to each side and to the front. We caught and identified individuals in the field if possible or collected and identified them in the laboratory. No bumblebee queens were collected to avoid impacts on respective populations. We surveyed butterflies and bumblebees each four times per site, between 1 June and August 23 in 2016. To avoid observer bias, the surveyors inventoried all habitats and to reduce bias due to activity patterns of the insects during the day, the order of sites visited on the same day was randomized. The surveys were only conducted on days with dry vegetation, temperatures above 17°C when sunny and above 20°C when cloudy and only between 10:00 and 16:00 h.

For butterflies and plants, we calculated the richness of grassland specialists and the total richness of all species, according to the classifications in Öckinger et al. (2012). Any species that occurred in our study but were not included in this list were classified according to our knowledge (Supporting information). Because bumblebees forage in a wide range of habitat types, we did not attempt to classify them into grassland specialists and only calculated total richness (Supporting information).

Current and historical land cover

We used maps of two time periods to calculate current and historical grassland cover, in a 2 km radius around each of the surveyed road verges and power line corridors (Fig. 1). Previous studies found effects of historical land cover on the 2 km scale on the studied taxa in semi-natural grasslands (Lindborg and Eriksson 2004, Krauss et al. 2010, Bommarco et al. 2014). Creating individual buffers around each study site meant that buffers included land outside of the initial landscape grids, but allowed us to get site-specific estimates of current and historical land cover in the respective surroundings. Buffers around the three habitats within each landscape grid overlapped, and in two cases buffers around the same habitat type of two separate landscape grids overlapped (with 7.1 and 12.2%; see below for how this was accounted for in the analyses). For the historical land cover, we used published digitisations of the 1940s–1960s Swedish Economic Map (Ekonomiska kartan, hereafter '1950s map') (Auffret et al. 2017a,b). Digitisations show land cover in four categories at a resolution of 1 m; arable, forest, grassland (mostly consisting of semi-natural grassland habitat, but also includes other open land cover types, such as wetlands and urban land uses; cf. Auffret et al. 2018) and surface water. For the current land cover, we used the National Land Cover Database (Nationella marktäckedata) showing land cover data of Sweden from 2017 to 2019 (Naturvårdsverket 2020) (hereafter '2017 map'). This database classifies Sweden into 25 categories of land cover (of



Map period	1900	1950s	1970s	2017
Habitat age	✓	✓	✓	✓
Grassland cover		✓		✓

Figure 1. Overview of the four maps used to assess linear infrastructure habitat age and grassland cover in a 2 km buffer (represented) in different time periods. Pictures of maps show the original; the 1950s map was digitised and the land cover categories of the 1950s and 2017 map were reclassified before analyses.

which 16 are various types of forest) at a resolution of 10 m. These more detailed land cover types were grouped to fit to the four broader land cover types of the 1950s map (Supporting information), while we aggregated and resampled (nearest neighbour) the pixels in the 1950s map to match the grid of the 2017 map in R (package 'raster': Hijmans et al. 2022, www.r-project.org). We then created a 2 km buffer around the start coordinates of the transects used in the diversity survey (package 'rgdal': Bivand et al. 2021a, package 'rgeos': Bivand et al. 2021b), calculating the proportion of grassland within each buffer at each time period. Because the 2017 map does not differentiate species-rich semi-natural grassland from other grassland types, we additionally calculated the proportion of pixels within each buffer that was classified as grassland both in the 1950s and in the 2017 maps (hereafter 'continuous grasslands').

Habitat age

To define the age of the studied linear infrastructure habitats, we used four points in time (Fig. 1). In addition to the two maps we used for the land cover calculations (from the 1950s and 2017), we also used two other non-digitised sources: geo-referenced aerial photographs, taken between 1970 and 1976 ('1970s map'), and a historical map created between 1859 and 1911 for our landscapes (Häradsekonomiska kartan, '1900 map'). We manually examined in which map a respective contemporary infrastructure habitat appeared for the first time and grouped all respective habitats into four categories corresponding to the four points in time (Supporting information). Some roads changed course slightly over time, but were categorised as present if the majority of the stretch overlapped. We have no knowledge on the exact management history of our road verges, but assume that the vegetation has always been kept relatively open. Furthermore, although the time periods between available maps and aerial photographs differ in their distance, the points in time represent relevant time periods for the land use change in Sweden (Eriksson et al. 2002, Cousins et al. 2015) and the creation and expansion of power line corridors and road networks. All map sources except the 1900 map were geo-referenced and the habitats were examined using QGIS ver. 3.10 (QGIS.org 2020). For the 1900 map, we manually located the contemporary habitats using unaltered landmarks.

Data analysis

Statistical approach

We investigated the effects of habitat age and surrounding grassland cover on the richness of plants (total richness and number of specialist species), butterflies (total and specialists) and bumblebees (total only) in two prevalent grassland habitats: road verges and power line corridors. Given their relevance to our questions, habitat age and surrounding grassland cover were fixed predictors in all models. Because landscape grassland cover from different time periods can have smaller or larger effects on species richness in novel habitats depending on the infrastructure habitat and taxon in focus (Lampinen et al. 2018, Auffret and Lindgren 2020, Dániel-Ferreira et al. 2020), we wanted to include the most relevant landscape predictor (surrounding grassland cover in 1950s, 2017, or continuous) in each of our ten models. These values were non-independent and correlated (highest $|r_{Pearson}| = 0.77$, Supporting information), and so we used a statistical approach using single-predictor models to select which grassland cover was the best predictor for each species group in each habitat.

Single-predictor models

We built a suite of single-predictor GLMs to determine the predictive power of each of the three candidate grassland cover variables individually for each of the five species groups in the two novel habitat types (cf. Auffret et al. 2018, total 30 models; Supporting information). Within each species group-habitat combination, we calculated the R squared value for each model (package 'rsq': Zhang 2021, www.r-project.org), with the surrounding grassland cover measurement explaining the most variation in species richness in each case being selected for the final model. Since insect richness can depend on plant species richness, for each of the insect models we included either grassland specialist or total plant richness as a potential predictor variable. Because these were also highly correlated ($|r_{\text{Pearson}}|$ between 0.90 and 0.95; Supporting information) we also created single-predictor GLMs to determine which plant richness variable had a higher predictive power for the respective insect groups within each habitat type (six models; Supporting information).

Full models

We created ten full models, which had total or grassland specialist richness of our three species groups in the two infrastructure habitats as a response variable. All models had the following fixed predictor variables: 1) habitat age and 2) surrounding grassland cover as determined from the single-predictor models. All insect models also included 3) total or grassland specialist plant richness as determined from the single-predictor models. To account for spatial autocorrelation, we calculated the Moran's I autocorrelation coefficient using an inversed distance matrix (package ape: Paradis and Schliep 2019, Supporting information). For models including spatially autocorrelated data (i.e. where Moran's I was significant at the 0.05 level), we therefore included 4) the first axis of a principal coordinates of neighbour matrix (PCNM) as an additional fixed predictor variable (package 'vegan': Oksanen et al. 2020). Road verge models also included 5) the type of road (gravel or paved), as well as a random effect for landscape identity, since each study landscape contained two road verge study sites (one of each type). Gravel roads were mostly younger than paved roads, but there was no correlation between road type and habitat age. Models for power-line corridors were generalised linear models (GLM), while for road verges we used a generalised linear mixed modelling approach (GLMM) due to the random effect for landscape identity.

Model selection

All ten models were built as a full model with all relevant predictor variables, before we performed a backwards model selection to determine the best-performing model. 1) Habitat age and 2) surrounding grassland cover were set as obligatory fixed factors, as well as 3) the PCNM if applicable. There was no collinearity among the final predictors that could be expected to considerably interfere with model selection or prediction in any of the models (highest $|r_{\text{Pearson}}| = -0.53$ and 0.25) (Dormann et al. 2013, Supporting information). We used the Akaike information criterion for small sample sizes (AICc) to select the final predictors for every model and to test for the importance of two-way interaction effects between all variables (package 'MuMIn': Bartoń 2022, Supporting information). However, due to model convergence issues, interactions between 2) surrounding grassland cover and 5) road type and between 1) habitat age and 5) road type were excluded. If multiple models were selected with AICc < 2, we chose the model with the lowest AICc. For the final models, we conducted model diagnostics using fitted versus residual plots, Q-Q plots ('stats' package: base R, www.r-project.org) and additional overdispersion tests (package 'performance': Lüdecke et al. 2021). To account for overdispersion when needed, we included an observation-level random effect, and for under-dispersed data we used mean-parameterized Conway–Maxwell–Poisson distribution (package 'glmmTMB': Brooks et al. 2017). For the final models we conducted pairwise comparisons for each combination of habitat age categories, using Tukey-adjusted p-values (package 'emmeans': Lenth et al. 2022, Supporting information).

Results

Overall, we recorded 121 plant species of which 70 were classified as grassland specialists, 49 butterfly species including 22 grassland specialist species, and 18 bumblebee species (Supporting information). The cover of surrounding grassland in the 1950s varied between 0.3 and 28.7%, with an average of 10.5% (Supporting information), while in 2017 there was an overall mean of 15.7% of grassland cover, varying between 5.1 and 15.7%. Despite this apparent increase, less than one fifth of the surrounding grassland cover in 2017 was continuous grasslands that already existed in the 1950s (on average 2.9% of the landscape).

In general, the difference in explanatory power between the single-predictor models comparing the different grassland cover variables was quite small (between 0.001 and 0.029, Supporting information). Nonetheless, in nine out of ten cases the most informative variable was related to historical land use, being either 1950s grassland cover or grassland cover that has been continuous since the 1950s. Butterflies in power line corridors were the exception to these findings, with both total and specialist richness showing the most variation in explanatory power across the single-predictor models.

Plants

The total plant species richness in road verges was on average 47.3% higher along historical roads already existing in 1900 than along roads only established before 2017 (Fig. 2A). For grassland specialist richness, we found no difference between road verges of different ages (Fig. 2B). The total and specialist plant richness was higher along gravel roads than along paved roads (Supporting information). In power line corridors, the total plant species richness tended to be higher in habitats first appearing in the 2017 map than in those already existing in the 1970s (Fig. 2C). Corridors that already existed in the 1950s had on average 65.8% more specialist plants than those that first appeared in the 1970s (Fig. 2D). The respectively selected grassland cover in the surrounding landscapes did not affect the total or specialist plant species richness, neither in road verges nor in power line corridors. In the single-predictor

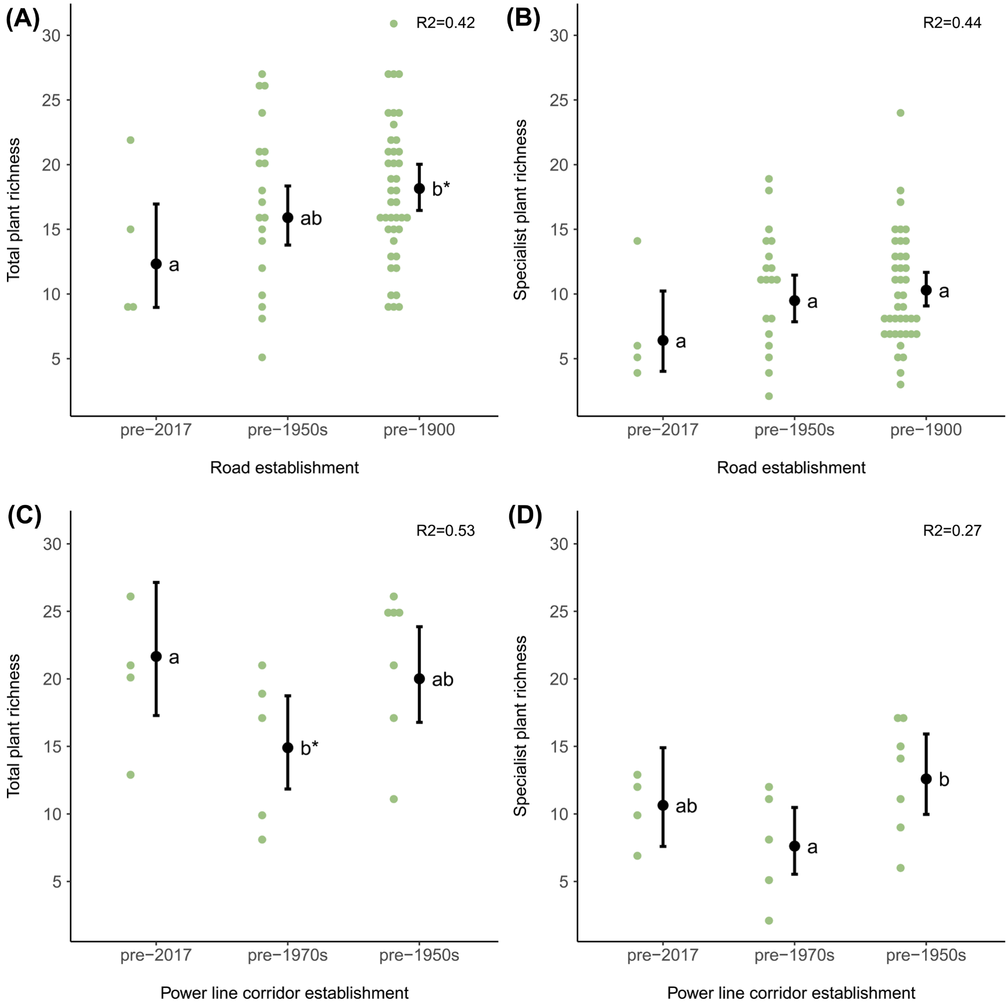


Figure 2. Effect plots for the relationship of habitat age and the richness of (A) all plant species and (B) grassland specialist plant species in road verges, and (C) all plant species and (D) grassland specialist plant species in power line corridors. Green dots represent raw data. Black dots show the predicted value of the estimated mean richness, error bars indicate the 95% confidence interval of the predicted mean. Means sharing a letter are not statistically different ($p < 0.05$), asterisk letters show marginal statistical differences ($p < 0.07$) (Tukey-adjusted pairwise comparisons).

analyses, the potential grassland cover variables showed a low difference in explanatory power (Supporting information).

Butterflies and bumblebees

We found a strong positive relationship between the richness of specialist plant species and the richness of butterfly species in road verges, for both the grassland specialist butterflies (Fig. 3A) and the total butterfly species richness (Supporting information). Furthermore, specialist and total butterfly species richness were highest in road verges first appearing in the 2017 map (Supporting information), with around 50% fewer total butterfly species in road verges from before 1900 and the 1950s than in road verges first appearing in the 2017 map. In power line corridors, there was no relationship between habitat age and total butterfly species richness or specialist butterfly species richness. Surprisingly, the number of specialist butterflies was negatively related to the cover of

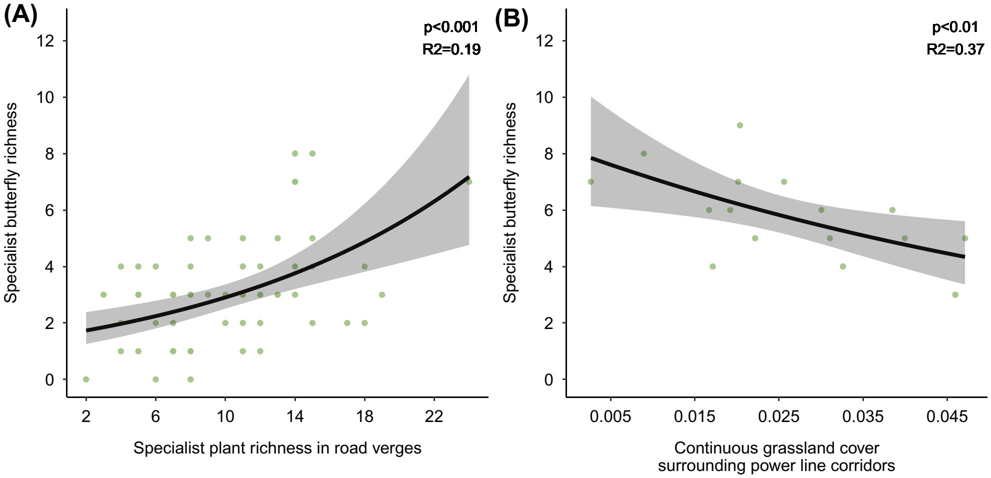


Figure 3. Effect plots for grassland specialist butterfly richness in two different infrastructure habitats, depending on (A) the richness of specialist plants in road verges and (B) the proportional cover of continuous grassland surrounding power line corridors. Green dots represent raw data. Black lines show the predicted value of the estimated mean richness, grey areas indicate the 95% confidence interval of the predicted mean richness.

continuous grasslands around power line corridors (Fig. 3B), and the total butterfly richness negatively related to the cover of current grasslands in 2017 (Supporting information). The difference in explanatory power between potential surrounding grassland cover variables was high for power line corridors but lower for road verges (Supporting information).

For bumblebees in road verges, there was a strong positive relationship with the total richness of plants, as well as with the surrounding grassland cover from the 1950s (Fig. 4A–B). We found no relationship between habitat age and bumblebee species richness in road verges, but in power line corridors bumblebee species richness was higher in corridors first

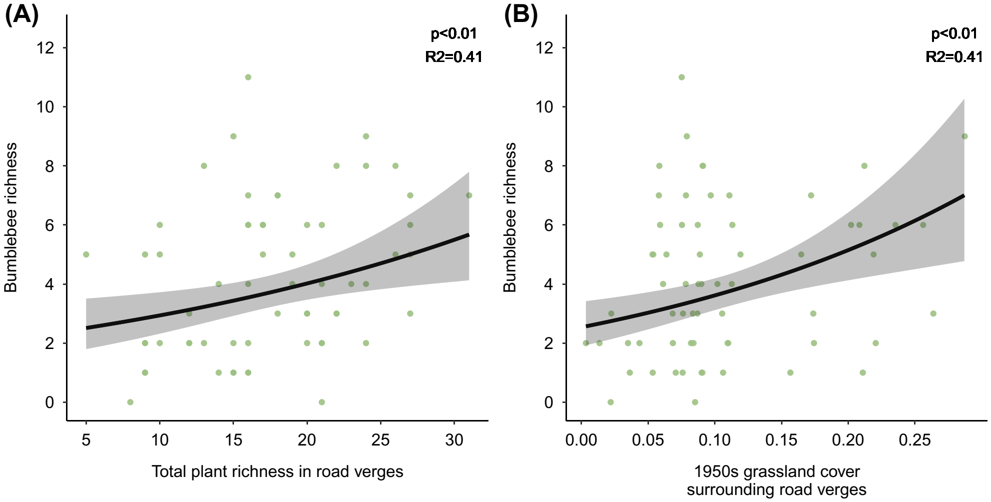


Figure 4. Effect plots for the bumblebee species richness in road verges, depending on (A) the richness of total plants and (B) the proportional cover of grasslands in the 1950s in the surrounding landscape. Green dots represent raw data. Black lines show the predicted value of the estimated mean richness, grey areas indicate the 95% confidence interval of the predicted mean richness.

appearing in the 2017 map compared to those visible in the 1970s map. The difference in explanatory power between potential grassland cover variables was low for both habitats (Supporting information).

Discussion

Our study shows that in general, both habitat age and landscape history can be drivers of contemporary species richness in linear infrastructure habitats. However, the effects differed between road verges and power line corridors, as well as among plants, butterflies and bumblebees. We found more plant species in older linear infrastructure habitats, and road verges with a higher plant species richness supported higher numbers of both butterfly and bumblebee species. In power line corridors, butterfly species richness was driven by landscape effects rather than by local resource availability.

Our results provide evidence that the accumulation of plant species in a novel grassland habitat can take a long time. In road verges, the overall plant species richness was higher along historical roads that already existed in 1900 than along young roads that first appeared on the 2017 map, with intermediate levels of species richness along roads constructed in the intervening period. This result concurs with Auffret and Lindgren (2020), who found plant richness to be highest in verges along roads that are older than 100 years. For power line corridors, we found a higher number of specialist plant species in older habitats, i.e. in those that were established before the 1950s compared to before the 1970s. Lampinen et al. (2015) also found that specialist plant species richness increased with power line corridor age, even when looking back < 50 years. Due to the construction of electricity networks mainly in the 20th century, it was unfortunately not possible to study the relationship between plant species richness and landscape composition further back in time. It should be noted that even though the time periods between the maps were of different length, this does not affect our main conclusions, since our aim was not to quantify the exact length of time lags in species accumulation. For semi-natural grasslands, the positive effects of long-term continuous management of mowing or grazing on plant diversity are well-established (Cousins and Eriksson 2002, Gustavsson et al. 2007, Eriksson 2013). Although we have no knowledge on the exact management history of our infrastructure habitats, we assume that the vegetation has always been relatively open, and that the long-term, low-intensity management of road verges has benefitted plant richness. Based on our results, we expect that plant species richness will further increase with advancing time since establishment of linear infrastructures, if current conditions remain. However, it may take over a century to see significant differences.

We found no relationship between continuous or historical grassland cover on plant species richness in linear infrastructure habitats. Nearby grasslands could in theory act as source habitats for colonization to novel habitats (Helsen et al. 2013, Damschen et al. 2019), while high levels of historical grassland cover might indicate the existence of remnant communities despite losses in core habitat (Lindborg and Eriksson 2004, Scherreiks et al. 2022). However, < 3% of the landscape surrounding our infrastructure habitats consisted of grassland habitat that has existed since the 1950s. This could help explain why the increase of plant species richness in the studied infrastructure habitats is slow, and raises the question of whether a larger area of continuously available high-quality grassland in the surroundings would enable a more efficient colonization of road verges and power line corridors. It is possible that the assembly of grassland communities in our study habitats was based on low-frequency long-distance dispersal events that could not be predicted by the landscape immediately surrounding the target site (Trakhtenbrot et al. 2005).

From a community-assembly point of view, it was surprising that the total plant richness tended to be lower in power line corridors established before the 1970s than pre-2017. Nonetheless, this was not the case for grassland specialists, and we can only speculate that this might be due to a decline in species adapted to forest conditions that existed before the creation of the corridors. Although all studied power line corridors are currently surrounded by forest, several of them had previously been pastures that were later afforested, a common trend in Swedish landscapes (Cousins et al. 2015). Previous work has indicated that relatively high richness in some power line corridors could be the result of time-lagged extinctions from previous land uses (Lampinen et al. 2018), and that power line corridors might even contribute to the maintenance of landscape-scale grassland biodiversity (Dániel-Ferreira et al. 2020). These findings and the results of our study highlight the importance of older power line corridors and their appropriate vegetation management, in order to retain the plant species in the long term.

By combining plants, pollinators and herbivores in the same study, we were able to assess how these interacting species groups react to land use changes. In road verges, the number of butterfly and bumblebee species were positively related to the richness of plant species. Other studies have found that road verges can support an abundance and richness in both flowers and pollinators comparable to or higher than in semi-natural grasslands (Phillips et al. 2020). In our study, the overall and specialist butterfly richness increased with the number of grassland specialist plant species, which likely reflects the presence of a range of nectar and host plants. This relationship between the plant and butterfly richness was also found by Ekroos et al. (2013). Thus, we can expect that road verges with a higher richness of specialist plants can support more butterfly species with diverse requirements. Bumblebee species richness was positively related to total plant species richness, probably because bumblebees respond to the general availability of various forb species (Steinert et al. 2020). This is supported by the observation that road age was not a significant predictor for bumblebee richness, even though total plant richness increases with age. We also found that the number of bumblebee species in road verges positively relates to the proportion of grasslands from the 1950s. Swedish landscapes previously dominated by open habitat have undergone a large-scale increase in forest cover and abandonment of grasslands (Cousins et al. 2015, Auffret et al. 2018). We therefore suspect that landscapes that had a larger area of grasslands in the past are composed of a mosaic of higher forest cover and different-aged, abandoned grasslands today, and that this heterogeneous landscape promotes bumblebee diversity (Rundlöf et al. 2008).

Butterfly and bumblebee species richness were surprisingly high in young road verges and power line corridors. We suggest that this means that butterflies and bumblebees can colonize infrastructure habitats relatively fast, if the local conditions are suitable. All roads in the youngest age class were gravel roads and all but one were dead-end roads leading into forests. Such forest roads typically have very low traffic intensity and are managed less intensively than larger roads, both of which could have a positive effect on insect diversity (cf. Berg et al. 2011, Dániel-Ferreira et al. 2022). In addition, grassland plant richness was higher along gravel roads than along paved roads, so the resource availability was probably higher (cf. Munguira and Thomas 1992, Saarinen et al. 2005).

In contrast to our expectations, total and specialist butterfly richness in power line corridors were negatively related to the proportion of current and continuous grassland in the surrounding landscape, respectively. While several studies found positive relationships between the local butterfly diversity in semi-natural grasslands and the amount of grasslands in the surrounding landscape (Öckinger and Smith 2006, Bergman et al. 2018), studies focussing specifically on butterfly diversity in power line corridors have not found similar patterns (Berg et al. 2011, Lampinen et al. 2018, Dániel-Ferreira et al. 2023). We consider that a concentration effect of more attractive habitats is a possible explanation for the negative relationship between butterfly species richness and grassland cover in our study. Old continuous grasslands potentially contain a higher richness of specialist plants due to the long management continuity (Cousins and Eriksson 2002), and therefore specialist butterflies might have been attracted to these more suitable habitats instead of to the power line corridors, while the total butterfly richness reacted to the availability of all current grassland habitats. Regardless of the mechanism, the conclusion of this finding is that novel grasslands are particularly important butterfly habitats in landscapes where few other grasslands remain, highlighting their importance as replacement or supplementary habitat.

To address the ongoing biodiversity crisis, it has become clear that in addition to the conservation of existing valuable habitats, the restoration of degraded habitats and the appropriate management of novel and marginal habitats also have an important role to play. Our study fits well within the context of the Kunming-Montreal Global Biodiversity Framework and upcoming EU-level legislation on nature restoration. Both acknowledge the importance of urban green space, and aim on reversing pollinator declines and enabling the long-term recovery of biodiversity (Convention on Biological Diversity 2022, European Union 2022). While our study habitats are located in rural landscapes, our results and those of similar studies emphasise their potential for biodiversity and we argue that they should be considered under the biodiversity-inclusive urban planning emphasised in the Global Biodiversity Framework. By identifying a prominence of temporal, rather than spatial factors affecting species accumulation in novel grassland habitats we highlight two conclusions of relevance for management and conservation of grassland habitats. First, management decisions should consider past habitat changes and potential time lags in the (future) establishment of local diversity (as discussed in Watts et al. 2020). Second, we show that with little grassland cover left in the landscape, the establishment of plant species in a novel habitat appears to be slow, and therefore is it of importance to conserve and restore existing valuable habitat on a landscape scale, increasing both habitat area and connectivity. Importantly, the slow assembly of plant communities can then have direct impact on pollinator diversity. Continued management of linear infrastructure habitats is therefore vital for supporting biodiversity across taxa. However, the weak or non-existent patterns for grassland specialist species highlight the importance of identifying road verges and power line corridors with local conditions that suit specialists for targeted management, while active conservation efforts such as seed sowing may be required to promote grassland biodiversity in more intensive landscapes.

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Author contributions

Svenja Horstmann: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Alistair G. Auffret**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Juliana Dániel-Ferreira**: Data curation (equal); Writing – review and editing (supporting). **Erik Öckinger**: Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data are available from the Swedish National Data Service: https://doi.org/10.5878/et9j-1p32 (Horstmann et al. 2023).

Supporting information

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

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SUPPORTING INFORMATION

Species accumulation in novel grassland habitats is linked to land cover history

Figures

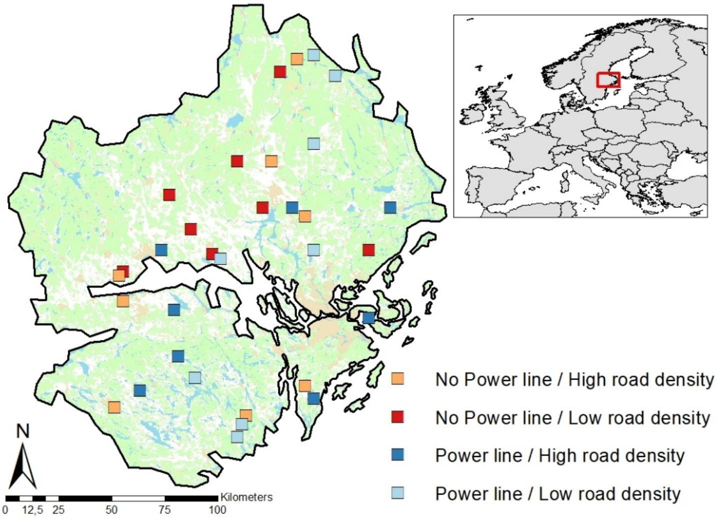

Figure S1. Location of the 32 landscapes in Sweden, from the original study design as used by Dániel-Ferreira et al. (2020), copied by permit of the Creative Commons license https://creativecommons.org/licenses/by/4.0/.

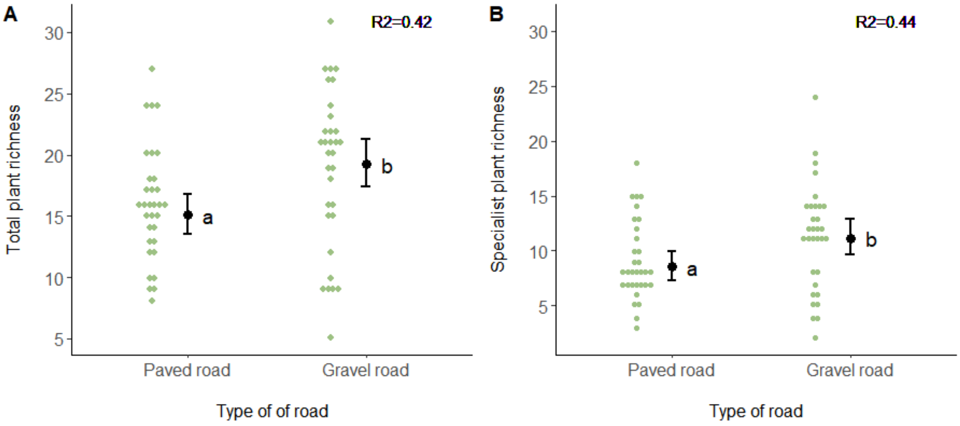

Figure S2. Effect plots for the difference between road types on (A) total plant richness and (B) grassland specialist plant richness in road verges. Green dots represent raw data. Black dots show the predicted value of the estimated mean richness, error bars indicate the 95 % confidence interval of the predicted mean. Means sharing a letter are not statistically different ($p<0.05$) (Tukey-adjusted pair-wise comparisons).

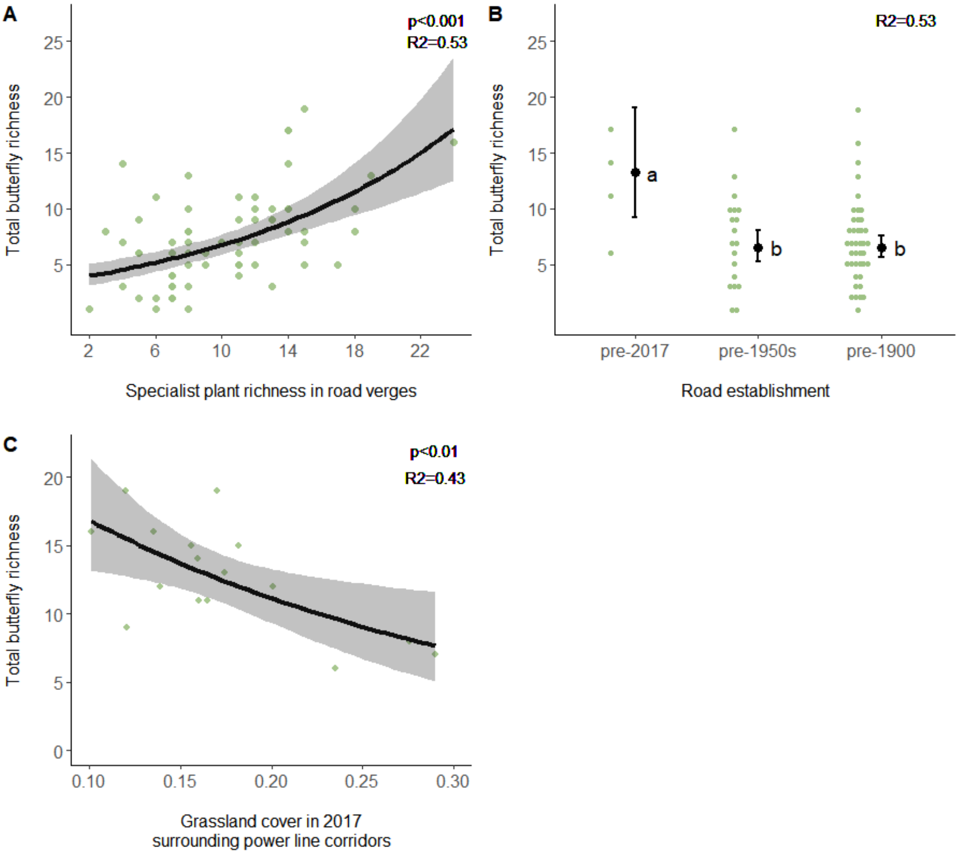

Figure S3. Effect plots for the total butterfly richness depending on (A) the richness of grassland specialist plants in road verges, (B) the age of the road and (C) the proportional cover of grasslands in 2017 surrounding power line corridors in a 2 km landscape. Green dots represent raw data. Black dots or black lines show the predicted value of the estimated mean richness, error bars or grey areas indicate the 95 % confidence interval of the predicted mean. Means sharing a letter are not statistically different ($p<0.05$) (Tukey-adjusted pair-wise comparisons).

Tables

Table S1. List of assessed plant species and the classification of grassland specialists.

Plant Species	Grassland Specialists (1 Yes/0 No)	Plant Species	Grassland Specialists (1 Yes/0 No)	Plant Species	Grassland Specialists (1 Yes/0 No)
Achillea millefolium	1	*Lathyrus pratensis*	1	*Cirsium palustre*	0
Achillea ptarmica	1	*Leucanthemum vulgare*	1	*Convallaria majalis*	0
Agrimonia eupatoria	1	*Lotus corniculatus*	1	*Elymus repens*	0
Agrostis capillaris	1	*Luzula campestris*	1	*Epilobium angustifolium*	0
Alchemilla glabra	1	*Phleum pratense*	1	*Epilobium montanum*	0
Alchemilla glaucescens	1	*Pimpinella major*	1	*Filipendula ulmaria*	0
Alchemilla monticola	1	*Pimpinella saxifraga*	1	*Galium boreale*	0
Alopecurus pratensis	1	*Plantago lanceolata*	1	*Geranium sylvaticum*	0
Anthoxanthum odoratum	1	*Plantago media*	1	*Geum urbanum*	0
Briza media	1	*Poa pratensis*	1	*Gnaphalium sylvaticum*	0
Campanula persicifolia	1	*Polygala amarella*	1	*Hieracium sylvaticiformia*	0
Campanula rotundifolia	1	*Polygala vulgaris*	1	*Hieracium vulgatiformia*	0
Carex hirta	1	*Potentilla anserina*	1	*Juncus articulatus*	0
Carex ovalis	1	*Potentilla reptans*	1	*Juncus compressus*	0
Carex pallescens	1	*Potentilla tabernaemontani*	1	*Juncus effusus*	0
Centaurea jacea	1	*Prunella vulgaris*	1	*Juniperus communis*	0
Cerastium fontanum	1	*Ranunculus acris*	1	*Leontodon autumnalis*	0
Dactylis glomerata	1	*Rhinanthus minor*	1	*Myosotis arvensis*	0
Danthonia decumbens	1	*Rumex acetosa*	1	*Oxalis acetosella*	0
Daucus carota	1	*Stellaria graminea*	1	*Plantago major*	0
Deschampsia cespitosa	1	*Succisa pratensis*	1	*Poa annua*	0
Deschampsia flexuosa	1	*Tragopogon pratensis*	1	*Poa nemoralis*	0
Dianthus deltoides	1	*Trifolium arvense*	1	*Potentilla argentea*	0
Euphrasia nemorosa	1	*Trifolium pratense*	1	*Potentilla erecta*	0
Euphrasia stricta	1	*Trifolium repens*	1	*Quercus robur*	0
Festuca ovina	1	*Veronica chamaedrys*	1	*Rubus idaeus*	0
Festuca pratensis	1	*Veronica officinalis*	1	*Rubus saxatilis*	0
Festuca rubra	1	*Vicia cracca*	1	*Rumex acetosella*	0
Filipendula vulgaris	1	*Viola canina*	1	*Rumex crispus*	0
Fragaria vesca	1	*Acer platanoides*	0	*Sedum telephium*	0
Fragaria viridis	1	*Agrostis gigantea*	0	*Solidago virgaurea*	0
Galium verum	1	*Agrostis stolonifera*	0	*Tanacetum vulgare*	0
Geum rivale	1	*Alnus glutinosa*	0	*Taraxacum erythrosperma*	0
Helianthemum nummularium	1	*Anthriscus sylvestris*	0	*Taraxacum vulgare*	0
Hieracium pilosella	1	*Arrhenatherum pratensis*	0	*Trifolium hybridum*	0
Hypericum maculatum	1	*Betula pendula*	0	*Trifolium medium*	0
Hypericum perforatum	1	*Calluna vulgaris*	0	*Urtica dioica*	0
Hypochaeris maculata	1	*Carex nigra*	0	*Vaccinium myrtillus*	0
Juncus conglomeratus	1	*Carex panacea*	0	*Vaccinium vitis-idaea*	0

Knautia arvensis	1	*Cirsium arvense*	0	*Vicia sepium*	0
Lathyrus linifolius	1				

Table S2. List of observed butterfly species and the classification of grassland specialists. The butterfly species *Leptidea juvernica* and *L. sinapis* were pooled together because of difficulties of separating them in the field.

Butterfly Species	**Grassland Specialists (1 Yes/0 No)**	**Butterfly Species**	**Grassland Specialists (1 Yes/0 No)**	**Butterfly Species**	**Grassland Specialists (1 Yes/0 No)**
Aphantopus hyperantus	1	*Polyommatus icarus*	1	*Lasiommata maera*	0
Argynnis adippe	1	*Polyommatus semiargus*	1	*Lasiommata petropolitana*	0
Argynnis aglaja	1	*Zygaena filipendulae*	1	*Limenitis populi*	0
Argynnis niobe	1	*Zygaena lonicerae*	1	*Melitaea athalia*	0
Aricia artaxerxes	1	*Zygaena viciae*	1	*Nymphalis antiopa*	0
Boloria euphrosyne	1	*Aglais urticae*	0	*Ochlodes sylvanus*	0
Boloria selene	1	*Anthocharis cardamines*	0	*Pieris brassicae*	0
Coenonympha arcania	1	*Argynnis paphia*	0	*Pieris napi*	0
Coenonympha pamphilus	1	*Brenthis ino*	0	*Pieris rapae*	0
Erynnis tages	1	*Callophrys rubi*	0	*Plebejus argus*	0
Glaucopsyche alexis	1	*Carterocephalus silvicola*	0	*Plebejus idas*	0
Hesperia comma	1	*Celastrina argiolus*	0	*Plebejus optilete*	0
Lasiommata megera	1	*Erebia ligea*	0	*Polygonia c album*	0
Leptidea sinapis juvernica	1	*Gonepteryx rhamni*	0	*Thecla betulae*	0
Lycaena phlaeas	1	*Inachis io*	0	*Thymelicus lineola*	0
Maniola jurtina	1	*Issoria lathonia*	0	*Vanessa cardui*	0
Polyommatus amandus	1				

Table S3. List of observed bumblebee species. Three bumblebee individuals could not be clearly identified as either *Bombus terrestris* or *B. lucorum* and were grouped with *B. terrestris*; on the respective study sites no other individuals of these species was observed and therefore the richness was not affected by this decision.

Bombus bohemicus	*Bombus lapidarius*	*Bombus rupestris*
Bombus campestris	*Bombus lucorum*	*Bombus soroeensis*
Bombus distinguendus	*Bombus muscorum*	*Bombus subterraneus*
Bombus hortorum	*Bombus pascuorum*	*Bombus sylvarum*
Bombus humilis	*Bombus pratorum*	*Bombus sylvestris*
Bombus hypnorum	*Bombus ruderarius*	*Bombus terrestris*

Table S4. Reclassification of land cover categories used in the Swedish National Land Cover Database (NMD, Nationella marktäckedata) to fit the land use categories of the 1950s map.

Code	NMD Classification (original)	NMD Classification (translated)	Reclassified Code	Reclassified Land Cover
111	Tallskog utanför våtmark	Pine forest outside wetlands	3	Forest
112	Granskog utanför våtmark	Spruce forest outside wetlands	3	Forest
113	Barrblandskog utanför våtmark	Coniferous forest outside wetlands	3	Forest
114	Lövblandad barrskog utanför våtmark	Deciduous coniferous forest outside wetlands	3	Forest
115	Triviallövskog utanför våtmark	Trivial deciduous forest outside wetlands	3	Forest
116	Ädellövskog utanför våtmark	Hardwood forest outside wetlands	3	Forest
117	Triviallövskog med ädellövinslag utanför våtmark	Trivial deciduous forest with deciduous elements outside wetlands	3	Forest
118	Temporärt ej skog utanför våtmark	Temporary no forest outside wetlands	3	Forest
121	Tallskog på våtmark	Pine forest in wetlands	3	Forest
122	Granskog på våtmark	Spruce forest in wetlands	3	Forest
123	Barrblandskog på våtmark	Coniferous forest in wetlands	3	Forest
124	Lövblandad barrskog på våtmark	Deciduous coniferous forest in wetlands	3	Forest
125	Triviallövskog på våtmark	Trivial deciduous forest in wetlands	3	Forest
126	Ädellövskog på våtmark	Hardwood forest in wetlands	3	Forest
127	Triviallövskog med ädellövinslag på våtmark	Trivial deciduous forest with deciduous elements in wetlands	3	Forest
128	Temporärt ej skog på våtmark	Temporarily not forest in wetlands	3	Forest
2	Våtmark	Wetland	2	Open
3	Åkermark	Arable land	1	Arable
41	Övrig öppen mark utan vegetation	Other open land without vegetation	2	Open
42	Övrig öppen mark med vegetation	Other open land with vegetation	2	Open
51	Exploaterad mark, byggnad	Exploited land, building	2	Open
52	Exploaterad mark, ej byggnad eller väg/järnväg	Exploited land, not building or road/rail	2	Open
53	Exploaterad mark, väg/järnväg	Exploited land, road/rail	2	Open
61	Sjö och vattendrag	Lake and watercourses	4	Water
62	Hav	Sea	4	Water

Table S5. Information on habitat age and proportional grassland cover in all respective maps, and the richness of all species groups.

Landscape	Habitat	Age (i.e. first appearance)	1950s Grassland	2017 Grassland	Continuous Grassland	Grassland Specialist Plant Richness	Plant Richness	Butterfly richness	Grassland Specialist Butterfly Richness	Bumblebee Richness
1037	Paved Road	1900	0.036	0.105	0.009	9	16	5	3	1
1037	Power line	1970s	0.036	0.101	0.009	11	17	16	8	3
1037	Gravel Road	1950s	0.035	0.105	0.009	11	20	11	5	2
1278	Paved Road	1950s	0.113	0.161	0.032	11	14	7	4	4
1278	Power line	1970s	0.083	0.139	0.022	8	19	12	5	3
1278	Gravel Road	1900	0.078	0.142	0.023	24	31	16	7	7
1450	Paved Road	1900	0.071	0.165	0.019	3	9	8	3	1

1450	Gravel Road	1900	0.076	0.161	0.025	12	20	11	3	3
1605	Paved Road	1900	0.208	0.178	0.062	5	10	9	3	6
1605	Gravel Road	1900	0.211	0.180	0.064	5	9	2	1	1
1851	Paved Road	1900	0.090	0.295	0.040	15	24	7	2	4
1851	Power line	1950s	0.062	0.276	0.019	17	26	8	6	4
1851	Gravel Road	1900	0.064	0.280	0.022	11	19	5	1	5
2014	Paved Road	1900	0.087	0.226	0.033	10	20	7	2	3
2014	Power line	1950s	0.085	0.235	0.033	15	25	6	4	3
2014	Gravel Road	1900	0.085	0.234	0.033	12	21	5	1	0
2156	Paved Road	1900	0.091	0.155	0.029	9	16	6	5	1
2156	Gravel Road	1950s	0.110	0.151	0.034	4	10	3	1	2
2333	Paved Road	1900	0.054	0.112	0.011	7	15	2	1	1
2333	Power line	1950s	0.089	0.121	0.017	14	25	9	4	5
2333	Gravel Road	1900	0.053	0.112	0.012	17	27	5	2	5
2844	Paved Road	1950s	0.091	0.140	0.012	15	24	5	5	8
2844	Power line	1950s	0.054	0.174	0.017	11	21	13	6	4
2844	Gravel Road	1950s	0.102	0.109	0.012	11	21	9	3	4
3897	Paved Road	1900	0.078	0.176	0.025	7	16	2	1	4
3897	Power line	1970s	0.113	0.290	0.046	2	8	7	3	3
3897	Gravel Road	1900	0.110	0.172	0.026	11	21	6	3	2
4091	Paved Road	1900	0.111	0.181	0.040	10	16	7	3	7
4091	Power line	2017	0.078	0.159	0.026	13	26	14	7	7
4091	Gravel Road	1900	0.061	0.154	0.019	13	23	9	3	4
4319	Paved Road	1900	0.079	0.177	0.018	13	24	9	5	9
4319	Gravel Road	1950s	0.091	0.145	0.018	18	26	10	2	8
5041	Paved Road	1900	0.059	0.132	0.030	7	17	6	3	6
5041	Gravel Road	1900	0.069	0.155	0.040	11	24	5	3	2
5166	Paved Road	1900	0.058	0.103	0.019	8	18	8	5	7
5166	Gravel Road	1900	0.058	0.102	0.019	13	22	10	3	8
5561	Paved Road	1900	0.090	0.144	0.033	8	15	6	3	1
5561	Power line	1970s	0.084	0.135	0.030	12	21	16	6	6
5561	Gravel Road	1900	0.088	0.134	0.026	14	19	10	3	4
5683	Paved Road	1900	0.087	0.168	0.024	8	16	3	0	6
5683	Gravel Road	1950s	0.075	0.148	0.022	8	16	8	4	11
5798	Paved Road	1900	0.084	0.111	0.031	7	12	3	2	2
5798	Power line	1950s	0.091	0.182	0.038	17	25	15	6	6
5798	Gravel Road	1950s	0.097	0.121	0.035	14	27	10	4	7
5834	Paved Road	1900	0.174	0.144	0.038	18	27	8	4	3
5834	Power line	2017	0.192	0.160	0.040	12	21	11	5	6
5834	Gravel Road	1900	0.256	0.156	0.054	14	27	14	7	6
5847	Paved Road	1900	0.075	0.089	0.010	8	17	13	3	6
5847	Gravel Road	1900	0.068	0.088	0.009	12	22	10	2	3
6437	Paved Road	1950s	0.165	0.100	0.035	13	17	3	3	5
6437	Gravel Road	1950s	0.119	0.128	0.045	2	5	1	0	5
6836	Paved Road	1900	0.174	0.241	0.075	8	15	1	1	2
6836	Gravel Road	2017	0.157	0.243	0.071	5	9	6	4	1

7073	Paved Road	1900	0.106	0.142	0.041	7	14	4	2	1
7073	Gravel Road	2017	0.106	0.140	0.042	14	22	17	7	3
7080	Paved Road	1900	0.082	0.167	0.019	6	9	2	2	2
7080	Power line	1950s	0.084	0.165	0.020	9	17	11	9	2
7080	Gravel Road	1950s	0.076	0.160	0.023	12	15	7	4	1
7103	Paved Road	1900	0.014	0.171	0.005	8	16	5	1	2
7103	Power line	1950s	0.007	0.170	0.003	6	11	19	7	5
7103	Gravel Road	1950s	0.003	0.168	0.002	11	21	4	2	2
7411	Paved Road	1900	0.054	0.067	0.009	7	10	4	3	5
7411	Gravel Road	1950s	0.044	0.051	0.006	6	9	1	0	2
8329	Paved Road	1900	0.083	0.159	0.030	7	13	7	2	2
8329	Gravel Road	1950s	0.084	0.152	0.026	7	12	3	2	3
8337	Paved Road	1950s	0.022	0.156	0.012	5	8	6	3	0
8337	Gravel Road	1950s	0.022	0.153	0.007	14	18	17	8	3
8768	Paved Road	1950s	0.264	0.109	0.040	12	20	9	3	3
8768	Power line	2017	0.150	0.120	0.020	10	20	19	7	7
8768	Gravel Road	1950s	0.235	0.103	0.035	8	16	10	3	6
9889	Paved Road	1900	0.212	0.161	0.049	8	13	7	3	8
9889	Power line	1970s	0.193	0.156	0.047	5	10	15	5	5
9889	Gravel Road	1900	0.202	0.127	0.042	15	21	8	4	6
9931	Paved Road	1900	0.172	0.099	0.022	14	18	8	4	7
9931	Gravel Road	2017	0.287	0.116	0.056	6	15	11	4	9
10099	Paved Road	1900	0.221	0.169	0.043	4	12	7	2	2
10099	Gravel Road	1950s	0.219	0.182	0.047	19	26	13	3	5
10156	Paved Road	1900	0.113	0.202	0.031	15	20	19	8	6
10156	Power line	2017	0.112	0.201	0.031	7	13	12	5	5
10156	Gravel Road	2017	0.089	0.184	0.025	4	9	14	4	5

Table S6. Pairwise correlation of potential predictors for the generalized linear models. Values higher than 0.7 are in bold.

Habitat	Predictor variables	Road Type	Habitat Age	1950s Grassland	2017 Grassland	Continuous Grassland	Grassland Specialist Plant Richness
Power line corridor	1950s Grassland		-0.526				
	2017 Grassland		0.207	-0.033			
	Continuous Grassland		-0.236	**0.760**	0.379		
	Grassland Specialist Plant Richness		0.160	-0.192	-0.053	-0.160	
	Total plant richness		0.047	-0.150	-0.111	-0.164	**0.945**
Road verge	Habitat Age	-0.437					
	1950s Grassland	0.003	-0.141				
	2017 Grassland	-0.051	0.095	0.054			
	Continuous Grassland	0.005	-0.090	**0.767**	0.416		

	Grassland Specialist Plant Richness	0.239	0.091	0.005	0.009	-0.141	
	Total plant richness	0.251	0.157	-0.012	0.023	-0.140	**0.902**

Table S7. R2 values retrieved from single-predictor GLMs to determine the most informative grassland cover predictor for every main model. The highest R2 values and the respective chosen predictor for each comparison are in bold.

Habitat	Response Variable	Estimate	Std. Error	z value	p value	R2 value	Predictor
Power line corridor	Total Plant Richness	-4.044	4.678	-0.865	0.387	**0.020**	**Continuous Grassland**
		-0.947	1.198	-0.791	0.429	0.019	1950s Grassland
		-0.659	1.124	-0.586	0.558	0.012	2017 Grassland
	Grassland Specialist Plant Richness	-5.088	6.288	-0.809	0.418	0.019	Continuous Grassland
		-1.578	1.624	-0.972	0.331	**0.031**	**1950s Grassland**
		-0.404	1.501	-0.269	0.788	0.003	2017 Grassland
	Total Butterfly Richness	-8.591	5.751	-1.494	0.135	0.133	Continuous Grassland
		-0.555	1.460	-0.380	0.704	0.009	1950s Grassland
		-4.245	1.511	-2.810	0.005	**0.406**	**2017 Grassland**
	Grassland Specialist Butterfly Richness	-12.368	8.525	-1.451	0.147	**0.328**	**Continuous Grassland**
		-2.003	2.203	-0.909	0.363	0.142	1950s Grassland
		-2.419	2.128	-1.137	0.255	0.200	2017 Grassland
	Bumblebee Richness	3.629	9.471	0.383	0.702	0.018	Continuous Grassland
		2.170	2.327	0.932	0.351	**0.117**	**1950s Grassland**
		-2.087	2.365	-0.882	0.378	0.092	2017 Grassland
Road verge	Total Plant Richness	-2.893	1.880	-1.538	0.124	**0.018**	**Continuous Grassland**
		-0.063	0.466	-0.136	0.892	0.000	1950s Grassland
		0.167	0.659	0.253	0.800	0.001	2017 Grassland
	Grassland Specialist Plant Richness	-3.765	2.474	-1.522	0.128	**0.018**	**Continuous Grassland**
		0.030	0.608	0.050	0.960	0.000	1950s Grassland
		0.085	0.864	0.099	0.921	0.000	2017 Grassland
	Total Butterfly Richness	-0.754	2.848	-0.265	0.791	0.000	Continuous Grassland
		1.138	0.687	1.656	0.098	**0.020**	**1950s Grassland**
		-0.416	1.021	-0.408	0.684	0.001	2017 Grassland
	Grassland Specialist Butterfly Richness	-0.035	4.399	-0.008	0.994	0.000	Continuous Grassland
		0.799	1.077	0.741	0.458	**0.009**	**1950s Grassland**
		-1.096	1.602	-0.684	0.494	0.006	2017 Grassland
	Bumblebee Richness	0.853	3.810	0.224	0.823	0.000	Continuous Grassland
		2.149	0.899	2.389	0.017	**0.055**	**1950s Grassland**
		-2.346	1.423	-1.648	0.099	0.026	2017 Grassland

Table S8. R2 values retrieved from single-predictor GLMs to determine the most informative plant richness predictor for every main model. The highest R2 values and the respective chosen predictor for each comparison are in bold.

		Estimate	Std. Error	z value	p value	R2 value	Predictor
Power line corridor	Total Butterfly Richness	-0.010	0.012	-0.850	0.395	**0.035**	**Total Plant Richness**
		-0.012	0.017	-0.684	0.494	0.021	Grassland Specialist Plant Richness
	Grassland Specialist Butterfly Richness	0.004	0.018	0.220	0.826	0.007	Total Plant Richness
		0.009	0.025	0.344	0.731	**0.016**	**Grassland Specialist Plant Richness**
	Bumblebee Richness	0.016	0.021	0.755	0.450	**0.076**	**Total Plant Richness**
		0.019	0.028	0.659	0.510	0.053	Grassland Specialist Plant Richness
Road verge	Total Butterfly Richness	0.045	0.008	5.559	0.000	0.215	Total Plant Richness
		0.060	0.010	6.000	0.000	**0.257**	**Grassland Specialist Plant Richness**
	Grassland Specialist Butterfly Richness	0.039	0.012	3.151	0.002	0.155	Total Plant Richness
		0.058	0.015	3.767	0.000	**0.215**	**Grassland Specialist Plant Richness**
	Bumblebee Richness	0.037	0.011	3.386	0.001	**0.114**	**Total Plant Richness**
		0.043	0.014	3.153	0.002	0.099	Grassland Specialist Plant Richness

Table S9. Moran's I autocorrelation coefficient, with p<0.05 indicating spatial autocorrelation (in bold).

	Variable	Observed	Expected	Standard Deviation	p value
Power line corridor	Total Plant Richness	0.121	-0.067	0.077	**0.015**
	Grassland Specialist Plant Richness	0.059	-0.067	0.076	0.098
	Total Butterfly Richness	-0.026	-0.067	0.077	0.598
	Grassland Specialist Butterfly Richness	-0.101	-0.067	0.075	0.648
	Bumblebee Richness	0.003	-0.067	0.078	0.371
Road verge	Total Plant Richness	0.059	-0.016	0.107	0.485
	Grassland Specialist Plant Richness	-0.123	-0.016	0.106	0.309
	Total Butterfly Richness	0.103	-0.016	0.106	0.260
	Grassland Specialist Butterfly Richness	0.003	-0.016	0.105	0.854
	Bumblebee Richness	0.231	-0.016	0.106	**0.020**

Table S10. Selection of the final predictors for every model on power line corridors, including tests of two-way interaction effect between all variables, using the Akaike Information Criterion for small sample sizes (AICc).

Response Variable	Grassland Cover Predictor (GCP)	Plant Richness Predictor (PRP)	Statistical model	Candidate Model	AICc	ΔAICc
Total Plant Richness	Continuous Grassland	NA	Generalized linear model (GLM), family=poisson, link=log	Age + GCP + Pcnm1	107.564	0.000
				Age + GCP + Pcnm1 + Age:GCP	114.710	7.146

Grassland Specialist Plant Richness	1950s Grassland	NA	Generalized linear model (GLM), family=poisson, link=log	Age + GCP	98.802	0.000
				Age + GCP + Age:GCP	100.445	1.643
Total Butterfly Richness	2017 Grassland	Total Plant Richness	Generalized linear model (GLM), family=poisson, link=log	Age + GCP	91.509	0.000
				Age + GCP + PRP	93.906	2.397
				Age + GCP + PRP + GCP:PRP	98.618	7.108
				Age + GCP + Age:GCP	100.883	9.374
				Age + GCP + PRP + Age:GCP	104.454	12.945
				Age + GCP + PRP + Age:PRP	104.681	13.172
				Age + GCP + PRP + Age:PRP + GCP:PRP	112.742	21.233
				Age + GCP + PRP + Age:GCP + GCP:PRP	112.935	21.426
				Age + GCP + PRP + Age:GCP + Age:PRP	123.656	32.147
				Age + GCP + PRP + Age:GCP + Age:PRP + GCP:PRP	139.655	48.146
Grassland Specialist Butterfly Richness	Continuous Grassland	Grassland Specialist Plant Richness	Generalized linear model (GLMM), family=compoisson, link=log	Age + GCP	67.053	0.000
				Age + GCP + PRP	72.137	5.084
				Age + GCP + PRP + GCP:PRP	77.685	10.633
				Age + GCP + Age:GCP	77.787	10.734
				Age + GCP + PRP + Age:PRP	83.129	16.076
				Age + GCP + PRP + Age:GCP	86.258	19.205
				Age + GCP + PRP + Age:PRP + GCP:PRP	94.503	27.450
				Age + GCP + PRP + Age:GCP + GCP:PRP	96.731	29.678
				Age + GCP + PRP + Age:GCP + Age:PRP	106.175	39.122
				Age + GCP + PRP + Age:GCP + Age:PRP + GCP:PRP	129.391	62.338
Bumblebee Richness	1950s Grassland	Grassland Specialist Plant Richness	Generalized linear model (GLMM), family=compoisson, link=log	Age + GCP	66.899	0.000
				Age + GCP + PRP	70.809	3.910
				Age + GCP + PRP + GCP:PRP	77.438	10.539
				Age + GCP + Age:GCP	77.747	10.848
				Age + GCP + PRP + Age:GCP	80.552	13.654
				Age + GCP + PRP + Age:PRP	85.343	18.444
				Age + GCP + PRP + Age:GCP + GCP:PRP	89.596	22.698
				Age + GCP + PRP + Age:PRP + GCP:PRP	96.696	29.797
				Age + GCP + PRP + Age:GCP + Age:PRP	107.102	40.204
				Age + GCP + PRP + Age:GCP + Age:PRP + GCP:PRP	126.091	59.192

Table S11. Selection of the final predictors for every model on road verges, including tests of two-way interaction effect between all variables, using the Akaike Information Criterion for small sample sizes (AICc). Due to model convergence issues, interactions between the (b) grassland cover predictor (GCP) and (d) road type (RT) and between (a) habitat age and (d) road type (RT) were excluded.

Response Variable	Grassland Cover Predictor (GCP)	Plant Richness Predictor (PRP)	Statistical model	Candidate Model	AICc	Δ AICc
Total Plant Richness	Continuous Grassland	NA	Generalized linear model (GLMM), family=poisson, link=log	Age + GCP + RT	408.702	0.000
				Age + GCP + RT + Age:GCP	413.686	4.984
				Age + GCP	419.083	10.381

				Age + GCP + Age:GCP	423.998	15.296
Grassland Specialist Plant Richness	Continuous Grassland	NA	Generalized linear model (GLMM), family=poisson, link=log	Age + GCP + RT	371.687	0.000
				Age + GCP	375.029	3.342
				Age + GCP + RT + Age:GCP	376.845	5.159
				Age + GCP + Age:GCP	380.099	8.412
Total Butterfly Richness	1950s Grassland	Grassland Specialist Plant Richness	Generalized linear model (GLMM), family=poisson, link=log	Age + GCP + PRP	333.734	0.000
				Age + GCP + PRP + GCP:PRP	335.633	1.899
				Age + GCP + RT + PRP	336.069	2.335
				Age + GCP + RT + PRP + RT:PRP	336.105	2.371
				Age + GCP + RT + PRP + GCP:PRP	338.189	4.455
				Age + GCP + PRP + Age:GCP	338.198	4.464
				Age + GCP + RT + PRP + GCP:PRP + RT:PRP	338.235	4.501
				Age + GCP + PRP + Age:PRP	338.472	4.738
				Age + GCP + PRP + Age:GCP + GCP:PRP	340.301	6.567
				Age + GCP + PRP + Age:PRP + GCP:PRP	340.395	6.661
				Age + GCP + RT + PRP + Age:PRP	340.762	7.028
				Age + GCP + RT + PRP + Age:GCP	340.801	7.067
				Age + GCP + RT + PRP + Age:GCP + RT:PRP	340.906	7.173
				Age + GCP + RT + PRP + Age:PRP + RT:PRP	341.606	7.872
				Age + GCP + RT + PRP + Age:PRP + GCP:PRP	342.984	9.250
				Age + GCP + RT + PRP + Age:GCP + GCP:PRP	343.083	9.349
				Age + GCP + PRP + Age:GCP + Age:PRP	343.148	9.414
				Age + GCP + RT + PRP + Age:GCP + GCP:PRP + RT:PRP	343.302	9.568
				Age + GCP + RT + PRP + Age:PRP + GCP:PRP + RT:PRP	343.927	10.193
				Age + GCP + PRP + Age:GCP + Age:PRP + GCP:PRP	345.386	11.652
				Age + GCP + RT + PRP + Age:GCP + Age:PRP	345.787	12.053
				Age + GCP + RT + PRP + Age:GCP + Age:PRP + RT:PRP	346.768	13.034
				Age + GCP + RT + PRP + Age:GCP + Age:PRP + GCP:PRP	348.272	14.538
				Age + GCP + RT + PRP + Age:GCP + Age:PRP + GCP:PRP + RT:PRP	349.382	15.648
				Age + GCP + RT	358.720	24.987
				Age + GCP	362.825	29.091
				Age + GCP + RT + Age:GCP	363.423	29.689
				Age + GCP + Age:GCP	367.498	33.765
Grassland Specialist Butterfly Richness	1950s Grassland	Grassland Specialist Plant Richness	Generalized linear model (GLMM), family=poisson, link=log	Age + GCP + PRP	241.350	0.000
				Age + GCP + RT + PRP	242.134	0.784
				Age + GCP + PRP + Age:GCP	243.446	2.096
				Age + GCP + RT + PRP + Age:GCP	243.717	2.367
				Age + GCP + PRP + GCP:PRP	243.875	2.526
				Age + GCP + RT + PRP + RT:PRP	244.666	3.316
				Age + GCP + RT + PRP + GCP:PRP	244.666	3.317
				Age + GCP + PRP + Age:GCP + GCP:PRP	246.144	4.794
				Age + GCP + RT + PRP + Age:GCP + RT:PRP	246.275	4.925
				Age + GCP + PRP + Age:PRP	246.482	5.133

				Age + GCP + RT + PRP + Age:GCP + GCP:PRP	246.526	5.176
				Age + GCP + RT + PRP + GCP:PRP + RT:PRP	247.301	5.951
				Age + GCP + RT + PRP + Age:PRP	247.375	6.026
				Age + GCP + PRP + Age:GCP + Age:PRP	248.808	7.458
				Age + GCP + PRP + Age:PRP + GCP:PRP	249.196	7.847
				Age + GCP + RT + PRP + Age:GCP + GCP:PRP + RT:PRP	249.200	7.850
				Age + GCP + RT + PRP + Age:GCP + Age:PRP	249.334	7.984
				Age + GCP + RT + PRP + Age:PRP + RT:PRP	249.970	8.620
				Age + GCP + RT + PRP + Age:PRP + GCP:PRP	250.128	8.779
				Age + GCP + PRP + Age:GCP + Age:PRP + GCP:PRP	251.717	10.368
				Age + GCP + RT + PRP + Age:GCP + Age:PRP + RT:PRP	251.978	10.629
				Age + GCP + RT + PRP + Age:GCP + Age:PRP + GCP:PRP	252.365	11.015
				Age + GCP + RT + PRP + Age:PRP + GCP:PRP + RT:PRP	252.855	11.505
				Age + GCP + RT + PRP + Age:GCP + Age:PRP + GCP:PRP + RT:PRP	255.140	13.790
				Age + GCP	255.305	13.955
				Age + GCP + RT	257.744	16.394
				Age + GCP + Age:GCP	258.001	16.651
				Age + GCP + RT + Age:GCP	260.599	19.249
Bumblebee Richness	1950s Grassland	Total Plant Richness	Generalized linear model (GLMM), family=poisson, link=log	Age + GCP + Pcnm1 + PRP	276.875	0.000
				Age + GCP + Pcnm1 + RT + PRP	278.859	1.984
				Age + GCP + Pcnm1 + PRP + GCP:PRP	279.148	2.273
				Age + GCP + Pcnm1 + RT + PRP + RT:PRP	280.927	4.052
				Age + GCP + Pcnm1 + RT + PRP + GCP:PRP	281.110	4.234
				Age + GCP + Pcnm1 + PRP + Age:PRP	281.451	4.576
				Age + GCP + Pcnm1	281.602	4.727
				Age + GCP + Pcnm1 + PRP + Age:GCP	281.811	4.936
				Age + GCP + Pcnm1 + RT + PRP + Age:PRP	283.010	6.134
				Age + GCP + Pcnm1 + RT + PRP + GCP:PRP + RT:PRP	283.307	6.432
				Age + GCP + Pcnm1 + RT + PRP + Age:GCP	283.734	6.859
				Age + GCP + Pcnm1 + PRP + Age:PRP + GCP:PRP	283.783	6.908
				Age + GCP + Pcnm1 + RT	284.086	7.211
				Age + GCP + Pcnm1 + PRP + Age:GCP + GCP:PRP	284.357	7.482
				Age + GCP + Pcnm1 + RT + PRP + Age:PRP + GCP:PRP	285.174	8.299
				Age + GCP + Pcnm1 + RT + PRP + Age:PRP + RT:PRP	285.854	8.979
				Age + GCP + Pcnm1 + RT + PRP + Age:GCP + RT:PRP	285.967	9.092
				Age + GCP + Pcnm1 + RT + PRP + Age:GCP + GCP:PRP	286.310	9.435
				Age + GCP + Pcnm1 + Age:GCP	286.692	9.816
				Age + GCP + Pcnm1 + PRP + Age:GCP + Age:PRP	286.770	9.895
				Age + GCP + Pcnm1 + RT + PRP + Age:GCP + Age:PRP	288.140	11.265
				Age + GCP + Pcnm1 + RT + PRP + Age:PRP + GCP:PRP + RT:PRP	288.168	11.293

	Age + GCP + Pcnm1 + RT + PRP + Age:GCP + GCP:PRP + RT:PRP	288.676	11.801
	Age + GCP + Pcnm1 + PRP + Age:GCP + Age:PRP + GCP:PRP	289.359	12.484
	Age + GCP + Pcnm1 + RT + Age:GCP	289.376	12.501
	Age + GCP + Pcnm1 + RT + PRP + Age:GCP + Age:PRP + GCP:PRP	290.563	13.688
	Age + GCP + Pcnm1 + RT + PRP + Age:GCP + Age:PRP + RT:PRP	291.217	14.342
	Age + GCP + Pcnm1 + RT + PRP + Age:GCP + Age:PRP + GCP:PRP + RT:PRP	293.814	16.939

Table S12. Results for the selected generalized linear models from Tables S10 and S11. Pcnm1 refers to the first axis of a principal coordinates of neighbour matrix (pcnm), which we included as an additional predictor variable for spatial autocorrelated data (as documented in Table S9). P-values < 0.05 are bold, values between 0.05 and 0.08 are italic.

	Habitat	Predictor	Estimate	SE	z value	p value	R2 value
Total Plant Richness	Power line corridor	Age 1970s	-0.374	0.163	-2.291	**0.022**	0.526
		Age 1950s	-0.079	0.153	-0.518	0.604	
		Landscape: Continuous Grassland	2.981	5.444	0.548	0.584	
		Pcnm1	-0.701	0.254	-2.765	**0.006**	
	Road verge	Habitat Gravel road	0.243	0.068	3.588	**0.000**	0.419
		Age 1950s	0.255	0.175	1.460	0.144	
		Age 1900	0.387	0.168	2.302	**0.021**	
		Landscape: Continuous Grassland	-1.987	2.630	-0.755	0.450	
Grassland Specialist Plant Richness	Power line corridor	Age 1970s	-0.334	0.233	-1.436	0.151	0.274
		Age 1950s	0.169	0.229	0.739	0.460	
		Landscape: 1950s Grassland	-0.345	2.009	-0.172	0.864	
	Road verge	Habitat Gravel road	0.270	0.109	2.489	**0.013**	0.441
		Age 1950s	0.392	0.255	1.535	0.125	
		Age 1900	0.473	0.249	1.902	*0.057*	
		Landscape: Continuous Grassland	-2.375	3.353	-0.708	0.479	
Total Butterfly Richness	Power line corridor	Age 1970s	-0.068	0.182	-0.372	0.710	0.426
		Age 1950s	-0.082	0.178	-0.462	0.644	
		Landscape: 2017 Grassland	-4.141	1.587	-2.609	**0.009**	
	Road verge	Grassland Specialist Plant Richness	0.067	0.012	5.753	**0.000**	0.527
		Age 1950s	-0.709	0.216	-3.283	**0.001**	
		Age 1900	-0.707	0.194	-3.640	**0.000**	
		Landscape: 1950s Grassland	0.716	0.957	0.748	0.454	
Grassland Specialist Butterfly Richness	Power line corridor	Age 1970s	-0.097	0.140	-0.693	0.488	0.368
		Age 1950s	-0.115	0.134	-0.858	0.391	
		Landscape: Continuous Grassland	-13.321	4.606	-2.892	**0.004**	
	Road verge	Grassland Specialist Plant Richness	0.065	0.016	4.153	**0.000**	0.192
		Age 1950s	-0.637	0.275	-2.322	**0.020**	
		Age 1900	-0.681	0.259	-2.634	**0.008**	
		Landscape: 1950s Grassland	0.179	1.117	0.160	0.873	
Bumblebee Richness	Power line corridor	Age 1970s	-0.429	0.175	-2.452	**0.014**	0.369
		Age 1950s	-0.374	0.185	-2.019	**0.043**	
		Landscape: 1950s Grassland	0.562	1.599	0.351	0.725	

	Road verge	Total Plant Richness	0.031	0.012	2.723	**0.006**	0.406
		Age 1950s	-0.234	0.293	-0.797	0.425	
		Age 1900	-0.313	0.280	-1.118	0.264	
		Landscape: 1950s Grassland	3.538	1.089	3.250	**0.001**	
		Pcnm1	2.603	0.569	4.574	0.000	

Table S13. Pairwise comparisons for each combination of habitat age categories, using Tukey-adjusted p-values. P-values < 0.05 are bold, values between 0.05 and 0.08 are italic.

	Habitat	Pairwise Comparison	Estimate	SE	t/z value	p
Total Plant Richness	Power line corridor	1970s - 1950s	-0.29	0.15	-1.97	0.12
		2017 - 1950s	0.08	0.15	0.52	0.86
		2017 - 1970s	0.37	0.16	2.29	*0.06*
	Road verge	2017 - 1900	-0.39	0.17	-2.30	*0.06*
		2017 - 1950s	-0.25	0.17	-1.46	0.32
		1950s - 1900	-0.13	0.09	-1.54	0.28
Grassland Specialist Plant Richness	Power line corridor	1970s - 1950s	-0.50	0.21	-2.45	**0.04**
		2017 - 1950s	-0.17	0.23	-0.74	0.74
		2017 - 1970s	0.33	0.23	1.44	0.32
	Road verge	2017 - 1900	-0.47	0.25	-1.90	0.15
		2017 - 1950s	-0.39	0.26	-1.54	0.28
		1950s - 1900	-0.08	0.12	-0.70	0.77
Total Butterfly Richness	Power line corridor	1970s - 1950s	0.01	0.17	0.08	1.00
		2017 - 1970s	0.07	0.18	0.37	0.93
		2017 - 1950s	0.08	0.18	0.46	0.89
	Road verge	1950s - 1900	0.00	0.12	-0.02	1.00
		2017 - 1900	0.71	0.19	3.64	**0.00**
		2017 - 1950s	0.71	0.22	3.28	**0.00**
Grassland Specialist Butterfly Richness	Power line corridor	1970s - 1950s	0.02	0.13	0.14	0.99
		2017 - 1970s	0.10	0.14	0.69	0.77
		2017 - 1950s	0.12	0.13	0.86	0.68
	Road verge	1950s - 1900	0.04	0.16	0.27	0.96
		2017 - 1950s	0.64	0.27	2.32	*0.06*
		2017 - 1900	0.68	0.26	2.63	**0.03**
Bumblebee Richness	Power line corridor	1970s - 1950s	-0.05	0.17	-0.31	0.95
		2017 - 1950s	0.37	0.19	2.02	0.15
		2017 - 1970s	0.43	0.17	2.45	*0.08*
	Road verge	1950s - 1900	0.08	0.14	0.55	0.85
		2017 - 1950s	0.23	0.29	0.80	0.71
		2017 - 1900	0.31	0.28	1.12	0.51

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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

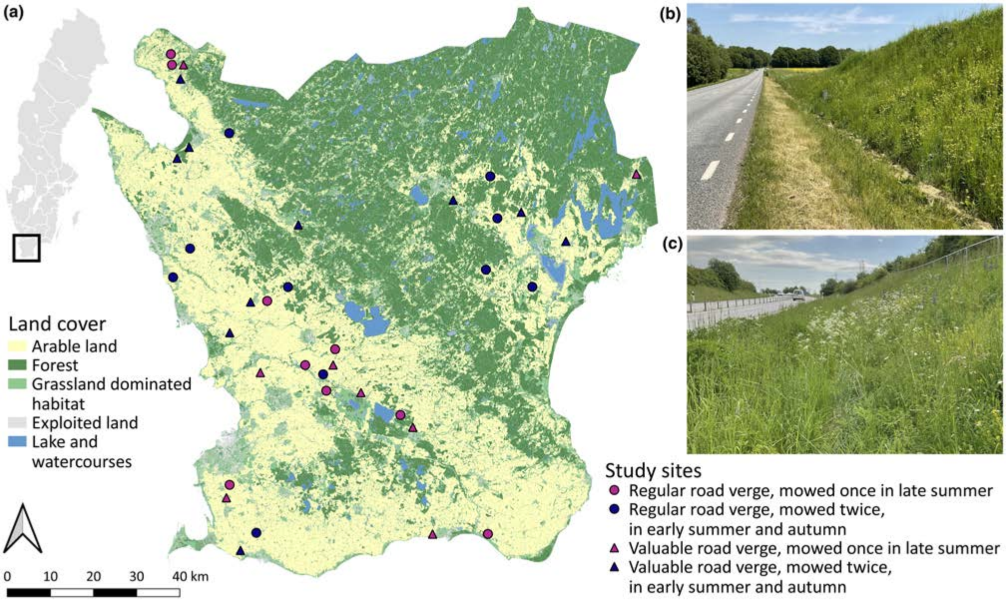

FIGURE 1 (a) Location of the 37 road verge sites in southern Sweden, showing the crossed study design to separate effects of road verge classification and mowing regime on biodiversity. Within each of the four categories for each combination of classification and mowing regime, the study sites were selected 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).

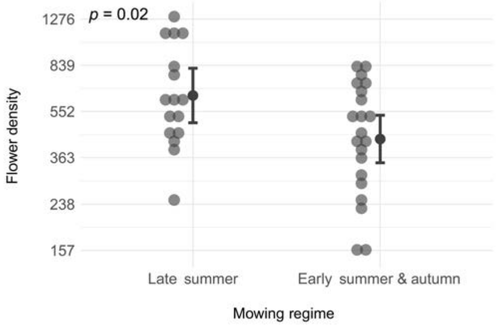

FIGURE 2 Differences in flower density (total abundance in three visits divided by width of road verge) in road verges in southern Sweden ($n=37$) depending on mowing regime. Only the early summer mowing occurred during our study period. Flower density was log-transformed for the analyses. Dots represent 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

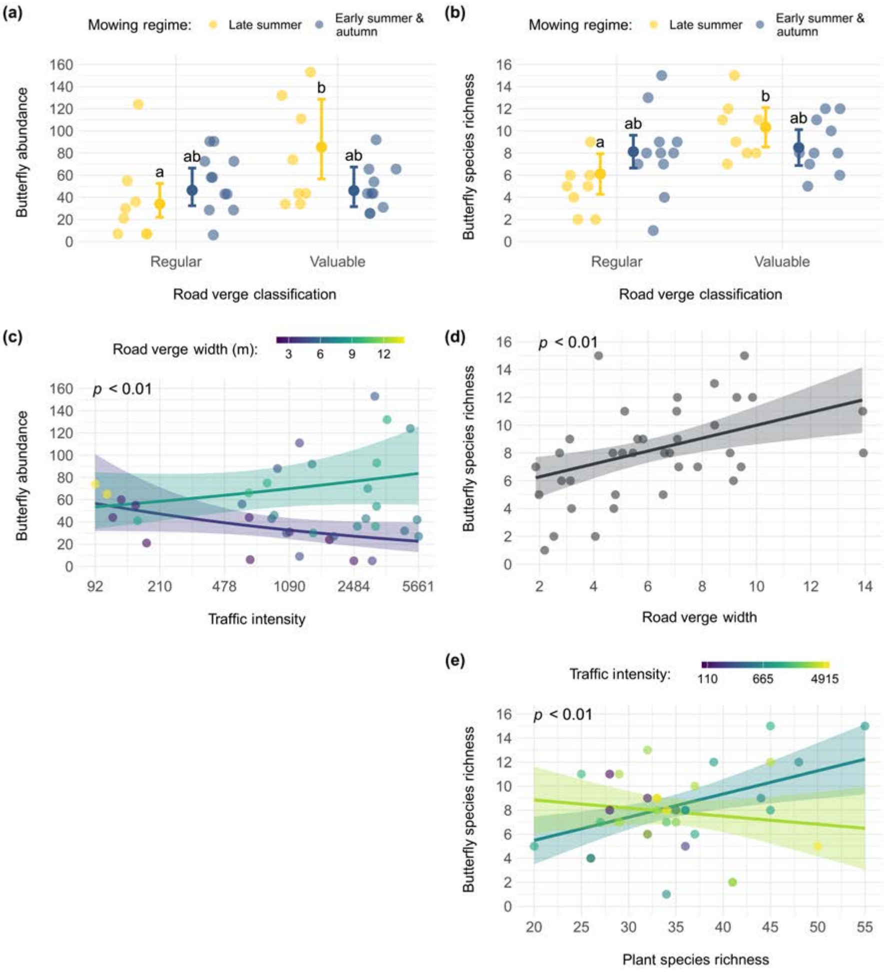

FIGURE 3 Predicted effects on butterfly abundance (left) and richness (right), depending on (a,b) the interaction between mowing regime and road verge classification, (c) the interaction between road verge width and traffic intensity for butterfly abundance, (d) the road verge width as additive effect 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

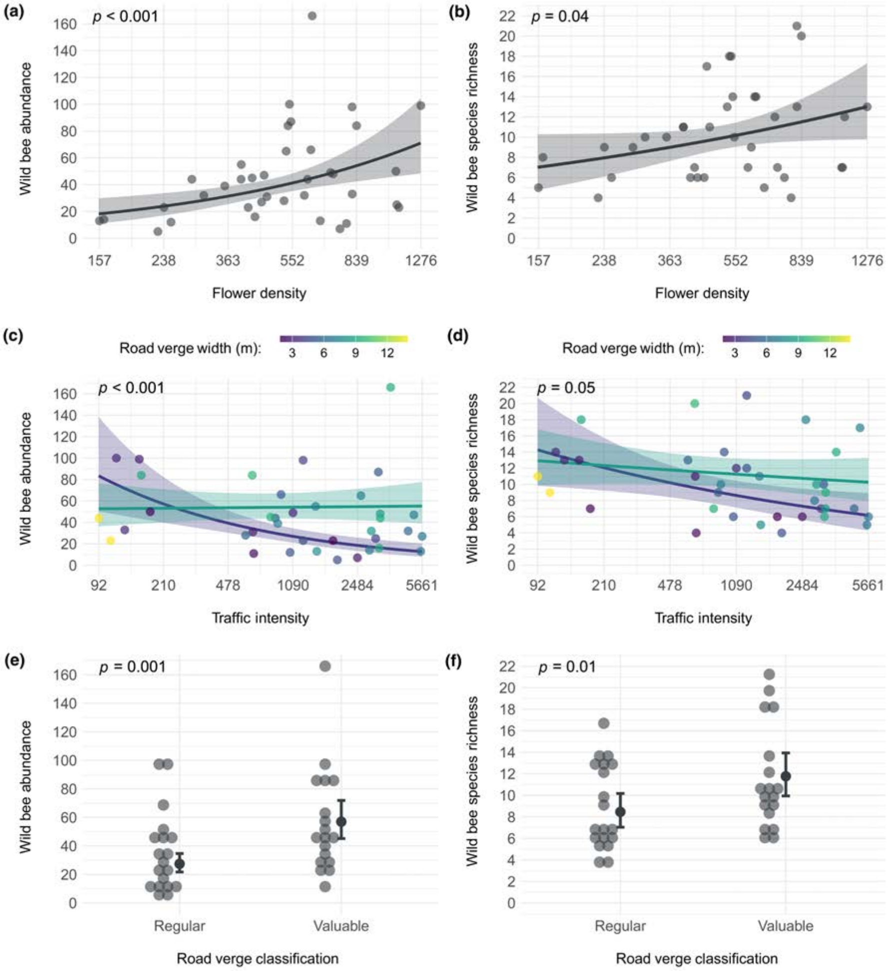

FIGURE 4 Predicted effects on wild bee abundance (left) and species richness (right) in (a, b) relation to flower density, (c, d) the interaction of traffic intensity and (e, f) road verge width and the road verge classification. Traffic intensity and flower density were log-transformed for the analyses. 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.

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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

($p < 0.05$) 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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SUPPORTING INFORMATION

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

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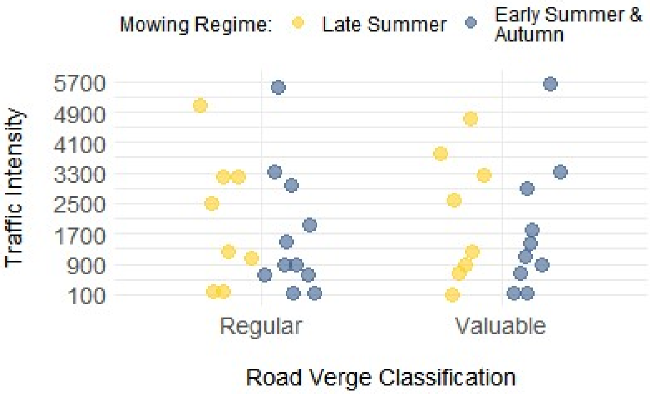
Figures



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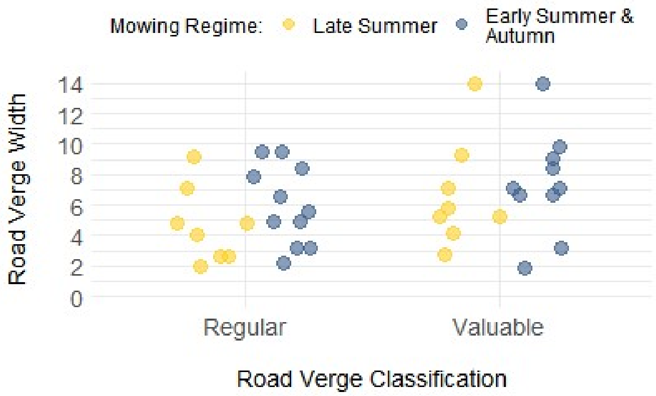

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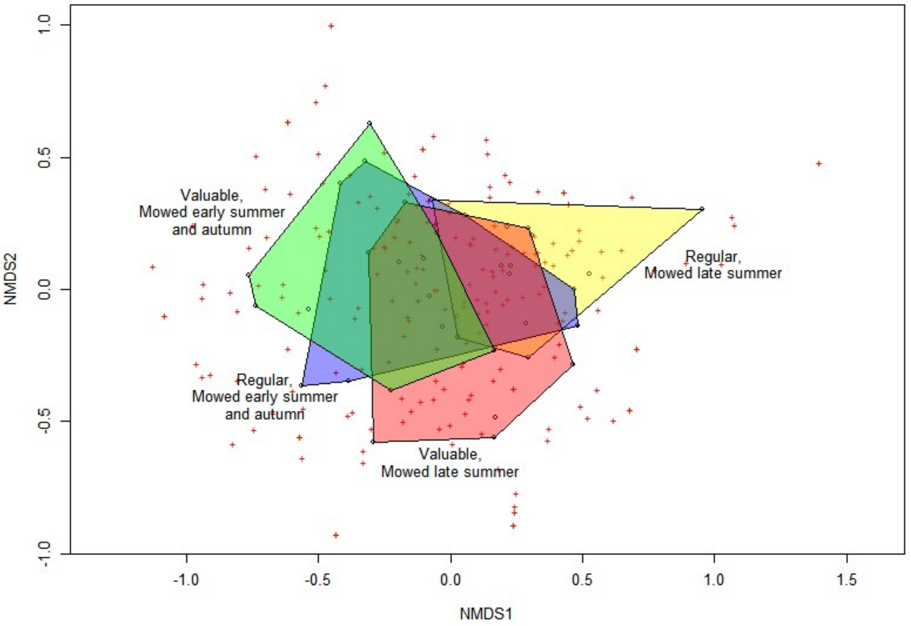

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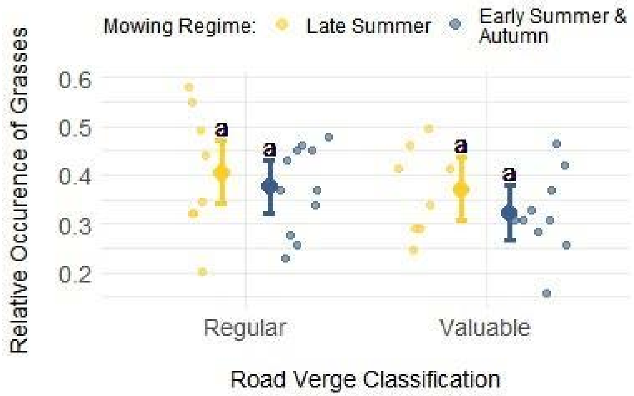

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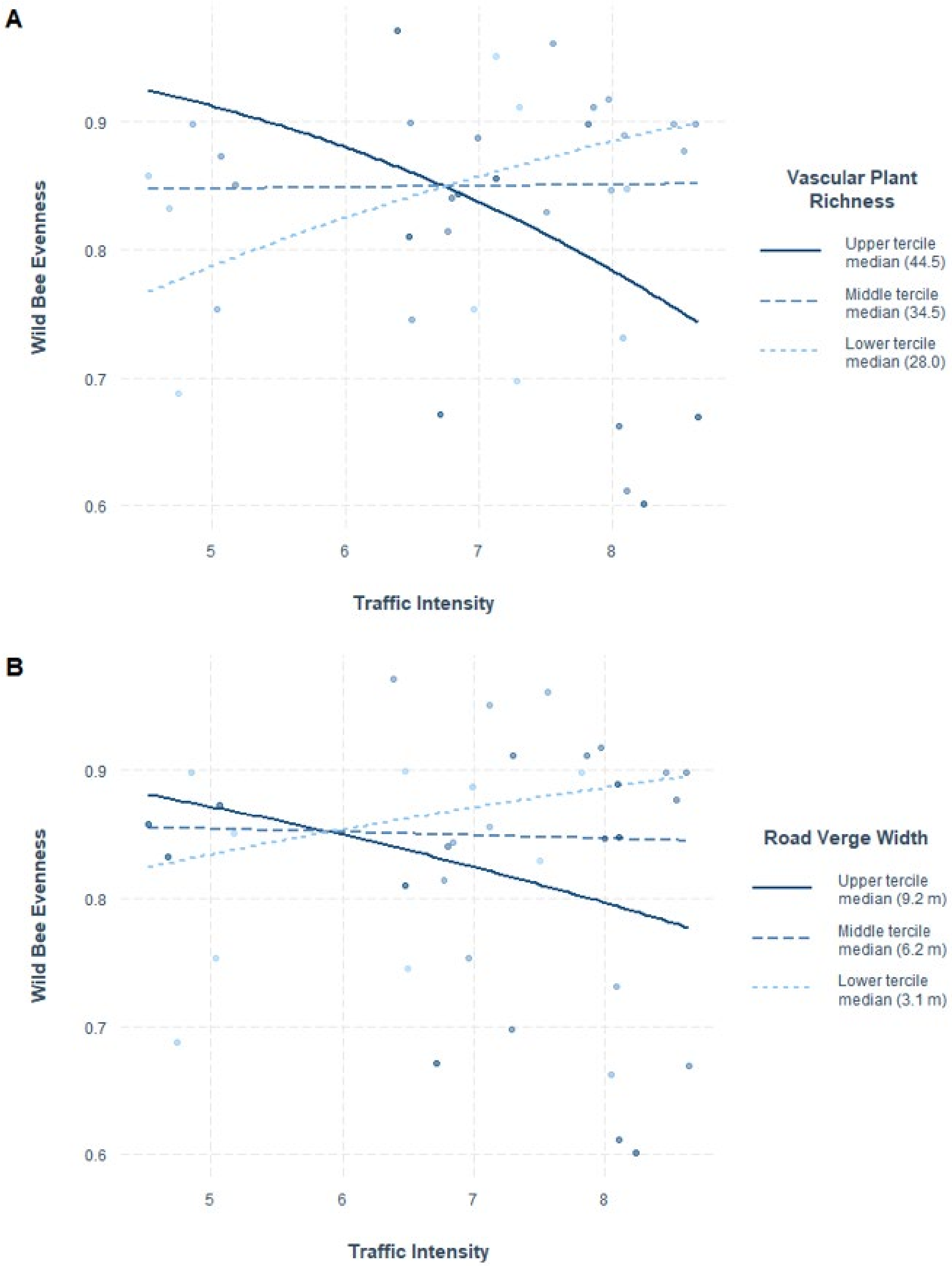

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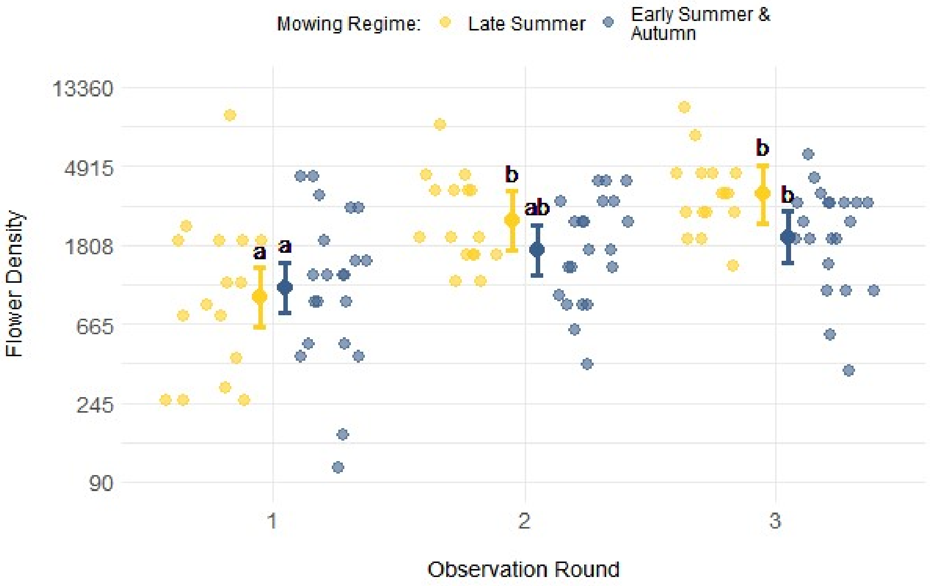

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Tables

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.*

Code	NMD Classification (original)	NMD Classification (translated)	Reclassified Code	Reclassified Land Cover
111	Tallskog utanför våtmark	Pine forest outside wetlands	3	Forest
112	Granskog utanför våtmark	Spruce forest outside wetlands	3	Forest
113	Barrblandskog utanför våtmark	Coniferous forest outside wetlands	3	Forest
114	Lövblandad barrskog utanför våtmark	Deciduous coniferous forest outside wetlands	3	Forest
115	Triviallövskog utanför våtmark	Trivial deciduous forest outside wetlands	3	Forest
116	Ädellövskog utanför våtmark	Hardwood forest outside wetlands	3	Forest
117	Triviallövskog med ädellövinslag utanför våtmark	Trivial deciduous forest with deciduous elements outside wetlands	3	Forest
118	Temporärt ej skog utanför våtmark	Temporary no forest outside wetlands	3	Forest
121	Tallskog på våtmark	Pine forest in wetlands	3	Forest
122	Granskog på våtmark	Spruce forest in wetlands	3	Forest
123	Barrblandskog på våtmark	Coniferous forest in wetlands	3	Forest
124	Lövblandad barrskog på våtmark	Deciduous coniferous forest in wetlands	3	Forest
125	Triviallövskog på våtmark	Trivial deciduous forest in wetlands	3	Forest
126	Ädellövskog på våtmark	Hardwood forest in wetlands	3	Forest
127	Triviallövskog med ädellövinslag på våtmark	Trivial deciduous forest with deciduous elements in wetlands	3	Forest
128	Temporärt ej skog på våtmark	Temporarily not forest in wetlands	3	Forest
2	Våtmark	Wetland	2	Open
3	Åkermark	Arable land	1	Arable
41	Övrig öppen mark utan vegetation	Other open land without vegetation	2	Open
42	Övrig öppen mark med vegetation	Other open land with vegetation	2	Open
51	Exploaterad mark, byggnad	Exploited land, building	5	Exploited
52	Exploaterad mark, ej byggnad eller väg/järnväg	Exploited land, not building or road/rail	5	Exploited
53	Exploaterad mark, väg/järnväg	Exploited land, road/rail	5	Exploited
61	Sjö och vattendrag	Lake and watercourses	4	Water
62	Hav	Sea	4	Water
255	Moln/Oklassat	Cloud/Unclassified	0	NA
0	Moln/Oklassat 2	Cloud/Unclassified	0	NA

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.*

Study Site ID	**Coordinates (WGS 84)**	**Quality**	**Mowing Regime**	**Traffic Intensity**	**Mean Road Verge Width**	**Vascular Plant Richness**	**Flower Density**	**Butterfly Abundance**	**Butterfly Richness**	**Wild Bee Abundance**	**Wild Bee Richness**	**Butterfly Evenness**	**Wild Bee Evenness**	**Vascular Plant Evenness**	**Arable Land Cover (%)**	**Forest Land Cover (%)**
0B	56.1283769553672, 13.8309127167964	Valuable	2	158	9.03	35	536.16	41	8	84	18	0.89	0.87	0.91	37.83	32.45
0C	56.0919996988494, 13.9965212541784	Regular	2	128	3.12	32	815.49	60	9	33	13	0.89	0.90	0.90	72.18	12.37
0D	55.9098591272408, 13.1475269784705	Regular	1	177	1.98	36	1084.29	21	5	50	7	0.82	0.85	0.93	85.14	2.67
1A	55.7810472611079, 13.3973929627945	Valuable	1	92	13.92	28	394.94	74	11	44	11	0.85	0.86	0.92	88.58	2.99
1B	55.3899290623592, 13.0740201585901	Valuable	2	107	13.94	28	238.74	65	8	23	9	0.77	0.83	0.91	74.59	3.13
1C	55.427421398679, 13.1303741033096	Regular	2	115	3.18	26	541.53	44	4	100	14	0.79	0.69	0.94	88.83	1.65
1D	55.8138796858352, 13.4036480653451	Regular	1	154	2.81	32	1276.08	55	6	99	13	0.62	0.75	0.92	81.06	9.58
2A	56.1873654092395, 14.5133705739595	Valuable	1	654	2.74	36	467.31	44	8	31	11	0.92	0.90	0.91	32.70	44.39
2C	56.1790736453034, 13.9679724068046	Regular	2	597	5.62	44	522.56	56	9	28	13	0.83	0.97	0.93	54.84	33.12
3A	55.4986933629804, 13.0170414872814	Valuable	1	871	5.45	36	609.46	43	8	44	9	0.57	0.81	0.91	82.41	2.21
3B	56.1052637891307, 14.0848692720075	Valuable	2	650	9.85	48	838.87	66	12	84	20	0.90	0.81	0.92	52.07	29.32
3C	55.98449528255, 13.9567367125803	Regular	2	822	9.56	55	424.36	75	15	45	7	0.83	0.67	0.93	53.99	25.09
3D	55.5257263886938, 13.0275179030362	Regular	2	662	2.19	34	785.59	6	1	11	4	1.00	0.75	0.90	83.90	2.02
4A	56.366994577017, 12.7995772417275	Valuable	2	899	7.08	39	354.94	46	12	39	10	0.88	0.84	0.92	52.34	17.88
4B	55.8425524835997, 13.0119843196558	Valuable	2	1091	3.14	37	708.11	31	6	49	12	0.91	0.89	0.93	82.39	4.37
4C	55.7610046416661, 13.3613503499024	Regular	2	938	5.05	45	622.53	88	8	66	14	0.58	0.84	0.94	72.61	5.20

4D	56.417814000239, 12.7608791887679	Regular	1	1052	4.80	20	249.97	30	5	12	6	0.72	0.75	0.92	62.52	13.04
5A	55.6547401713388, 13.6964386894241	Valuable	1	1242	4.18	45	814.83	111	15	98	21	0.84	0.86	0.92	40.50	24.60
5B	56.0459960922703, 14.2528545509001	Valuable	2	1456	7.06	25	395.38	92	11	55	11	0.74	0.70	0.91	71.06	6.04
5C	55.9501141788948, 14.1300752360367	Regular	2	1479	7.83	27	156.80	30	7	13	5	0.85	0.91	0.90	60.41	15.27
5D	55.6798228690502, 13.6499360872609	Regular	1	1242	4.74	26	1105.30	9	4	23	12	0.83	0.95	0.90	36.62	39.00
6A	55.7247474054853, 13.5024708046008	Valuable	1	2595	7.13	35	530.10	36	7	65	18	0.87	0.91	0.92	54.75	17.27
6B	56.0700303387886, 13.2557451962731	Valuable	2	1818	1.86	34	413.61	24	7	23	6	0.85	0.83	0.91	27.51	39.31
6C	55.9399004934327, 13.2234089789421	Regular	2	1921	4.70	35	229.49	27	8	5	4	0.91	0.96	0.91	62.50	25.45
6D	55.7269697657157, 13.3744968318773	Regular	1	2482	2.53	41	752.70	5	2	7	6	0.72	0.90	0.90	61.56	15.29
7A	56.3966386010831, 12.8092376139056	Valuable	1	3240	5.14	29	546.60	153	11	87	10	0.52	0.73	0.91	36.05	35.49
7B	56.2253555156508, 12.8401660976779	Valuable	2	2892	6.80	33	161.39	43	8	14	8	0.82	0.92	0.92	34.75	40.49
7C	56.2572036247982, 12.9885833079833	Regular	2	2962	8.45	32	309.59	70	13	32	10	0.82	0.85	0.90	36.18	32.91
7D	56.3956453564341, 12.7661524993306	Regular	1	3132	4.06	41	1090.77	5	2	25	7	0.97	0.66	0.92	59.26	13.73
8A	55.7613587467669, 13.1292117524266	Valuable	1	3788	9.28	45	628.05	132	12	166	14	0.82	0.60	0.92	85.37	2.46
8B	55.9067250847047, 13.0859342716348	Valuable	2	3316	8.46	37	720.13	54	10	48	7	0.79	0.61	0.90	76.81	3.53
8C	55.9534015067537, 12.7957977052281	Regular	2	3321	9.43	29	286.49	93	7	44	9	0.81	0.85	0.93	69.34	2.90
8D	55.7793067451218, 13.2943072141329	Regular	1	3271	9.15	32	432.39	36	6	16	6	0.85	0.89	0.90	77.04	5.36
9A	55.4330342693422, 13.7759952628636	Valuable	1	4735	5.82	33	596.51	32	9	32	7	0.77	0.90	0.92	44.12	5.05
9B	56.2014552800413, 12.7964262172781	Valuable	2	5661	6.56	50	451.36	27	5	27	6	0.94	0.67	0.93	52.05	33.32
9C	56.0143860261252, 12.8554148743133	Regular	2	5558	6.60	34	661.95	42	8	13	5	0.81	0.90	0.92	85.42	4.53

9D	55.4350570337926, 13.9785053313856	Regular	1	5095	7.08	33	458.99	124	9	47	17	0.85	0.88	0.92	59.42	5.25

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

	Mowing	**Verge Width Mean**	**Vascular Plant Richness**	**Road Verge Classification**	**Traffic Intensity (log)**
Verge Width Mean	0.160				
Vascular Plant Richness	0.126	0.000			
Road Verge Classification	-0.024	0.277	0.125		
Traffic Intensity (log)	-0.095	-0.027	0.179	0.037	
Flower Density (log)	-0.367	-0.438	0.305	-0.090	-0.153

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

	Observed	**Expected**	**SD**	**p-value**
Flower Density	-0.039	-0.028	0.048	0.816
Vascular Plant Richness	-0.083	-0.028	0.047	0.242
Butterfly Abundance	-0.100	-0.028	0.047	0.125
Butterfly Richness	-0.025	-0.028	0.048	0.961
Butterfly Evenness	-0.127	-0.028	0.047	**0.035**
Wild Bee Abundance	-0.066	-0.028	0.046	0.398
Wild Bee Richness	0.067	-0.028	0.048	**0.049**
Wild Bee Evenness	-0.002	-0.028	0.048	0.596

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). Abbreviations: FlowDens = Flower Density (log), RVC = Road Verge Classification (valuable or regular), TI = Traffic Intensity (log), PR = (Vascular) Plant Richness, VWM = Verge Width Mean. PCNM1 is the first axis of a principal coordinates of neighbour matrix, included for models in which the response variable is spatially autocorrelated.*

	Statistical Model	**Candidate Model**	**AICc**	**Δ AICc**
Flower Density	Linear model (lm)	Mowing + RVC + TI	59.259	0.000
		Mowing + RVC + TI + Mowing:RVC	61.564	2.305
		Mowing + RVC + TI + VWM	263.975	0.000

Vascular Plant Richness	Negative binomial model (glm.nb)	Mowing + RVC + TI + VWM + Mowing:RVC	266.732	2.757
Butterfly Abundance	Negative binomial model (glm.nb)	FlowDens + Mowing + RVC + TI + VWM + Mowing:RVC + TI:VWM	367.216	0.000
		Mowing + RVC + TI + Vasc_Rich + VWM + Mowing:RVC + TI:VWM	367.263	0.047
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + Mowing:RVC	368.592	1.376
		Mowing + RVC + TI + Vasc_Rich + VWM + Mowing:RVC + TI:Vasc_Rich + TI:VWM	368.986	1.770
		FlowDens + Mowing + RVC + TI + VWM + TI:VWM	369.177	1.961
		Mowing + RVC + TI + Vasc_Rich + VWM + TI:VWM	369.200	1.984
		FlowDens + Mowing + RVC + TI + VWM + Mowing:RVC	369.605	2.389
		Mowing + RVC + TI + Vasc_Rich + VWM + Mowing:RVC	369.745	2.529
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + Mowing:RVC + TI:VWM	370.452	3.236
		Mowing + RVC + TI + Vasc_Rich + VWM + TI:Vasc_Rich + TI:VWM	370.533	3.317
		Mowing + RVC + TI + Vasc_Rich + VWM	371.076	3.860
		FlowDens + Mowing + RVC + TI + VWM	371.110	3.894
		Mowing + RVC + TI + Vasc_Rich + VWM + Mowing:RVC + TI:Vasc_Rich	371.572	4.356
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI	371.968	4.752
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + TI:VWM	372.649	5.433
		Mowing + RVC + TI + Vasc_Rich + VWM + TI:Vasc_Rich	372.932	5.716
Butterfly Richness	Linear model (lm)	Mowing + RVC + TI + PR + VWM + Mowing:RVC + TI:PR	185.243	0.000
		Mowing + RVC + TI + PR + VWM + Mowing:RVC + TI:PR + TI:VWM	186.344	1.101
		Mowing + RVC + TI + PR + VWM + TI:PR	188.440	3.197
		Mowing + RVC + TI + PR + VWM + TI:PR + TI:VWM	189.080	3.837
		Mowing + RVC + TI + PR + VWM + Mowing:RVC	190.802	5.558
		Mowing + RVC + TI + PR + VWM + Mowing:RVC + TI:VWM	190.964	5.720
		Mowing + RVC + TI + PR + VWM + TI:VWM	193.295	8.051
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + Mowing:RVC	193.304	8.060
		Mowing + RVC + TI + PR + VWM	193.612	8.368
		FlowDens + Mowing + RVC + TI + VWM + Mowing:RVC	193.760	8.517
		FlowDens + Mowing + RVC + TI + VWM + Mowing:RVC + TI:VWM	194.089	8.846
		FlowDens + Mowing + RVC + TI + VWM + TI:VWM	196.669	11.426
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + Mowing:RVC + TI:VWM	196.748	11.504
		FlowDens + Mowing + RVC + TI + VWM	197.061	11.817
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI	197.583	12.339
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + TI:VWM	199.928	14.684
Butterfly Evenness	Beta-regression model (betareg)	Mowing + PCNM1 + RVC + TI + PR + VWM	-53.016	0.000
		Mowing + PCNM1 + RVC + TI + PR + VWM + TI:PR	-50.872	2.144
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM	-50.823	2.193
		Mowing + PCNM1 + RVC + TI + PR + VWM + Mowing:RVC	-50.612	2.404
		Mowing + PCNM1 + RVC + TI + PR + VWM + TI:VWM	-50.149	2.867
		Mowing + PCNM1 + RVC + TI + PR + VWM + Mowing:RVC + TI:PR	-48.177	4.839
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + Mowing:RVC	-48.042	4.974
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + TI:VWM	-47.831	5.184
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + FlowDens:TI	-47.784	5.231
		Mowing + PCNM1 + RVC + TI + PR + VWM + TI:PR + TI:VWM	-47.364	5.651

		Mowing + PCNM1 + RVC + TI + PR + VWM + Mowing:RVC + TI:VWM	-47.233	5.783
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + FlowDens:TI + Mowing:RVC	-44.768	8.248
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + Mowing:RVC + TI:VWM	-44.559	8.457
		Mowing + PCNM1 + RVC + TI + PR + VWM + Mowing:RVC + TI:PR + TI:VWM	-44.223	8.793
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + FlowDens:TI + TI:VWM	-44.044	8.971
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + FlowDens:TI + Mowing:RVC + TI:VWM	-40.586	12.430
Wild Bee Abundance	Negative binomial model (glm.nb)	FlowDens + Mowing + RVC + TI + VWM + TI:VWM	334.927	0.000
		FlowDens + Mowing + RVC + TI + VWM + Mowing:RVC + TI:VWM	334.928	0.001
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + TI:VWM	338.048	3.121
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + Mowing:RVC + TI:VWM	338.682	3.755
		Mowing + RVC + TI + PR + VWM + TI:VWM	339.861	4.934
		Mowing + RVC + TI + PR + VWM + Mowing:RVC + TI:VWM	342.226	7.299
		Mowing + RVC + TI + PR + VWM + TI:PR + TI:VWM	343.378	8.451
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + Mowing:RVC	345.727	10.800
		Mowing + RVC + TI + PR + VWM + Mowing:RVC + TI:PR + TI:VWM	346.010	11.083
		FlowDens + Mowing + RVC + TI + VWM + Mowing:RVC	347.091	12.164
		FlowDens + Mowing + RVC + TI + VWM	348.104	13.177
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI	348.455	13.528
		Mowing + RVC + TI + PR + VWM	354.272	19.345
		Mowing + RVC + TI + PR + VWM + Mowing:RVC	355.889	20.962
		Mowing + RVC + TI + PR + VWM + TI:PR	357.420	22.492
		Mowing + RVC + TI + PR + VWM + Mowing:RVC + TI:PR	359.377	24.450
Wild Bee Richness	Negative binomial model (glm.nb)	FlowDens + Mowing + PCNM1 + RVC + TI + VWM + TI:VWM	218.249	0.000
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM	218.458	0.210
		Mowing + PCNM1 + RVC + TI + PR + VWM + TI:VWM	220.162	1.914
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + FlowDens:TI	220.446	2.197
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + Mowing:RVC	221.178	2.930
		Mowing + PCNM1 + RVC + TI + PR + VWM	221.259	3.011
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + Mowing:RVC + TI:VWM	221.521	3.272
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + FlowDens:TI + TI:VWM	222.041	3.793
		Mowing + PCNM1 + RVC + TI + PR + VWM + TI:PR + TI:VWM	222.983	4.734
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + FlowDens:TI + Mowing:RVC	223.173	4.924
		Mowing + PCNM1 + RVC + TI + PR + VWM + TI:PR	223.405	5.156
		Mowing + PCNM1 + RVC + TI + PR + VWM + Mowing:RVC + TI:VWM	223.896	5.647
		Mowing + PCNM1 + RVC + TI + PR + VWM + Mowing:RVC	224.637	6.388
		FlowDens + Mowing + PCNM1 + RVC + TI + VWM + FlowDens:TI + Mowing:RVC + TI:VWM	225.603	7.354
		Mowing + PCNM1 + RVC + TI + PR + VWM + Mowing:RVC + TI:PR + TI:VWM	227.005	8.757
		Mowing + PCNM1 + RVC + TI + PR + VWM + Mowing:RVC + TI:PR	227.055	8.806
Wild Bee Evenness	Beta-regression model (betareg)	Mowing + RVC + TI + PR + VWM + TI:PR + TI:VWM	-62.372	0.000
		FlowDens + Mowing + RVC + TI + VWM	-61.185	1.187
		Mowing + RVC + TI + PR + VWM + TI:PR	-61.017	1.355
		FlowDens + Mowing + RVC + TI + VWM + TI:VWM	-60.017	2.355
		Mowing + RVC + TI + PR + VWM + Mowing:RVC + TI:PR + TI:VWM	-59.595	2.777
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + TI:VWM	-58.879	3.493

		Mowing + RVC + TI + PR + VWM	-58.852	3.520
		Mowing + RVC + TI + PR + VWM + TI:VWM	-58.208	4.164
		FlowDens + Mowing + RVC + TI + VWM + Mowing:RVC	-58.182	4.190
		Mowing + RVC + TI + PR + VWM + Mowing:RVC + TI:PR	-58.005	4.367
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI	-57.906	4.466
		FlowDens + Mowing + RVC + TI + VWM + Mowing:RVC + TI:VWM	-56.886	5.486
		Mowing + RVC + TI + PR + VWM + Mowing:RVC	-56.368	6.004
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + Mowing:RVC + TI:VWM	-56.299	6.073
		Mowing + RVC + TI + PR + VWM + Mowing:RVC + TI:VWM	-55.594	6.778
		FlowDens + Mowing + RVC + TI + VWM + FlowDens:TI + Mowing:RVC	-54.664	7.708

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

Genus	Epithet	Genus	Epithet	Genus	Epithet
Acer	platanoides	Fallopia	convovulus	Prunus	padus
Achillea	millefolium	Festuca	rubra	Prunus	spinosa
Aegopodium	podagraria	Fraxinus	excelsior	Quercus	robur
Agrostis	agg	Fumaria	officinalis	Ranunculus	acris
Agrostis	capillaris	Galeopsis	bifida	Ranunculus	repens
Agrostis	vinealis	Galium	aparine	Ribes	alpinum
Alliaria	petiolata	Galium	mollugo	Ribes	uva-crispa
Allium	oleraceum	Galium	verum	Rosa	villosa
Allium	scorodoprasum	Geranium	dissectum	Rosa	virginiana
Allium	vineale	Geranium	molle	Rubus	caesius
Alopecurus	pratensis	Geranium	robertianum	Rubus	idaeus
Anchusa	officinalis	Geum	urbanum	Rubus	plicatus
Anisantha	tectorum	Glechoma	hederacea	Rubus	saxatilis
Anthemis	arvensis	Gnaphalium	uligonosum	Rumex	acetosa
Anthoxanthum	odoratum	Heracleum	sphondilium	Rumex	acetosella
Anthriscus	sylvestris	Hieracium	sect. vulgata	Rumex	longifolius
Anthyllis	vulneraria	Hieracium	umbellatum	Salix	caprea
Apera	spica-venti	Holcus	lanatus	Salix	cinerea
Arabidopsis	thaliana	Holcus	mollis	Saponaria	officinalis
Arenaria	serpyllifolia	Hylotelephium	telephium	Schedonorus	pratensis
Argentina	anserina	Hypericum	maculatum	Scorzoneroides	autumnalis
Armeria	maritima	Hypericum	perforatum	Scrophularia	nodosa
Arrhenaterum	elatius	Hypochaeris	radicata	Securigea	varia
Artemisia	campestris	Jacobea	vulgaris	Sedum	acre
Artemisia	vulgaris	Jasione	montana	Sedum	sexangulare
Astragalus	glycyphyllos	Juncus	conglomeratus	Senecio	vulgaris
Avena	fatua	Juncus	effusus	Silene	latifolia
Avenella	flexuosa	Knautia	arvensis	Silene	vulgaris

Ballota	nigra	Lamium	album	Solidago	gigantea
Barbarea	vulgaris	Lapsana	communis	Solidago	virgaurea
Betula	pendula	Lathyrus	pratensis	Sonchus	arvensis
Betula	pubescens	Lathyrus	sylvestris	Sonchus	asper
Bromopsis	inermis	Lens	culinaris	Sonchus	oleraceus
Bromus	hordeaceus	Leucanthemum	vulgare	Sorbaria	sorbifolia
Calamagrostis	epigejos	Linaria	vulgaris	Spergula	arvensis
Calluna	vulgaris	Lolium	perenne	Spergularia	rubra
Campanula	rotundifolia	Lotus	corniculatus	Stellaria	graminea
Capsella	bursa-pastoris	Lupinus	polyphyllus	Stellaria	holostea
Carduus	crispus	Luzula	campestris	Stellaria	media
Carex	divulsa	Matricaria	discoidea	Tanacetum	vulgare
Carex	hirta	Medicago	lupulina	Thlaspi	arvense
Carex	muricata agg	Medicago	sativa	Tilia	xvulgaris
Carex	spicata	Melampyrum	arvense	Tragopogon	pratensis
Carpinus	betulus	Melilotus	albus	Trifolium	arvense
Centaurea	cyanus	Myosotis	arvensis	Trifolium	campestre
Centaurea	jacea	Myosotis	ramosissima	Trifolium	dubium
Centaurea	scabiosa	Neslia	paniculata	Trifolium	hybridum
Cerastium	fontanum	Ononis	spinosa	Trifolium	medium
Chamaenerion	angustifolium	Origanum	vulgare	Trifolium	pratense
Chenopodium	album	Papaver	dubium	Trifolium	repens
Cichorium	intybus	Papaver	rhoeas	Tripleurospermum	inodorum
Cirsium	arvense	Pastinaca	sativa	Triticum	aestivum
Cirsium	vulgare	Persicaria	lapathifolia	Tussilago	farfara
Convallaria	majalis	Phacelia	tanacetifolia	Ulmus	glabra
Convolvulus	arvensis	Phleum	pratense	Urtica	dioica
Conyza	canadensis	Phragmites	australis	Valeriana	sambucifolia
Crataegus	monogyna	Pilosella	aurantiaca	Verbascum	nigrum
Crepis	tectorum	Pilosella	officinarum	Veronica	arvensis
Dactylis	glomerata	Pimpinella	saxifraga	Veronica	chamaedrys
Daucus	carota	Plantago	coronopus	Veronica	officinalis
Deschampsia	cespitosa	Plantago	lanceolata	Veronica	verna
Draba	verna	Plantago	maritima	Vicia	cracca
Echium	vulgare	Poa	annua	Vicia	hirsuta
Elymus	caninus	Poa	palustris	Vicia	sativa
Elytrigia	repens	Poa	pratensis	Vicia	sepium
Epilobium	hirsutum	Poa	trivialis	Vicia	tetrasperma
Epilobium	montanum	Polygonum	aviculare	Vicia	villosa
Epilobium	tetragonum	Populus	tremula	Viola	arvensis
Equisetum	arvense	Potentilla	argentea	Viola	canina
Equisetum	palustre	Potentilla	reptans	Viola	tricolor
Equisetum	pratense	Potentilla	subarenaria	Viscaria	vulgaris
Erigeron	acer	Primula	veris		
Erodium	cicutarium	Prunella	vulgaris		

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 ($p < 0.05$) and respective predictor variables are indicated in bold. Abbreviations: RVC = Road Verge Classification (valuable or regular), VWM = Verge Width Mean. PCNM1 is the first axis of a principal coordinates of neighbour matrix, included for models in which the response variable is spatially autocorrelated. For Mowing, "1" refers to road verges that are cut once in late summer, and "2" to road verges cut twice, in early summer and autumn.*

	Predictor	**Estimate**	**SE**	**t value**	**z value**	**P value**	**R2 value**
Flower Density	(Intercept)	7.045	0.490	14.380		<0.001	0.179
	Mowing (1 to 2)	-0.395	0.162	-2.442		**0.020**	
	RVC (Regular to Valuable)	-0.093	0.160	-0.583		0.564	
	log(Traffic Intensity)	-0.077	0.066	-1.174		0.249	
Vascular Plant Richness	(Intercept)	3.290	0.215		15.272	<0.001	0.074
	Mowing (1 to 2)	0.068	0.068		0.989	0.323	
	RVC (Regular to Valuable)	0.057	0.069		0.833	0.405	
	log(Traffic Intensity)	0.033	0.028		1.201	0.230	
	VWM	-0.004	0.012		-0.357	0.721	
Butterfly Abundance	(Intercept)	6.587	2.281		2.888	0.004	0.412
	log(Flower Density)	-0.083	0.226		-0.368	0.713	
	Mowing (1 to 2)	0.266	0.289		0.920	0.357	
	RVC (Regular to Valuable)	0.914	0.292		3.129	0.002	
	log(Traffic Intensity)	-0.497	0.203		-2.445	0.015	
	VWM	-0.340	0.159		-2.137	0.033	
	Mowing (1 to 2):RVC (Regular to Valuable)	-0.905	0.377		-2.399	0.016	
	log(Traffic Intensity):VWM	0.071	0.025		2.800	0.005	
Butterfly Richness	(Intercept)	-38.203	13.603	-2.809		0.009	0.533
	Plant Richness	1.250	0.408	3.067		0.005	
	Mowing (1 to 2)	2.016	1.152	1.750		0.091	
	RVC (Regular to Valuable)	4.214	1.247	3.378		0.002	
	log(Traffic Intensity)	5.355	1.914	2.798		0.009	
	VWM	0.464	0.140	3.323		**0.002**	
	Mowing (1 to 2):RVC (Regular to Valuable)	-3.847	1.601	-2.403		**0.023**	
	Plant Richness: log(Traffic Intensity)	-0.163	0.057	-2.840		**0.008**	
Butterfly Evenness	(Intercept)	0.468	0.715		0.656	0.512	0.093
	Plant Richness	0.023	0.014		1.714	0.086	
	Mowing (1 to 2)	0.170	0.203		0.838	0.402	
	PCNM1	0.105	0.615		0.170	0.865	
	RVC (Regular to Valuable)	-0.045	0.203		-0.220	0.826	
	log(Traffic Intensity)	0.010	0.080		0.126	0.900	
	VWM	0.003	0.034		0.074	0.941	
Wild Bee Abundance	(Intercept)	4.095	1.879		2.180	0.029	0.611
	log**(Flower Density)**	0.649	0.191		3.398	**0.001**	
	Mowing (1 to 2)	-0.154	0.171		-0.900	0.368	
	RVC (Regular to Valuable)	0.731	0.169		4.322	**<0.001**	

	log(Traffic Intensity)	-0.806	0.167		-4.833	<0.001	
	VWM	-0.532	0.131		-4.055	<0.001	
	log(Traffic Intensity):VWM	0.097	0.021		4.641	**<0.001**	
Wild Bee Richness	(Intercept)	2.230	1.431		1.558	0.119	0.382
	log(Flower Density)	0.294	0.145		2.023	**0.043**	
	Mowing (1 to 2)	-0.126	0.131		-0.960	0.337	
	PCNM1	-0.402	0.371		-1.083	0.279	
	RVC (Regular to Valuable)	0.330	0.129		2.559	**0.010**	
	log(Traffic Intensity)	-0.314	0.125		-2.506	0.012	
	VWM	-0.158	0.096		-1.643	0.100	
	log(Traffic Intensity):VWM	0.030	0.015		1.972	**0.049**	
Wild Bee Evenness	(Intercept)	-8.712	3.067		-2.841	0.005	0.258
	Mowing (1 to 2)	0.040	0.186		0.218	0.828	
	RVC (Regular to Valuable)	-0.245	0.203		-1.209	0.227	
	log(Traffic Intensity)	1.590	0.437		3.637	0.000	
	Plant Richness	0.243	0.084		2.901	0.004	
	VWM	0.321	0.145		2.210	0.027	
	log(Traffic Intensity):Plant Richness	-0.036	0.012		-3.100	**0.002**	
	log(Traffic Intensity):VWM	-0.054	0.024		-2.312	**0.021**	
Relative Occurrence of Grasses	(Intercept)	-0.390	0.139		-2.793	0.005	0.095
	Mowing (1 to 2)	-0.124	0.184		-0.674	0.500	
	RVC (Regular to Valuable)	-0.143	0.199		-0.717	0.473	
	Mowing (1 to 2):RVC (Regular to Valuable)	-0.094	0.267		-0.353	0.724	

Table S8. *Results of permutational MANOVA for the pairwise comparisons of plant community composition between the four road verge categories. For Mowing, "1" refers to road verges that are cut once in late summer, and "2" to road verges cut twice, in early summer and autumn. Statistically significant p values (p < 0.05) are indicated in bold. P-value adjusted with Bonferroni method.*

	Regular, Mowed 1	**Valuable, Mowed 1**	**Regular, Mowed 2**
Valuable, Mowed 1	1.000		
Regular, Mowed 2	0.732	0.306	
Valuable, Mowed 2	**0.012**	0.402	0.102

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

Genus	**Epithet**
Adscita	statices
Aglais	io
Aglais	urticae
Anthocharis	cardamines
Aphantopus	hyperantus

Araschnia	levana
Aricia	agestis
Coenonympha	pamphilus
Cupido	minimus
Erynnis	tages
Favonius	quercus
Gonepteryx	rhamni
Lasiommata	maera
Lasiommata	megera
Limentitis	populi
Lycaena	phlaeas
Maniola	jurtina
Ochlodes	sylvanus
Pieris	brassicae
Pieris	napi
Pieris	rapae
Plebejus	argus
Plebejus	idas
Polyommatus	icarus
Satyrium	w-album
Thecla	betulae
Thymelicus	lineola
Vanessa	atalanta
Vanessa	cardui
Zygaena	filipendulae
Zygaena	lonicerae
Zygaena	viciae

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

Genus	Epithet	Genus	Epithet
Andrena	albofasciata	Colletes	fodiens
Andrena	carantonica	Colletes	marginatus
Andrena	cineraria	Dasypoda	hirtipes
Andrena	fulva	Epeolus	variegatus
Andrena	fulvago	Eucera	longicornis
Andrena	haemorrhoa	Halictus	confusus/tumulorum
Andrena	hattorfiana	Hylaeus	angustatus
Andrena	helvola	Hylaeus	brevicornis
Andrena	labiata	Hylaeus	confusus
Andrena	lathyri	Hylaeus	dilatatus
Andrena	minutula	Hylaeus	hyalinatus
Andrena	minutuloides	Hylaeus	incongruus

Andrena	nigriceps	Lasioglossum	aeratum
Andrena	nigroaenea	Lasioglossum	calceatum
Andrena	praecox	Lasioglossum	lativentre
Andrena	semilaevis	Lasioglossum	leucopus
Andrena	similis	Lasioglossum	leucozonium
Andrena	subopaca	Lasioglossum	morio
Andrena	wilkella	Lasioglossum	nitidiusculum
Anthidium	punctatum	Lasioglossum	punctatissimum
Bombus	campestris	Lasioglossum	quadrinotatum
Bombus	hortorum	Lasioglossum	villosulum
Bombus	humilis	Lasioglossum	xanthopus
Bombus	hypnorum	Macropis	europaea
Bombus	jonellus	Megachile	versicolor
Bombus	lapidarius	Megachile	willughbiella
Bombus	lucorum(coll)	Melitta	leporina
Bombus	pascuorum	Nomada	goodeniana
Bombus	pratorum	Nomada	guttulata
Bombus	ruderarius	Nomada	marshamella
Bombus	rupestris	Nomada	panzeri
Bombus	soroeensis	Nomada	ruficornis
Bombus	subterraneus	Panurgus	calcaratus
Bombus	sylvarum	Sphecodes	crassus
Bombus	sylvestris	Sphecodes	ephippius
Bombus	terrestris	Sphecodes	geoffrellus
Bombus	vestalis	Sphecodes	hyalinatus
Ceratina	cyanea	Sphecodes	puncticeps
Chelostoma	florisomme	Sphecodes	reticulatus
Colletes	daviesanus		

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Road verges may be an important resource for the conservation of flower-visiting insects. However, my research shows that traffic on the adjacent road can limit the species richness and abundance of wild bees and butterflies, the reproductive success of cavity-nesting insects and the number of flower visitors in the surrounding landscape. Road verge management can play a significant role in determining habitat quality for flower-visiting insects, and wide road verges offer the best opportunities for targeted conservation actions.

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