ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

SLU

DOCTORAL THESIS NO. 2021:63
FACULTY OF NATURAL RESOURCES AND AGRICULTURAL SCIENCES

Linear infrastructure habitats for the conservation of plants and pollinators

The value of road verges and power-line corridors for landscape-scale diversity and connectivity

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SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS

Uppsala 2021

Acta Universitatis Agriculturae Sueciae
2021:63

Cover: Plants, butterflies, and bumblebees in linear infrastructure habitats
(photos: Juliana Dániel-Ferreira)

ISSN 1652-6880
ISBN (print version) 978-91-7760-803-5
ISBN (electronic version) 978-91-7760-804-2

Print: SLU Service/Repro, Uppsala 2021

Linear infrastructure habitats for the conservation of plants and pollinators

Abstract

The substantial reduction in the area of semi-natural grasslands due to the intensification of agriculture and silviculture has resulted in a dramatic decline of species that depend on these habitats. Simultaneously, the area of grassland habitats along infrastructure such as power lines and roads continues to increase and can even surpass the area of semi-natural grasslands of high nature value. In this thesis, I aimed to explore to what extent linear infrastructure habitats contribute to the biodiversity of plants and flower-visiting insects and landscape connectivity. I showed that the presence of power-line corridors in the landscape positively influenced the alpha and gamma diversity of plants, but that this habitat had no effect on beta diversity. Road verges and power-line corridors had as high alpha diversity of plant and insect species as semi-natural pastures of high nature value. Despite the fact that road verges increase the structural connectivity in the landscape, they did not strongly influence the alpha, beta or gamma diversity of plants, butterflies or bumblebees in other grassland types. Further, I found that road verges are corridors for flower-visiting insects irrespective of their diversity of flowering plants. My results also showed that roads are barriers to the movements of flower-visiting insects regardless of the traffic intensity of the road, and that traffic mortality rates of bumblebee queens increase with increasing traffic intensity. Finally, my thesis highlights that the contribution of linear infrastructure habitats to landscape connectivity for flower-visiting insects can be constrained by the behavioural responses of individuals to these habitats and by an increased mortality risk.

Keywords: alpha-, beta-, gamma-diversity, functional connectivity, structural connectivity, road mortality, corridors, barriers, behaviour, semi-natural grasslands

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Linjära infrastrukturmiljöers betydelse för växter och pollinatörer

Abstract

Förlusten av slåtter- och betesmarker under de senaste decennier har resulterat i en kraftig minskning av arter som är beroende av dessa habitat. Samtidigt har arealen av linjära infrastrukturmiljöer såsom kraftledningsgator och vägkanter ökat kraftigt, och i Sverige är arealen av dessa miljöer större än den totala arealen av slåtter- och betesmarker med högt naturvärde. Syftet med denna avhandling var att undersöka i vilken utsträckning linjära infrastrukturmiljöer bidrar till mångfalden av växter och pollinerande insekter och till landskapets konnektivitet. Jag visade att landskap som korsades av kraftledningsgator hade högre alfa- och gamma-diversitet av växter, men att kraftledningsgator inte hade någon effekt på växternas beta-diversitet. Vägkanter och kraftledningsgator hade lika hög alfa-diversitet som betesmarker. Trots att vägkanter ökar landskapets strukturella konnektivitet hade de ingen stark påverkan på varken alfa-, beta- eller gamma-diversitet av växter, humlor eller fjärilar. Jag visade också att vägkanter fungerar som korridorer för blombesökande insekters rörelser oberoende av hur många blommande arter de innehåller. Dessutom visade jag att vägar fungerar som barriärer för blombesökande insekter oberoende av trafikintensiteten, och att mortaliteten av humledrottningar ökar med ökande trafikintensitet. Min avhandling understryker att linjära infrastrukturmiljöers bidrag till landskapets konnektivitet för blombesökande insekter kan begränsas av individens beteendemässiga reaktioner på dessa livsmiljöer och på en ökad mortalitetsrisk.

Nyckelord: alfa-diversitet, beta-diversitet, gamma-diversitet, funktionell konnektivitet, strukturell konnektivitet, mortalitet vid vägar, korridorer, barriärer, beteende, ängs- och betesmarker

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Dedication

"If two hundred years of history of environmentalism has taught us anything, it is that a change of heart occurs when people look beyond themselves to others, and then to the rest of life."
E. O. Wilson, 2002

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. Juliana Dániel-Ferreira, Riccardo Bommarco, Jörgen Wissman, Erik Öckinger (2020). Linear infrastructure habitats increase landscape-scale diversity of plants but not of flower-visiting insects. Scientific reports, 10:21374, 1-11.

II. Juliana Dániel-Ferreira, Yoan Fourcade, Riccardo Bommarco, Jörgen Wissman, Erik Öckinger. Communities in infrastructure habitats are species-rich but only partly support species associated with semi-natural grasslands. (manuscript)

III. Juliana Dániel-Ferreira, Åsa Berggren, Jörgen Wissman, Erik Öckinger. Road verges are corridors and roads barriers for flower-visiting insects. (submitted)

IV. Juliana Dániel-Ferreira, Åsa Berggren, Riccardo Bommarco, Jörgen Wissman, Erik Öckinger. Bumblebee queen mortality and behavior along roads with varying traffic and road verges with contrasting flowering plant diversity. (submitted)

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The contribution of Juliana Dániel-Ferreira to the papers included in this thesis was as follows:

- I. Main author. Participated in the development of ideas, analysed the data and led the writing of the manuscript.
- II. Main author. Participated in the development of ideas, analysed the data with YF and led the writing of the manuscript.
- III. Main author. Conceived the project together with EÖ, ÅB, and JW. Conducted the field experiment, analysed the data, and led the writing of the manuscript.
- IV. Main author. Conceived the project together with EÖ, ÅB, RB, and JW. Conducted the field experiment, analysed the data, and led the writing of the manuscript.

1. Background

1.1 Biological diversity

1.1.1 What is biodiversity and how do we measure it?

The number of species present in a system is a natural index of the structure of a community and is therefore often used in conservation research and management (Gotelli & Colwell 2011). Species richness seems like an intuitive measure that allows for comparisons among sites and conveys information about the saturation of local communities colonised from regional species pools (Gotelli & Colwell 2001). However, biological diversity has additional aspects that a simple measure, such as the number of species, fails to measure (Leinster & Cobbold 2012). For instance, a community in which only one species is highly abundant can be considered less diverse than a community with the same number of species but in which all species have more or less the same abundance. Similarly, a community composed of only bird species can be considered less diverse than a community composed of birds, mammals and insects. These aspects of diversity are encompassed not by the number of species but by the evenness of the community and by the evolutionary distinctiveness of the species in the community (Box 1). It is evident that species richness is an incomplete measure of biological diversity, and because of this, a myriad of indices to measure biodiversity have been developed (Wilsey et al. 2005). For example, species richness metrics can be as simple as the number of species in a sample (S), or can be the number of species but taking into account that species richness increases with the total number of individuals (Margalef diversity, S_{Margalef}).

Box 1: Aspects of diversity

Number of species (species richness): The number of species present in e.g. a site, habitat type, landscape, region or country.

Evenness: Equitability of the proportional abundances of the species in a community.

Evolutionary distinctiveness: Dissimilarity between species in a community based on their evolutionary relationships or functional traits.

Commonly used diversity metrics include Shannon diversity (H') which accounts for the abundance and evenness of the species, or Simpson diversity (1/D) which is used to calculate the probability that two individuals drawn at random from an infinite community would belong to the same species (Maurer & McGill 2011). Some measurements of species diversity are based on the observation that inevitably, some of the species in a community will be more abundant than others, and some of the species will be so rare that observing them requires a lot of effort. Different diversity indices take this into account by giving different weights to rare and common species. For instance, species richness (S) gives equal weight to rare and common species. In contrast, the Berger-Parker relative dominance index (C_{Rel}) does the opposite by completely ignoring rare species (Maurer & McGill 2011).

An evenness index provides information about the degree to which communities differ in terms of the proportions of species and can be a valuable tool when investigating which factors can influence the structure of communities (Magurran & McGill 2011). Typically, a high evenness index value represents a more or less even community in which most species have similar abundances. Conversely, a low evenness index value represents the opposite; a community in which a few species are considerably more abundant than others. Examples of evenness indices are Shannon evenness ($E_{Shannon}$) or Simpson evenness ($E_{Simpson}$).

An additional component of diversity is given by the degree of relatedness between species and how this affects the phenotypic characteristics that influence species performance (i.e. functional traits; Jonason et al. 2017).

Closely related species can be more similar in terms of dispersal ability, niche breadth or reproductive potential, which can make them phylogenetically and ecologically redundant (Ricotta et al. 2018). Species close to each other in the phylogenetic tree can respond similarly to habitat loss, a phenomenon observed for bees (Arbetman et al. 2017; Grab et al. 2019). This can be measured by estimating trait or functional diversity (i.e. the degree to which coexisting species vary in terms of their functional traits) or phylogenetic diversity (i.e. the quantification of diversity among species based on their evolutionary relationships).

1.1.2 The issue of spatial scale

At what spatial scale should we measure biodiversity? This is a difficult question, given that species distributions and abundance patterns vary with the spatial scale of observation (Levin 1992; Whittaker et al. 2001). This is partly because there is also an increase in the number of observed species with an increase in area. A larger habitat area enables larger population sizes and reduces extinction rates, allowing species to accumulate at the patch and landscape scales (MacArthur & Wilson 1967). This relationship between species richness and area, i.e. the species-area relationship, SAR (Arrhenius 1921), is so ubiquitous that it has been deemed one of the few general rules of ecology (Lawton 1999; Lomolino 2000). The spatial scale of observation can determine the conclusions drawn about a study system and can often lead to the detection of contrasting patterns or trends (Wiens 1989; Dornelas et al. 2014; McGill et al. 2015; Chase et al. 2019). Thus, there is no single natural scale at which ecological phenomena should be studied (Levin 1992; Rosenzweig 1995). Because of this, Whittaker (1960, 1972) proposed three types of diversity measures that are based on the spatial scale: alpha, beta and gamma diversity (Box 2).

While alpha and gamma diversity are relatively straightforward concepts once a spatial scale has been selected, the concept of beta diversity has been used for a wide variety of phenomena (Tuomisto 2010). For instance, beta diversity can be used to measure among-plot variability in species composition independently of the position of the plots or as the extent of change in species composition along a predefined environmental gradient (Vellend 2001). Beta diversity, defined here as a measure of the (dis)similarity in species composition between sites, can be measured as the

Box 2: Types of diversity based on spatial scale

Alpha (α) diversity: The number of species present in one community or location.

Beta (β) diversity: Change in community composition across space. It can be partitioned into:

- **Nestedness**: Reflects when the species composition at different sites are nested subsets of one another.
- **Turnover**: Reflects the replacement of species at some sites by a different set of species at other sites.

Gamma (ϒ) diversity: The number of species present in a landscape or region, based on the α and β diversity of the communities.

pairwise differences between sites or among multiple sites and can reflect two different phenomena: turnover or nestedness (Baselga 2010). Turnover occurs when some species are replaced by others and can reflect environmental filtering or spatial and historical constraints. Nestedness occurs when the species in sites with a lower number of species are a subset of the communities in sites with a higher number of species and reflect a non-random loss of species (Baselga 2010). Pairwise and multi-site dissimilarity in species composition can also be estimated using different measures, such as Sørensen pairwise dissimilarity (β_{sor}), Simpson pairwise dissimilarity (β_{sim}), Whittaker's beta (β_{w}), or Sørensen-based multiple site dissimilarity (β_{SOR}).

1.1.3 What determines community composition?

Ecologists are often asked about the large-scale impacts of anthropogenically driven environmental change on biodiversity. Answering such questions often requires scaling up the information collected at small spatial scales, which can be problematic because the factors that determine diversity may not scale up or down across spatial scales (Tylianakis et al. 2006). Further, data acquired by non-manipulative observational approaches are shaped by a myriad of assembly processes at different spatial and temporal scales that cannot be directly observed and that can lead to similar or even identical patterns (Ovaskainen et al. 2019). The species richness and composition of local communities are influenced by biogeographic and evolutionary processes at multiple spatial and temporal scales (Tscharntke et al. 2012; Cornell & Harrison 2014). Several ecological frameworks have been developed to make these processes more tractable and to enable the assessment of the influence of large-scale processes into analyses of community assembly (Cornell & Harrison 2014). Among these, the metacommunity concept is very useful in that it depicts local species communities (i.e. metacommunities) as dynamically interdependent systems connected by dispersal among localities (Leibold et al. 2004; Cornell & Harrison 2014). In other words, metacommunity theory explains how diversity results from an interplay of various stochastic (associated with extinction and dispersal) and deterministic (associated with biotic interactions and niche differentiation) processes (Ovaskainen et al. 2019). Each of these processes is more or less relevant at different spatial and temporal scales. For example, local factors such as habitat quality and type are important determinants of the presence of a species in a site (Duelli 1997; Weibull et al. 2003; Nielsen et al. 2011), but at larger spatial scales, diversity will also be influenced by the structure of the surrounding landscape (Dauber et al. 2003; Janišová et al. 2014). Metacommunity theory encompasses four different, but not mutually exclusive, frameworks that make different assumptions about the operating processes for community assembly (Fig. 1; Shmida & Wilson 1985; Leibold 2018):

- *Local environmental conditions*: local environmental filtering of species due to e.g. area, habitat quality, disturbance, biotic and abiotic interactions.
- *Colonisation-extinction dynamics*: related to the area and quality of a patch and the degree of connectivity between patches
- *Stochasticity*: niche differences among species in a community are unimportant.
- *Dispersal*: the ability of an individual or species to reach and establish in a new patch, regulated by the structure of the landscape and functional traits of the species.
- *Sources*: areas in which species have positive population growth.

- *Sinks*: areas where species have negative population growth in the absence of immigration.

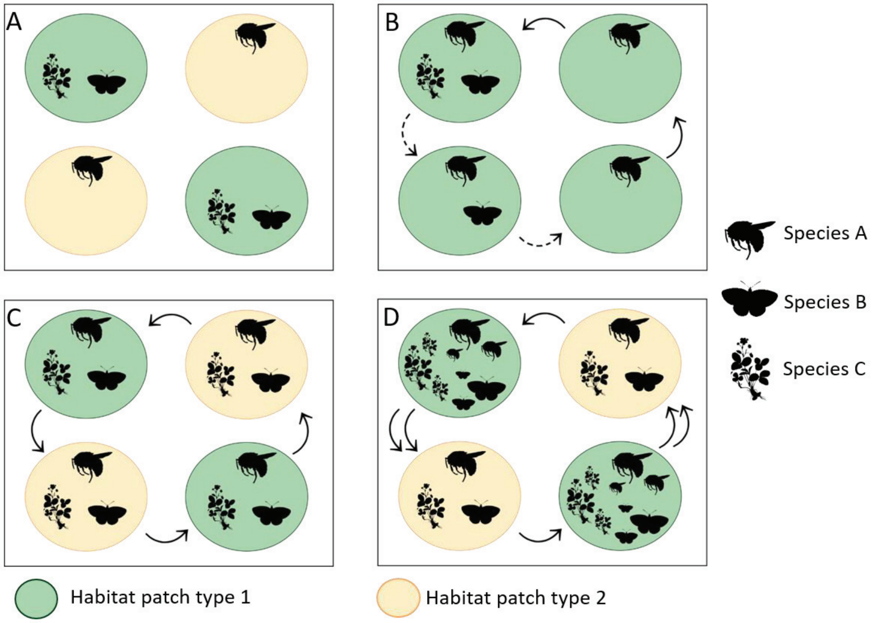

Figure 1. The theories of metacommunities. A) Species sorting: patch to patch differences in local environmental conditions allow a diverse number of species to coexist in a metacommunity, B) Patch dynamics: colonisation-extinction processes lead to a dynamic equilibrium that mediate how species coexist in a metacommunity (the dashed arrows indicate reduced dispersal) , C) Neutral theory: stochastic demography and dispersal (arrows) among patches influence local and metacommunity diversity, D) Mass-effects: species are present in both sources and sink habitats (Leibold et al. 2004; Leibold 2018). Adapted from Ovaskainen et al. (2019).

Metapopulation and metacommunity dynamics are theoretical frameworks that aim to study biodiversity patterns. They often assume a binary landscape composed of habitat and non-habitat, in which suitable habitat is seen as patches scattered across a less suitable matrix (Ricketts 2001). However, landscapes are heterogeneous and consist of dynamic mosaics of more or less suitable elements (Ouin et al. 2004). Loss of suitable habitat can affect biodiversity by driving species to extinction (locally and regionally) through species-area relationships, dispersal limitation, and by altering dominance patterns in communities so that already abundant species become even more abundant and rare species become rarer (Sang et al. 2010; Bommarco et al. 2012; Marini et al. 2014). Therefore, an essential question in ecology is how different landscape elements contribute to the overall diversity in a landscape, and which types of species (e.g. generalists vs specialists) benefit from different habitat elements. These questions can be investigated by exploring patterns of beta diversity, determining how different landscape elements contribute to the exchange of individuals between high-quality patches, or studying the demography of the species in the landscape.

1.1.4 Dispersal and landscape connectivity

Human activity has thoroughly transformed landscapes via habitat destruction, deforestation, fragmentation, urbanisation and agricultural conversion (Wagner et al. 2021). Such activities result in a disruption of landscape connectivity, defined as the degree to which a landscape facilitates or impedes movements, viewed from the landscape and the individual's perspectives (Taylor et al. 1993). Loss of landscape connectivity is a concern because it ultimately disrupts dispersal, a crucial process for the viability of populations. In metapopulation theory, the rate of dispersal among habitat patches affects the relative importance of local vs regional processes because it can determine the ability of a species to recolonise a patch, and influence patch occupancy rates, overall population size and the genetic diversity of a species (Schtickzelle & Baguette 2003; With 2019). Measuring landscape connectivity provides landscape ecologists with a way to explore how the pattern of a landscape influences ecological processes, also crucial in conservation planning (With 2019). Structural landscape connectivity refers to the physical aspects in the landscape that facilitate (e.g. habitat corridors or stepping stones) or impede movement (e.g. barriers such as rivers or roads) (Baguette & Van Dyck 2007). In contrast, functional connectivity incorporates the behavioural response of the organism to landscape structure, and it depends on how the organism perceives and responds to landscape structure within a hierarchy of spatial scales (Bélisle 2005). Measuring functional connectivity thus requires detailed knowledge of how the organism responds to e.g. habitat edges and their relative movement rates and mortality risks in different landscape elements or habitat types (Tischendorf & Fahrig 2000). Further, there are different types of movement and an individual may respond differently to habitat types depending on if they are, for example, foraging for food or searching for breeding territory. As such, detailed information about foraging behaviour will likely not explain how the same individual selects a breeding site within the same landscape (With 2019). To approach this problem, it is essential to directly study the movement and mortality risks within different landscape elements compared to others to determine whether or not they increase functional connectivity.

1.1.5 Corridors and barriers

Ecological corridors, i.e. long strips of habitat that connect otherwise isolated habitat patches, are frequently suggested to counteract the adverse effects of habitat loss and fragmentation on biodiversity (Haddad et al. 2003, 2014). Habitat corridors are thought to rescue isolated populations by enabling dispersal and enhancing gene flow (i.e. increasing landscape connectivity). For mobile animals, corridors are most likely to enhance connectivity when the vegetation structure is similar to the vegetation of their habitat (Eycott et al. 2012). Still, if a species avoids crossing habitat edges, the corridors are likely ineffective (Schtickzelle & Baguette 2003). Therefore, the presence of a corridor will increase structural connectivity, but whether it also increases functional connectivity depends on the habitat preferences, behaviour, and the life-history traits of the species (Ewers & Didham 2005; Öckinger et al. 2010). For instance, a forested corridor connecting two forest patches can enhance the movement of forest species between the patches, but may represent a barrier for grassland specialist species that prefer open habitats.

The positive effect of corridors can be confounded with habitat amount such that it is often unclear whether they enhance landscape connectivity or if they just provide additional habitat (Sutcliffe & Thomas 1996). Several attempts to determine whether conservation efforts should mainly focus on habitat area, habitat quality, or connectivity have been performed, but results are inconclusive (e.g. Doerr et al. 2011; Hodgson et al. 2011; Fahrig 2013; Haddad et al. 2017; Watling et al. 2020). Regardless, accumulating evidence has shown that corridors are, in general, effective at improving the exchange of individuals between populations (Tewksbury et al. 2002; Damschen 2006; Resasco 2019). In theory, this would imply that landscapes with higher connectivity (i.e. with habitat corridors) should differ in terms of species structure and composition when compared to landscapes with low habitat amount and low connectivity, as small and isolated populations tend to be more susceptible to genetic or environmental stochasticity and thus extinction (Baguette & Schtickzelle 2006).

Dispersal barriers have huge impacts on the organisation of life on Earth as they drive ecological processes such as speciation, gene flow, and population viability (Caplat et al. 2016). As with corridors, barriers to movement can also be structural (i.e. physical barriers such as fencing along roads or railway lines) or functional. Functional barriers affect the behaviour of an individual so that they avoid crossing specific areas due to, for example, non-preferred vegetation structure. For instance, despite being highly mobile animals with the capacity of long-distance dispersal, hoverflies have been observed to avoid crossing uncultivated field boundaries between agricultural fields (Wratten et al. 2003).

1.2 Semi-natural grasslands

1.2.1 Traditionally managed semi-natural grasslands

The agricultural landscape in Europe underwent drastic changes during the 20th century (Stoate et al. 2001). Traditionally, European landscapes comprised a system of arable fields, meadows, uncultivated land used for grazing, and pastures for collecting fodder and fuel (Eriksson et al. 2002). The maintenance of this farming system for an extended period allowed the preservation of a uniquely adapted flora and fauna that originated during the Pleistocene (Eriksson et al. 2002; Bråthen et al. 2020). Locally, managing grasslands by mowing or grazing allowed for a diverse plant community that often hosted an equally diverse community of other species groups such as insects (Cousins & Eriksson 2002; WallisDeVries et al. 2002). At the landscape scale, there was a high turnover of species among habitats with early successional stages, which resulted in an overall high number of species (WallisDeVries et al. 2002; Öckinger et al. 2006).

The increasing demand for food and fibre led to the intensification of land use by introducing fertilisers, pesticides, and large-scale monocultural farming and silviculture (Eriksson et al. 2002; Hoekstra et al. 2005; Cousins et al. 2015). In Scandinavia, traditionally managed semi-natural grasslands, i.e. grasslands modified and maintained by agricultural activity such as mowing and grazing, were largely replaced by crop fields on the most productive soils or forests on the less productive soil (Cousins & Eriksson

2002; Cousins et al. 2015). In Sweden, the area reduction of traditionally managed semi-natural grasslands between 1920 and 2000 is estimated to be around 90% (Eriksson et al. 2002). These changes in land use have resulted in less heterogeneous landscapes characterised by a decreased ability to fulfil the requirements of different species, and the consequences for flora and fauna have been profound (e.g. Chisté et al. 2018; Ekroos et al. 2010). Flower-visiting insects are especially affected by the loss of semi-natural grassland area because they largely depend on flower-rich semi-natural habitats for their survival (Milberg et al. 2016). In turn, the maintenance of the diversity of flowering plants largely depends on the pollination services provided by insects and other pollinators (Wei et al. 2021). Reductions in local species diversity, biotic homogenisation (loss of beta diversity) at larger spatial scales, and changes in community composition have been reported for plants (Nielsen et al. 2019; Tyler et al. 2020), butterflies (Van Dyck et al. 2009), and bumblebees (Bommarco et al. 2012; Goulson et al. 2015), among others. Apart from their high conservation value, traditionally managed semi-natural grasslands are the sources of a wide variety of ecosystem services such as pollination of crops and wild plants, water and climate regulation, erosion control, and biological control of pests (Öckinger & Smith 2007; Bengtsson et al. 2019). Despite conservation efforts and financial support through agri-environmental schemes, the area of traditionally managed semi-natural grasslands continues to decline (Hooftman & Bullock 2012; Cole et al. 2020), and the remaining patches are typically small, fragmented, and embedded in intensively managed landscapes (Cousins et al. 2015).

1.2.2 Linear infrastructure habitats

In intensively farmed agricultural landscapes, semi-natural grassland habitat typically remains as linear landscape elements such as grassy field borders, road verges and hedgerows (Öckinger & Smith 2007). Such linear landscape elements can have a positive effect on the diversity of plants and pollinators at several spatial scales by increasing habitat area and promoting landscape connectivity (Berggren et al. 2001; Cousins 2006; Van Geert et al. 2010; Cranmer et al. 2012; Moroń et al. 2017; Vanneste et al. 2020). In some cases, these habitats can harbour a high local diversity of plants and animals, including rare and endangered species (Gardiner et al. 2018). In addition, the

Table 1. Areas of managed grassland habitats in Sweden (Sources: (1) Jordbruksmarkens användning 2018; (2) http://www.jordbruksverket.se/tuva [access date: 06-08-2020]; (3) Stenmark 2012).

Land use	**Area (ha)**
Total area of pasture and meadows	450 900 (1)
-Of these*: semi-natural pastures of high nature value*	298 690 (2)
Grasslands in road verges	164 000 (3)
Grassland/ shrubland in power lines	223 000 (3)

area of linear infrastructure habitats, i.e. grassland habitats along linear infrastructure used for transportation, cover large areas and have a unique distribution in modern landscapes. Roads and road verges, power-line corridors and railway lines form a ubiquitous network that crosses forests, cities and agricultural land. In Sweden, the area of linear infrastructure habitats surpasses the remaining area of traditionally managed semi-natural grasslands (Table 1). One of the key strategies to increase connectivity in Europe includes using linear habitats along infrastructure (the European Union Strategy on Green Infrastructure). However, these habitats are rarely managed to promote biodiversity.

Recent reports suggest that insects are in a state of imminent population collapse (Hallmann et al. 2017; Goulson 2019; Van Klink et al. 2020). Among insects, pollinators are of particular economic concern (Wagner 2020). To ensure pollination service provision, the Swedish government allocated a part of the country's budget between 2020 and 2022 to increase knowledge on the status and importance of pollinators (Regeringskansliet, 70 miljoner för att gynna pollinerande insekter). Furthermore, the authorities in charge of managing road verges (Trafikverket) and power lines (Svenska Kraftnät) have received commissions from the Swedish government to promote and conserve biodiversity in the infrastructure habitats they are responsible for. With this goal in mind, there is a need for authorities to receive relevant knowledge regarding 1) to what extent these habitats are currently contributing to biodiversity and 2) when and where it is relevant to apply improvements to management.

Roads and road verges

Roads and road verges form a ubiquitous global network with a length extending to 64 million km, and an additional 25 million km are to be built by 2050 (van der Ree et al. 2015). The pervasive negative impacts of roads (Table 2) have given rise to a standalone branch of ecology, road ecology, that mainly focuses on studying how to mitigate the effects of roads on wildlife. Roads and traffic negatively affect animal abundance, movements and distribution, and there is a concern that roads might even cause wildlife populations to go extinct (Fahrig & Rytwinski 2009; Baxter-Gilbert et al. 2015; Muñoz et al. 2015; Keilsohn et al. 2018; Martin et al. 2018). At the landscape scale, road construction and maintenance are responsible for the fragmentation of habitat and the reduction of landscape connectivity (Fahrig & Rytwinski 2009; Wojcik & Buchmann 2012). Animal movements are mainly affected because roads act as physical and behavioural barriers, isolating populations on different sides of the road (Lesbarrères & Fahrig 2012). Thus, the persistence of animal populations is affected by roads depending on species characteristics such as road surface avoidance behaviour, population sensitivity to habitat loss, traffic mortality, population subdivision, and inaccessibility to food, mates, and breeding sites (Jaeger et al. 2005). The adverse effects of roads also depend on the specific characteristics of the road, such as the width, speed limit, and traffic intensity (Muñoz et al. 2015; Keilsohn et al. 2018). Consequently, fully understanding the effects of roads on insect populations requires disentangling the effect of the road itself from the effect of traffic intensity on the behaviour and mortality risk, respectively.

Roads have been shown to act as movement barriers for insects (Andersson et al. 2017; Fitch & Vaidya 2021), mammals (Oxley et al. 1974), reptiles and amphibians (Woltz et al. 2008). However, most studies on the impacts of roads on ecological communities have focused on vertebrates, and evidence of roads as barriers for insect movement is scarce and mainly focused on butterflies (Fitch & Vaidya 2021). Furthermore, it is still unclear whether road mortality is contributing to the decline of insect populations and whether the costs of road mortality can be outweighed by the beneficial effect of the vegetation in the road verges (Baxter-Gilbert et al. 2015).

Table 2. The ecological and genetic consequences of roads on populations. Adapted from Balkenhol & Waits (2009).

Effect of roads and/or traffic	Potential ecological consequences	Potential genetic consequences
Habitat loss	Decreased area of habitat patches Decreased size of local populations	Reduced effective population size Reduced genetic diversity
Barrier effect	Inaccessibility of resources Increased indirect mortality	Reduced gene flow Decreased genetic diversity
Road mortality	Inaccessibility of resources Increased direct mortality	Reduced effective population size Reduced gene flow Decreased genetic diversity
Fragmentation	Reduced local population sizes Reduced population connectivity Reduced overall population size	Reduced genetic connectivity Reduced genetic diversity Reduced effective population sizes

The type and quality of the habitat adjacent to the road can impact road mortality rates (Keilsohn et al. 2018). Most roads have associated bordering strips of land that are often subject to frequent disturbances and that are different from the adjacent land use (Phillips et al. 2020a). Vegetation in verges along roads is managed and kept in an early successional stage, and the species composition in road verges can highly resemble that in traditionally managed semi-natural grasslands (Auffret & Lindgren 2020; Vanneste et al. 2020). Because of this, road verges have the potential to partially mitigate the negative impacts of roads by increasing landscape connectivity for plants and insects and by increasing the available amount of grassland habitat area (Phillips et al. 2020a). However, invasive plant species are often observed along road verges, and concern that road verges along roads with a high traffic intensity are acting as ecological traps has been raised (Valtonen et al. 2006; Gardiner et al. 2018). Ecological traps arise when animals settle in habitats where their net population growth rate is negative (Gilroy & Sutherland 2007). If flower-visiting insects are attracted to road verges with high flowering plant diversity (i.e. of high habitat quality), and this increases their mortality rates such that population growth is negatively affected, road verges might act as ecological traps. Whether road verges act as ecological traps for pollinating insects or not will most likely depend on the landscape context. In landscapes where road verges support viable populations of pollinating insects, road verges will not act as ecological traps even if road mortality occurs. However, it is still unclear under what circumstances road verges are supporting insect populations and how this is affected by the quality of the road verge and traffic intensity.

Power-line corridors

Areas along power-line corridors are managed to keep the vegetation low and maintain an early successional stage to prevent the vegetation from interfering with the electrical lines (Russo et al. 2021). Consequently, the vegetation structure along this type of infrastructure can resemble vegetation in semi-natural grasslands (Berg et al. 2013; Eldegard et al. 2017). Research on the conservation potential of power-line corridors for pollinating insects has demonstrated their value as habitat for wild bees (Russell et al. 2005; Hill & Bartomeus 2016; Wagner et al. 2019; Steinert et al. 2020) and butterflies (Lensu et al. 2011; Berg et al. 2016). Power-line corridors have also been shown to improve landscape connectivity for carabid beetles (Noordijk et al. 2011), but evidence of these corridors improving connectivity for species associated with grasslands is insufficient (Suárez-Esteban et al. 2016; Villemey et al. 2018).

Power-line corridors can promote the spread of invasive species in the landscape (Lampinen et al. 2015) and act as dispersal barriers for birds and small mammals (Biasotto & Kindel 2018). Furthermore, the conservation value of power-line corridors for plants and pollinators depends on factors that are tightly linked with the type of management applied. Power-line corridors are cleared of tall vegetation in management cycles ranging from a few to twelve years (Berg et al. 2013; Eldegard et al. 2017; Wagner et al. 2019), depending on plant productivity. In the United States, power lines are often managed with a combination of extraction of tall vegetation and herbicides (Russell et al. 2005; Russo et al. 2021), which can either promote or impede the establishment of grassland plant species. Local abiotic conditions in power-line corridors such as light availability, soil moisture and soil productivity have also been shown to be strong determinants of plant and insect diversity (Berg et al. 2013; Steinert et al. 2018). Additional factors at different spatial and temporal scales, such as past and present connectivity between grassland habitats (Lampinen et al. 2018), age of the power line (Eldegard et al. 2017), or historical land use (Lampinen et al. 2015) influence species' compositions in power-line corridors.

2. Aims

My objective with this thesis was to explore to what extent linear infrastructure habitats contribute to the conservation of biodiversity linked to semi-natural grasslands. To achieve this, I aimed to:

- Explore whether the species richness and composition of plants and flower-visiting insects in linear infrastructure habitats is similar to that in traditionally managed semi-natural grasslands

- Investigate how linear infrastructure habitats contribute to landscape-scale biodiversity

- Investigate the influence of flowering plant diversity in road verges and traffic on the movements of flower-visiting insects

- Investigate whether flowering plant diversity in road verges and traffic intensity influence the populations of flower-visiting insects

3. Methods

3.1 Study organisms

This thesis focuses on the importance of linear infrastructure habitats for the diversity of vascular plants and flower-visiting insects (especially butterflies, burnet moths, and bees). Plants are primary producers and provide fundamental resources for herbivores and pollinators, and therefore have a profound influence on the distribution and diversity of other organisms (Tyler et al. 2020). Eighty-seven percent of the world's wild plants are pollinated by animals, and many plant species rely on them for the genetic exchange among individuals (Winfree et al. 2011). However, pollinators are currently facing multiple threats, including habitat loss, land-use intensity, climate change, pesticides, genetically modified crops, pathogens and invasive alien species (Potts et al. 2016). Bees are the main animal pollinators in most ecosystems, and they often rely on resources that are spread across multiple types of habitats. Oligolectic bees (species with specialised diets that display high fidelity for particular pollen taxa; Michener 2007) can be more susceptible to environmental change because they gather pollen from a small number of related flower species. Polylectic bees (extreme generalists that use pollen from various unrelated kinds of flowers; Michener 2007) such as bumblebees (*Bombus*) are pollen generalists, but even polylectic species with more specialised diets have shown population declines (Winfree 2010). Butterflies are typically specialised herbivores in their larval stage, but are less specialised flower visitors as adults. They are often restricted to specific habitats such as semi-natural grasslands, and often persist as metapopulations (Hanski & Thomas 1994). Highly specialised and less mobile butterfly species are therefore more susceptible to habitat loss than more mobile species or more generalist species (Öckinger et al. 2010).

Burnet moths are diurnal and have similar requirements to day-flying butterflies, and were therefore treated as additional butterfly species. Even though they were not directly studied in this thesis (only indirectly in **paper III**), hoverflies, i.e. species in the family Syrphidae, are also important pollinators and provide additional ecosystem services such as biocontrol of crop pests and waste recycling. As with other pollinators, the greatest hoverfly declines are found among specialised species and those with a single generation per year (Doyle et al. 2020).

3.2 Area of study

The data for this thesis was collected in east mid-Sweden between 2016 and 2020 in a total of 52 sites. The data for **papers I** and **II** were collected in the summer of 2016 within 32 landscapes located in the counties of Stockholm, Uppsala, Södermanland, and Västmanland. The data for **papers III** and **IV** were collected between the months of May and September of 2019 and 2020 in 20 sites spread across the counties of Uppsala, Stockholm, and Södermanland (Fig. 2).

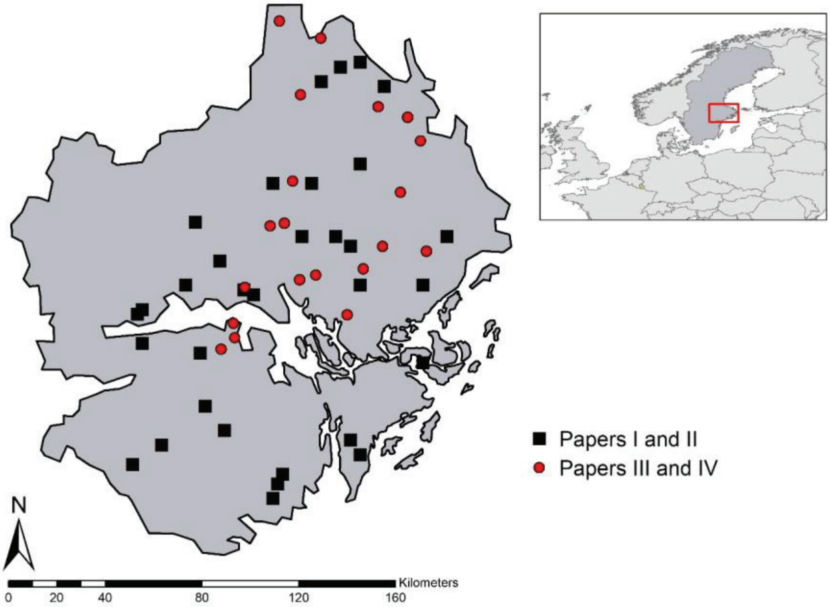

Figure 2. Location of the sites used in this thesis. The black squares represent the 32 landscapes in **papers I** and **II**. The red circles represent the 20 study sites in **papers III** and **IV**.

3.3 Data collection

3.3.1 Papers I and II

Study design

To evaluate if linear infrastructure habitats and semi-natural grasslands of high nature value (as identified in TUVA, the Swedish National Survey of semi-natural pastures and meadows http://www.jordbruksverket.se/tuva) in the landscape affect the biodiversity of plants and flower-visiting insects at different spatial scales, the communities of butterflies, bumblebees, and plants were surveyed in five types of grassland habitats within 32 landscapes with different amounts of grassland habitat (Fig. 3).

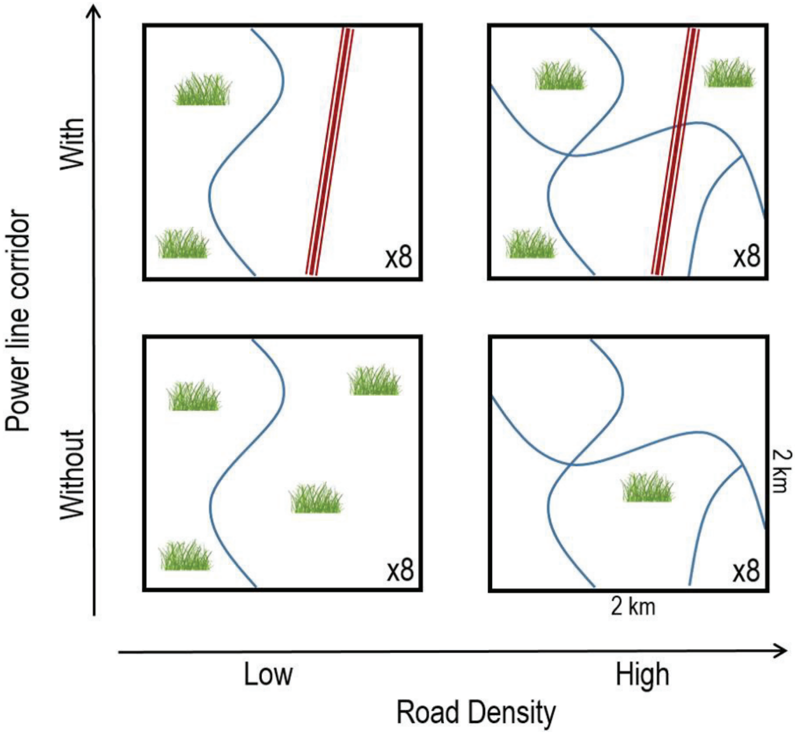

Figure 3. Study design for **papers I** and **II**. Each of the 32 selected landscapes fell into one of the four categories illustrated above. The grass illustrations represent that all landscapes had different amounts of semi-natural pastures of high nature value. Blue lines represent roads and red lines represent power-line corridors.

The landscapes had an area of 4 km^2 and were selected to achieve a design in which the amount of road verges, power-line corridors, and semi-natural grasslands of high nature value were the only source of variation. To achieve this, the amount of forest and arable land cover were held relatively constant among all landscapes to minimise the effects that these types of land-cover can have on plants and insects. The landscapes were forest dominated and varied from 45% to 81% forest cover. The selected landscapes comprised 16 landscapes crossed by at least one power-line corridor, and 16 landscapes without power-line corridors. The selection of landscapes crossed by power-line corridors was limited only to landscapes that were crossed by a power line of at least 1 km in length. The area of road verges in the landscapes was estimated using the density of roads as a proxy and varied from low- to high road density. To select landscapes with a low road density, the selection was limited only to landscapes with a maximum length of 8 km. The selection of landscapes with a high road density was limited to landscapes with at least 12 km in length. The proportion of semi-natural grasslands of high nature value in the landscapes varied from 0.8% to 9.9%.

Biodiversity surveys

Within each landscape, plants, bumblebees, and butterflies were surveyed in five types of prevalent grasslands: road verges along small gravel roads, road verges along big paved roads, power-line corridors, pastures, and uncultivated field borders (Fig. 4). The organisms were surveyed along 200 m long transects placed in each habitat. For the plant survey, all species present within four 1 x 1 m sample plots placed along the transect were identified. This allowed an estimation of the abundance of the plant species in each site. All bumblebees and butterflies along the transects were identified to species level and counted. Butterflies and burnet moths were surveyed by counting the number of individuals of each species observed within five meters from the observer (i.e. "Pollard walk", Pollard 1977). All individuals in road verges narrower than 5 m were noted. Bumblebees were surveyed by capturing and identifying all individuals present within 1 m at each side of the observer.

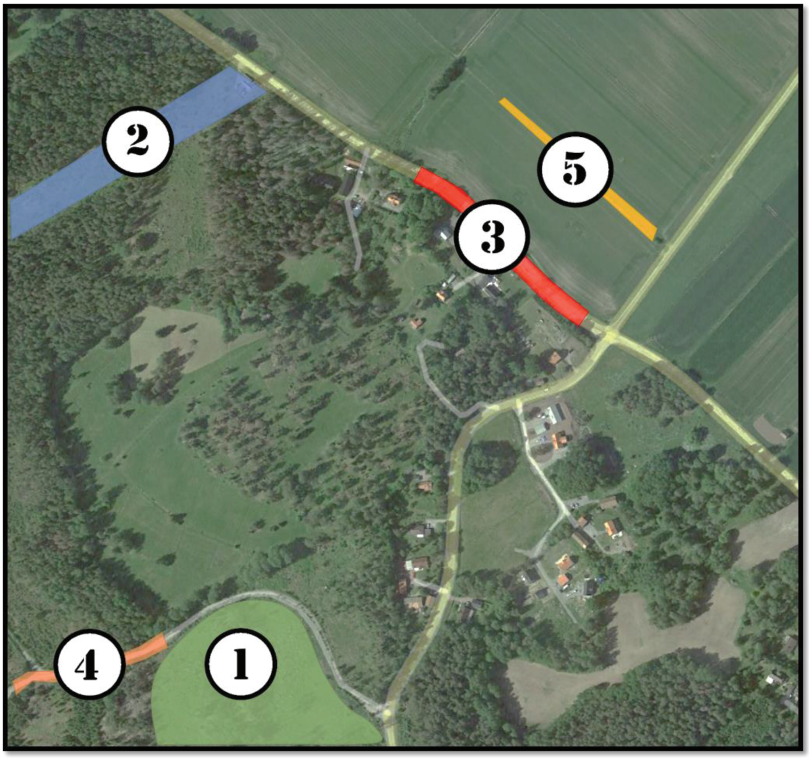

Figure 4. Example landscape to illustrate the five grassland habitat types surveyed for plants, bumblebees, and butterflies. Five types of grassland habitats were surveyed within the 32 4 km^2 landscapes: semi-natural pastures of high nature value (1), power-line corridors (2; only present in 16 landscapes), road verges along big roads (3), road verges along small roads (4), and uncultivated grasslands between fields (5; not present in all landscapes). Note that the presented landscape is not part of the study and is only used for illustration purposes.

3.3.2 Papers III and IV

Study design

To explore the effects of roads and traffic, and road verges and flowering plant diversity on the movements of flower-visiting insects and their populations, I conducted two separate studies. I selected 20 sites to achieve a study design where the interaction between the explanatory variables traffic intensity on the road (continuous) and flowering plant diversity in the road verge (factor: high or low) could be studied. The sites were matched in terms

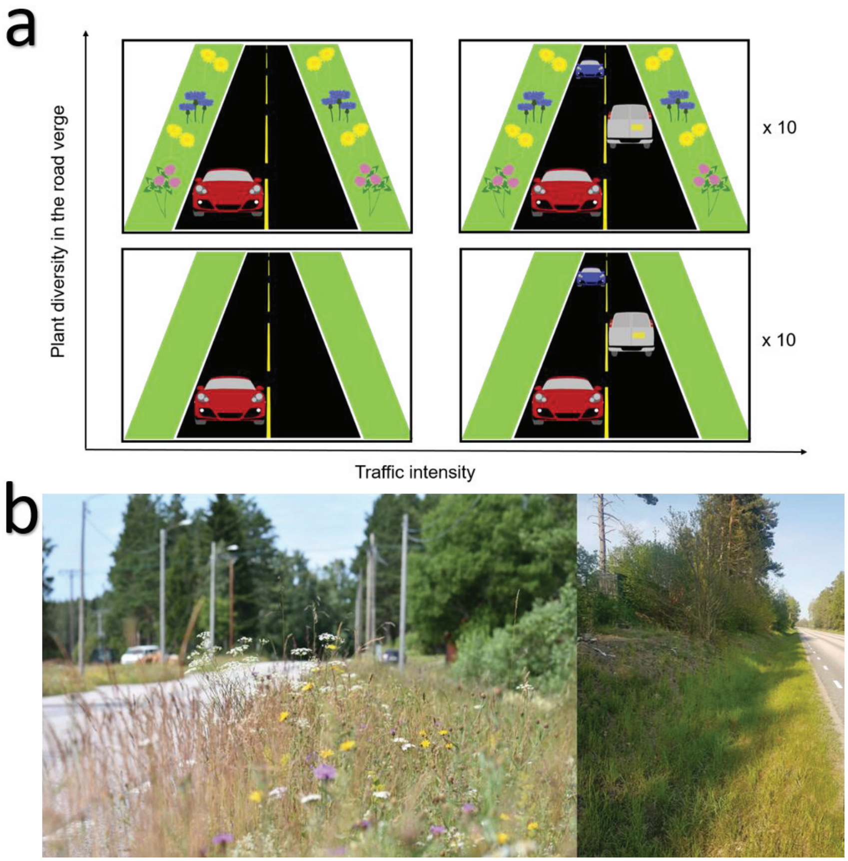

Figure 5. a) Study design for **papers III** and **IV**. Ten of the sites had a higher number of flowering plant species (high quality road verges) in the road verge in relation to the other ten, which were regular grassy road verges (low quality road verges). High quality sites had a traffic intensity gradient similar to the gradient in low quality sites. b) Example sites showing how the flowering plant communities differed between the two categories. To the left is an example of a site with high flowering plant diversity and to the right is an example of a site with low flowering plant diversity.

of traffic intensity but had contrasting flowering plant diversity in the road verge (Fig. 5). Ten of the twenty sites had road verges with high flowering plant diversity and a traffic intensity gradient varying from 125 to 6356 vehicles per day, while the other ten sites had regular grassy road verges and a similar traffic intensity gradient varying from 158 to 6168 vehicles per day. All of the selected roads were between 6 and 7 m wide and had speed limits of 70 or 80 km/h. The width of a road tends to be highly correlated with traffic intensity (Fitch & Vaidya 2021), so the road width was kept as constant as possible to be able to investigate the effect of traffic intensity without adding the effect of the area of the road itself. The quality status of the road verge was confirmed by surveying all flowering plants in six 1 m^2 plots placed at both sides of the road (i.e. three on each side of the road) in the centre of the road verge. This was done twice; during early and late summer in 2019.

Paper III: Exploring the movements of flower-visiting insects in road environments

During the summer of 2019, I performed an experiment aimed at exploring how traffic intensity and flowering plant diversity in the road verge affected the movements of day-flying flower-visiting insects (**paper III**). The experiment enabled tracking the movements of flower-visiting insects by mimicking pollen transfer between plants. At each site, six groups of potted plants with the highly attractive species *Scabiosa columbaria* were placed along the road verges, and two groups were placed in the adjacent habitat. Two of the groups along the road verges were marked with two colours of fluorescent dye powder. Any insect that visited the marked flower heads transferred the fluorescent dye to the unmarked groups, which enabled tracking the transfer of the powder along the road verges and into the adjacent habitat (Fig. 6). To ensure that the differences in flower resource density between sites did not influence the number of flower-visiting insects in the road verges, I visually counted all insects visiting the marked flowers at each side of the road once for 15 minutes (30 minutes per site).

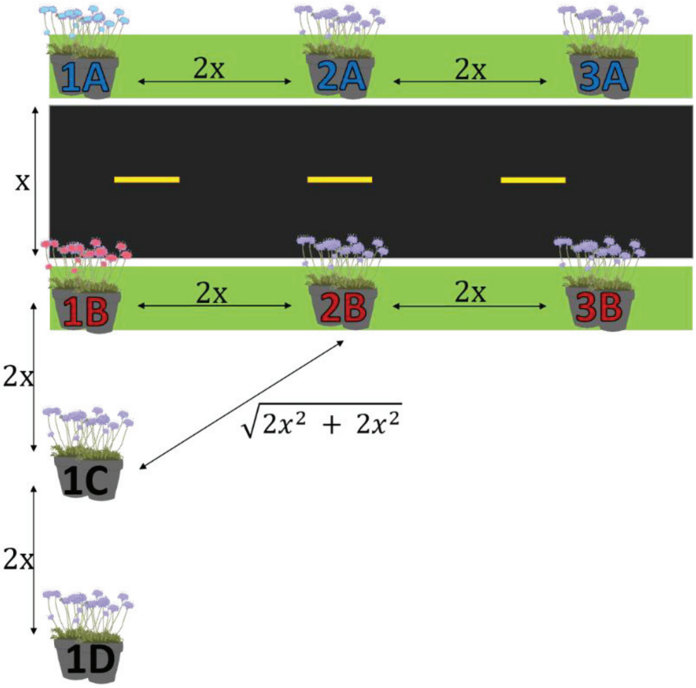

Figure 6. Illustration of the experimental set-up for **paper III**. At each site, I placed eight groups of pots with flowers of the species *Scabiosa columbaria*. The groups along the road verge were separated by a distance of two-times the width of the road. Groups 1A and 1B were marked with blue and red fluorescent dye, respectively, to track the movement frequencies of flower-visiting insects along the road verge, across the road, and perpendicular to the road.

Paper IV: Exploring the impacts of road verges and traffic on bumblebee populations

During the spring and late summer of 2020, dead and alive bumblebee queens were surveyed along a 1 km transect in the same sites as the previous experiment at both sides of the road (**paper IV**). All surveyed individuals were identified to species level when possible, and the behaviour of the living queens along the road verges was noted. During the spring, the bumblebee queens can be foraging, nest-seeking, passing, or resting. In the late summer, the newly emerged queens no longer present nest-seeking behaviour but can instead be seen mating, foraging, resting, flying along the road verge or looking for overwintering sites.

3.4 Analytical concepts and procedures

All statistical analyses were performed in R (R Core Team 2020). General models, generalised linear models, and generalised linear mixed models were often used to statistically evaluate the data. Additional methods used included multivariate statistics for visualisation of ecological communities, diversity partitioning to explore patterns of beta diversity, and indicator species analyses to identify species associations with individual habitat types.

To explore the importance of linear infrastructure habitats, I separated the studies into spatial scales. First, I explored the role of these habitats at the landscape scale (**paper I**), then at the local community scale, and among communities (**paper II**). Then, I explored in more detail how the movements at the local scale are influenced by roads and road verges (**paper III**) in an attempt to link back to landscape-scale diversity (**paper I**). Finally, to get a broader picture of the effects of road verges on pollinator populations, I went back to exploring the effects of road verges and traffic on bumblebee queen mortality, and extrapolated it to the landscape scale, and even to the regional scale (**paper IV**) (Fig. 7).

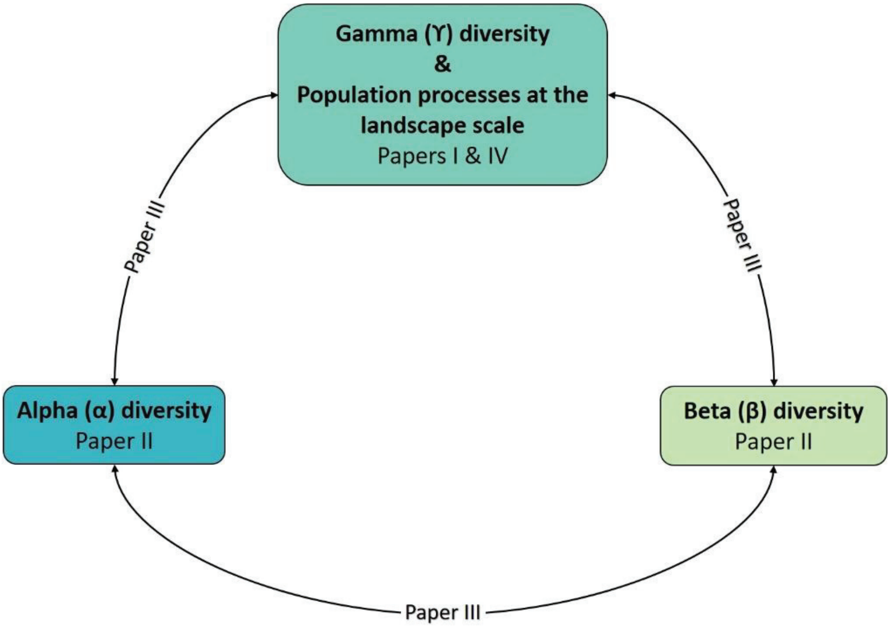

Figure 7. Graphical description of the relationship between the papers in this thesis. In **paper I**, I studied the effects of power lines and road verges in the landscape (ϒ diversity). In **paper II**, I explored patterns of beta and alpha diversity among grassland habitat types and their relation to the amount of habitat in the landscape. In **paper III**, I studied how roads and road verges influence functional connectivity for flower-visiting insects. In **paper IV**, I studied how roads and road verges influence the mortality rates of bumblebee queens.

3.4.1 Alpha and beta diversity

To explore if linear infrastructure habitats can harbour as many species as traditionally managed semi-natural pastures of high nature value, I started by comparing the species richness of plants, bumblebees and butterflies among the five types of grassland habitats (pastures, road verges along big and small roads, power-line corridors and field borders). I also explored whether species richness of each species group in individual habitat types was related to the area of grassland habitats in the landscape (**paper II**). The response variable was species richness in each of the habitats for each species group, separately. The explanatory variables were the type of grassland habitat (factor), the road verge density in the landscape (factor: high or low), the presence of a power line in the landscape (factor: present or not present), and the area of semi-natural pastures of high nature value in the landscape (continuous variable). A random effect for landscape was included to account for the nested nature of the design. Then, I investigated if the species compositions of individual species groups were (dis)similar among all habitat types by using multivariate statistics and by partitioning beta diversity into the nestedness and turnover components. A non-metric multidimensional scaling analysis (NDMS) allowed the visualisation of the degree of overlap between communities and a permutational analysis of variance (PERMANOVA) analysis was used to statistically confirm the differences among communities (**paper II**). For the PERMANOVA analysis, the explanatory variables were the same as before: type of grassland habitat, presence/absence of power-line corridors, road verge density, the amount of semi-natural pastures in the landscape and landscape identity as a nesting variable. Partitioning beta diversity into the nestedness and turnover components allowed me to determine whether communities in linear infrastructure habitats were a subset of the species present in semi-natural pastures or if they were a different set of species.

3.4.2 Gamma diversity

The importance of linear infrastructure habitats was analysed at the landscape (ϒ) scale by pooling the collected species data for bumblebees, butterflies, and plants (**paper I**). Given that half of the landscapes did not have a power-line corridor, including the data collected within the power-line corridors would have generated an unbalanced dataset in terms of sampling effort. Additionally, some of the landscapes did not have uncultivated field borders and would thus generate the same bias in sampling effort if included in the analysis. Thus, to calculate species richness at the landscape scale (ϒ diversity), I pooled the number of species in three habitats (semi-natural pastures of high nature value, and road verges along small and big roads) for each landscape. Using these data also enabled the estimation of the evenness and phylogenetic diversity at the landscape scale. The response variables were species richness, evenness, and phylogenetic diversity in the landscape. The explanatory variables were the area of semi-natural pastures of high nature value in the landscape (continuous variable), the road verge density in the landscape (factor: high or low), and the presence of a power line in the landscape (factor: present or not present).

3.4.3 Landscape connectivity

Alpha diversity, as well as turnover and nestedness, can be directly linked to the connectivity in the landscape. Therefore, I aimed at exploring the effects of flowering plant diversity (habitat quality) in the road verges and traffic intensity on the movements of flower-visiting insects (**paper III**). To do this, I estimated the frequency of movements a) along the road verges, b) across the road and c) across the road and then into the adjacent habitat. I used generalised linear mixed models with the number of marked flowers in each plant group as a response variable. The response variables were different for each type of movement to control for possible confounding effects of the number of insects present in each site, the distance to the marked plants, and the differences in flower density between the two sides of the road.

3.4.4 Mortality risk and behaviour

I explored whether the probability of an observed bumblebee queen being dead was affected by the flowering plant diversity in the road verges or by traffic intensity (**paper IV**). I modelled this probability as a response to the flowering plant diversity in the road verge (factor: high or low), traffic intensity (continuous variable) and the road verge width as a way of controlling the effect of habitat area on the number of individuals. I also investigated whether bumblebee queen behaviour was related to the flowering plant diversity in the road verge or the traffic intensity in an attempt to explain the observed mortality rates. Finally, to extrapolate my results to the landscape scale and the regional scale, I used two separate studies that estimated bumblebee nest density within different habitat types. With this, I was able to estimate the total number of bumblebee queens in the 20 landscapes of 1 km^2 in my study, which together with the observed mortality rates enabled me to perform a rough estimation of the total number of killed bumblebee queens along Swedish roads in a season.

4. Results and discussion

In this thesis, I present evidence that road verges, roads, and power-line corridors affected the diversity of plants and flower-visiting insects at several spatial scales (Table 3). In **paper II**, I showed that the alpha diversity of plants, butterflies and bumblebees was as high in road verges and power-line corridors as in semi-natural pastures. In this paper, I also showed that the community composition in road verges and power-line corridors was relatively similar to that in semi-natural pastures of high nature value. However, each habitat type also had a set of species that were much more common there than in any of the other habitats. Combined, these results indicate that linear infrastructure habitats are valuable for the persistence of grassland species, but that they can only support a part of the biodiversity found in semi-natural pastures of high nature value.

An open question before my study was if the patterns observed at the local community scale, i.e. the high alpha diversity that is often observed in road verges and power-line corridors, scale up to the metacommunity scale or the landscape scale. Remarkably, road verges and power-line corridors had contrasting effects on the landscape-scale diversity, and the response to the area of these habitat types by plants differed from the response by the two insect groups. The number of plant species benefitted at the local (α) and landscape (ϒ) scales from the presence of power-line corridors. In other words, landscapes crossed by a power-line corridor had on average more plant species both at the landscape (**paper I**) and the local community scales (**paper II**). However, road verge density in the landscape did not influence plant diversity at any spatial scale. Contrastingly, butterfly and bumblebee diversity did not show any relationship with the presence of a power-line corridor in the landscape at any spatial scale, but they did with the road verge density. Interestingly, in landscapes with a high road verge density, local

Table 3. Summary of the effects of high road verge density and the presence of power-line corridors in the landscape on the alpha (α), beta (β), and gamma (ϒ) diversities of plants, butterflies, and bumblebees.

	Road verges			**Power-line corridors**		
	Plants	**Butterflies**	**Bumblebees**	**Plants**	**Butterflies**	**Bumblebees**
α	No effect	Marginal negative effect	Marginal negative effect	Positive effect	No effect	No effect
β	No effect	No effect	No effect	No effect	No effect	No effect
ϒ	No effect	No effect	No effect	Positive effect	No effect	No effect

insect communities (α) tended to have a lower species richness than local communities in landscapes with low road verge density (**paper II**). Furthermore, despite a high local (α) species richness in road verges (**paper II**), landscapes with a high density of road verges had the same amount of plant and insect species compared to landscapes with a low density (**paper I**), indicating that the positive effect of this habitat type at the local community (α) scale does not scale up to the landscape (ϒ) scale. Finally, I found that neither the area of power-line corridors, road verges, nor semi-natural pastures in the landscape influenced the (dis)similarities in community composition among habitat types (β-diversity), indicating that linear infrastructure habitats are not currently facilitating dispersal (**paper II**). Given 1) the differing responses (or lack thereof) to power lines and road verges between the species groups (Table 2), 2) the opposing directions of the effects of power-line corridors and road verges on plant and insect diversity (Table 2), and 3) the differences in management between road verges and power-line corridors, I will discuss the relationship between each habitat type with plants and insects separately.

In **paper III**, I found that roads and road verges have opposite effects on the movements of flower-visiting insects. I disentangled the effect of the road surface from the effect of traffic on the movement frequencies of flower-visiting insects in road environments, and found that roads are movement barriers irrespective of the number of passing vehicles. Further, I found that road verges are corridors for flower-visiting insects independent of the flowering plant diversity in the verge. Notably, I found that flower-visiting insects crossed the road less frequently when the road verge had a high resource density. Finally, in **paper IV**, I found that the flowering plant diversity in the road verge does not have any effect on the road mortality risk of bumblebee queens. In other words, the road mortality risk of bumblebee queens increases with increasing traffic intensity independent of the amount of floral resources in the road verge. In this paper, I also showed that the nest-seeking behaviour presented by the queens in response to the flowering plant diversity in the road verge can potentially influence their traffic mortality risk.

4.1 The importance of power-line corridors for landscape-scale species diversity

4.1.1 Vascular plants

In **paper II**, I found that power-line corridors harboured as many plant species as semi-natural pastures of high nature value. Furthermore, I found that all habitat types in landscapes crossed by a power-line corridor had on average three plant species more compared to grassland habitats in landscapes without a power line. In **paper I**, I found that landscapes that are crossed by a power-line corridor have in average six more plant species than landscapes without. Together, these results indicate that power-line corridors are important for plants, either because they are increasing habitat area or connectivity in the landscape. The most parsimonious explanation for the observed patterns would be that power-line corridors add more habitat area to the landscapes and are thus able to harbour more species. However, neither of the insect groups presented a similar response to the presence of power-line corridors. In contrast to mobile animals, plants are slow dispersers and their response to environmental change can be very slow (Cousins 2009). This implies both that plants are slow to establish in newly created habitats, and that they are slow at disappearing from habitat patches after disturbances. In this context, a potential explanation for the observed patterns is that the additional habitat area provided by power lines slowed down the loss of plant species that has already occurred in landscapes that have no power-line corridors.

I found that the type of management and the neighbouring habitat (forests) can influence the community composition of plants in the power-line corridors. In **paper II**, I found that plant species associated with forests are often occurring in power-line corridors (e.g. *Betula pendula*, *Rubus idaeus*, or *Vaccinium vitis-idaea*). These species also occur in semi-natural pastures, but not as often as they do in power-line corridors, which might be due to differences in management intensity. Berg et al. (2013) showed that there were differences in vegetation structure (vegetation height, amount of shrubs and moisture) between power-line corridors and semi-natural pastures and that these differences were likely due to the different management regimes. However, I also found that the plant community composition in power lines had some degree of overlap with semi-natural pastures (Fig. 8), indicating that the applied management in power-line corridors benefits grassland plant species.

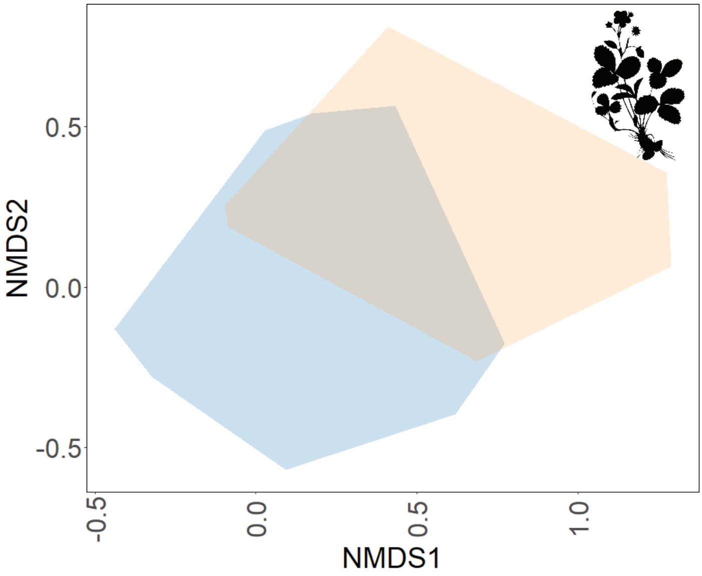

Figure 8. Non-metric multidimensional scaling (NMDS) ordination comparing the community composition of plants in semi-natural pastures of high nature value (blue) and power-line corridors (orange).

This was also reflected by the indicator species analysis in **paper II**, which showed that species that are common in semi-natural pastures, such as *Anthoxanthum odoratum*, *Agrostis capillaris* and *Hypericum maculatum*, were also common in power-line corridors. Overall, the results in **papers I** and **II** showed that power-line corridors are important for the alpha and gamma diversity of plants, most likely due to an increase in habitat area in the landscape.

Power-line corridors also influenced the evenness of plant communities. In landscapes with power-line corridors, plant communities were on average more even than in landscapes without, but only when all species, rare and common, had the same weight. When ignoring rare species, all landscapes had on average the same evenness (Fig. 9).

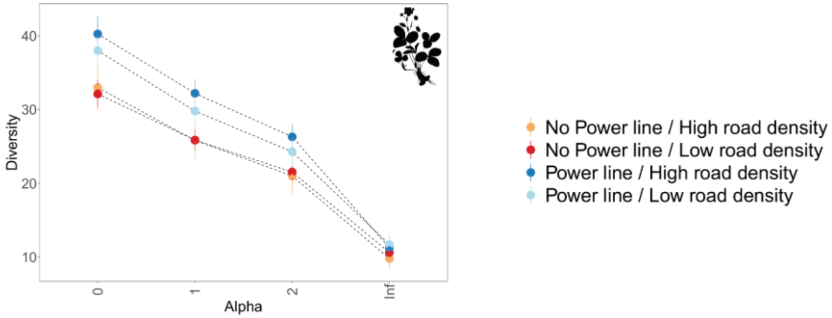

Figure 9. Diversity profile for plants in four types of landscapes varying in the amount of semi-natural grasslands. Each value of alpha represents a different biodiversity index: 0 = species richness, 1 = Shannon diversity, 2 = Simpson diversity and Inf = BergerParker. The indexes put different weights to rare and common species (i.e. rare species have the same weight as common species in alpha = 0 while Berger-Parker ignores rare species). Diversity is represented in Hill numbers, meaning that all indexes predict number of species and can thus be compared to each other. The bars represent the standard error of the mean.

Furthermore, in **paper I**, I found an interaction effect between the road verge density and power-line corridor in the landscape on the evenness of plants, so that evenness was similar when there was a low road density and an absence of a power line compared to when there was a high road density and a power line in the landscape. It is clear that power-line corridors influence the evenness of plant communities, but it is still unclear whether this was driven by an increase in habitat area or by an increase in landscape connectivity, or both. Marini et al. (2014) found that habitat area and connectivity can have opposite effects on species richness and evenness of grassland communities, but these mechanisms are difficult to isolate. From a conservation perspective, it is important to determine which mechanism, habitat area or connectivity, is the most important driver of differences in the composition of communities. If habitat area is more important, then conservation can focus on creating and restoring semi-natural grasslands. If connectivity is more important, conservation can focus on increasing the quality of the landscape with the aim of facilitating species dispersal. However, the most likely scenario is that the importance of these mechanisms will depend on the dispersal abilities and niche breath of the species in question. Ideally, conservation efforts should focus both in increasing habitat area and landscape connectivity to benefit as many species as possible.

4.1.2 Butterflies and bumblebees

In **paper II**, I found that power-line corridors had a similar community composition of bumblebees compared to semi-natural pastures (due to nestedness), and that there were similarities in the community composition of butterflies between the two habitats (Fig. 10). This indicates that power-line corridors can provide valuable resources for pollinators, and are thus supporting viable populations of these insects. Butterflies and bumblebees require different types of resources throughout their life cycles. Some butterflies are highly specialised as larvae, requiring the presence of certain plant species for their development. In **paper II**, I found that power-line corridors provide this type of resource for some butterfly species such as *Plebejus argus* and *P. idas*, which depend on *Calluna vulgaris*, a common species in power-line corridors, as a host species. Despite similarities in the community composition of insects between semi-natural pastures and power-line corridors, I found no evidence suggesting that the presence of power-line corridors in the landscape influence the alpha, beta, or gamma diversity of butterflies or bumblebees. This lack of effect can indicate that power-line corridors only provide a small increase in habitat so that large-scale effects are non-detectable. In **paper I**, I showed that all landscape types had a similar number of species, similar evenness and similar phylogenetic diversity. In addition, the results in **paper II** showed no effect of power-line corridors in the landscape on the alpha diversity or the dissimilarity of

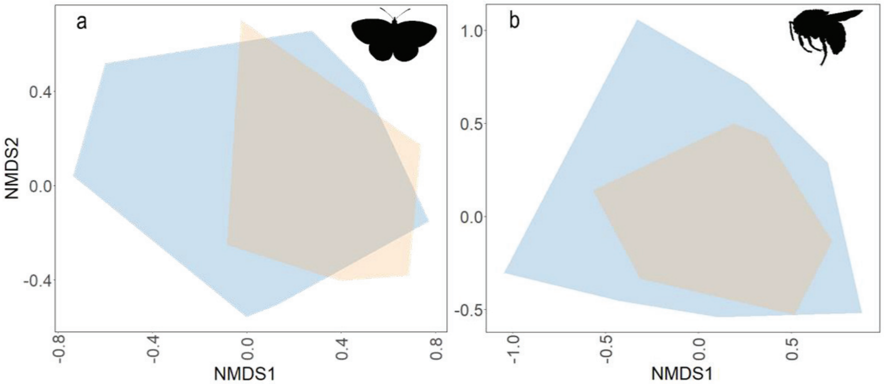

Figure 10. Non-metric multidimensional scaling (NMDS) ordination comparing the community composition of butterflies (left) and bumblebees (right) in semi-natural pastures of high nature value (blue) and power-line corridors (orange).

community compositions of butterflies and bumblebees in individual habitat types. The lack of effect of power-line corridors in the landscape on the beta diversity of butterflies and bumblebees indicate that this habitat type does not influence the connectivity between habitat types for these groups. However, the results in **paper II** suggest that the importance of power lines on landscape diversity will most likely depend on the surrounding landscape. In flower-poor landscapes where little or no semi-natural grasslands remain, and where additional resources found in forests are scarce, power-line corridors can be important for maintaining viable population sizes.

4.2 The importance of road verges for landscape-scale species diversity

4.2.1 Vascular plants

In contrast to power-line corridors, I did not find any evidence suggesting that road verge density in the landscape can influence any type of plant diversity. In **paper I**, landscape types differing in road verge density had a similar number of plant species, as well as similar community evenness and phylogenetic diversity. Further, in **paper II**, there was no effect of road verge density in the landscape on the alpha diversity of plants, indicating that the potential increase in habitat area provided by road verges does not directly result in the accumulation of species in the landscape. Plant community compositions in landscapes with high road density were different from those in landscapes with low road density, but road verge density did not influence the differences in community composition among habitat types. The lack of effect of road verges on alpha, beta or gamma diversity of plants can be due to several reasons. One possibility is that, as with the insects (see below), the positive effects of road verge area on plant diversity might be counteracted by roads and traffic. Of course, plants do not suffer from traffic mortality as mobile animals do, but there is evidence showing that roads and exhaust emissions from passing vehicles can, directly and indirectly, affect the composition of plant communities in the road verges (Angold 1997; Lee et al. 2012). Motor vehicles emit reactive nitrogen, carbon dioxide, carbon monoxide, methane, heavy metals, and other pollutants that can influence plant communities (Lee et al. 2012). Additional compounds are also applied to the roads during winter in some countries to prevent slippery roads, which can influence the pH and the salt concentrations of the soil in the road verges and thus the plant communities. Moreover, the width of the road verge, time and frequency of management, the soil type, the adjacent land use, and the age of the road can also influence plant establishment in the road verge (Jimenez et al. 2013; Auffret & Lindgren 2020; Monasterolo et al. 2020). Thus, not only the size of the road verges but the habitat degradation resulting from the roads and traffic can limit their effectiveness as seed sources (cf. Hooftman et al. 2021). Although it is difficult to isolate the exact mechanism leading to this lack of effect at small and large spatial scales, the results in **paper II** indicate that local environmental factors in the road verges are strong determinants of the species composition of plants. This is because

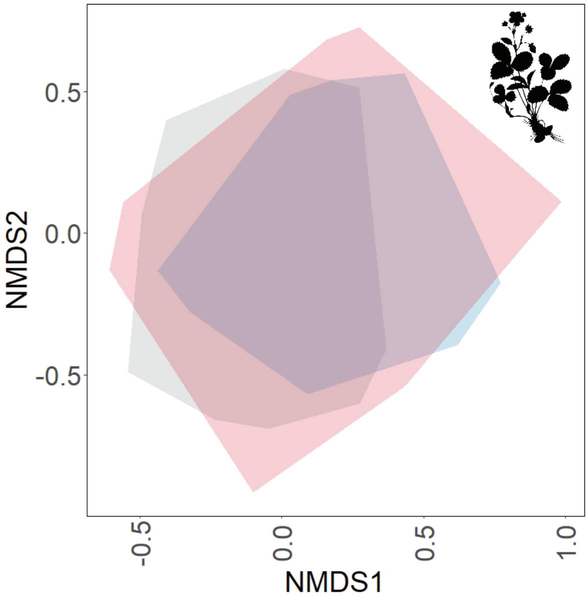

Figure 11. Non-metric multidimensional scaling (NMDS) ordination comparing the community composition of plants in semi-natural pastures of high nature value (blue), road verges along small roads (pink) and road verges along big roads (grey).

the community composition of plants in both road verge types was different from that in semi-natural pastures (Fig. 11).

The results showed that plants with a strong association to semi-natural pastures were species that are specialised on continuously managed grasslands, and that indicator species in road verges along big roads (*Rumex acetosella* and *Arrhenatherum pratensis*) and in small roads (*Plantago major* and *Poa annua*) were generalist species that prefer dry, calcareous soils. This suggests that the environmental conditions in road verges favour generalist species that benefit from repeated disturbances, while more specialised species remain in the semi-natural pastures of high nature value. I also found that there were significant differences in the community composition of plants between road verges of small and big roads. Often, traffic intensity is positively correlated with the width of the road verge (as I found in **paper III** and **IV**), which might lead to more species in wider road verges as a result of species-area relationships (cf. Monasterolo et al. 2020). However, this was not the case for this study because the verges along big and small roads had on average the same width (big roads: 2.8 m, small roads: 2.9 m). Additional causes for the differences between road verge types can be distance to the nearest source habitat (cf. Öckinger & Smith 2007) or the age of the roads (cf. Auffret & Lindgren 2020). Despite the differences, road verges and pastures had several species in common, such as *Achillea millefolium*, *Trifolium pratense*, and *Lotus corniculatus*, confirming previous evidence (e.g. Cousins 2006; Vanneste et al. 2020) that road verges can harbour a considerable proportion of the grassland species pool. However, I show that road verges cannot substitute core semi-natural grasslands. Therefore, the conservation and restoration of core habitat should be prioritised as well as improving management of the road verges to promote plant diversity.

4.2.2 Butterflies and bumblebees

In **paper II**, I found that there were significant differences in the community compositions of bumblebees and butterflies between semi-natural pastures of high nature value and road verges. The community composition of butterflies differed among all habitat types, but the differences between semi-natural pastures and the two types of road verges are worth noting (Fig. 12a). Along big roads (presumably with higher traffic intensity), the number of butterfly species was lowest and the indicator species analysis showed that there were no specific species associations with this habitat type. In contrast, road verges along small roads had a similar number of butterfly species compared to semi-natural pastures, and the indicator species analysis showed that both generalists and forest species (e.g. *Melitaea athalia*) can utilise this type of habitat. Moreover, the ordination analysis showed a large variation in the community composition of butterflies in road verges along small roads, indicating that more species can occur in this habitat type, compared to verges along big roads. Patterns of beta diversity for butterflies was also mostly driven by turnover, indicating that verges along small and big roads might provide different types of resources for butterflies. However, the overall results in **paper II** show that most butterfly species are present in all habitat types, and as such, differences in community composition can be driven mostly by more specialised species.

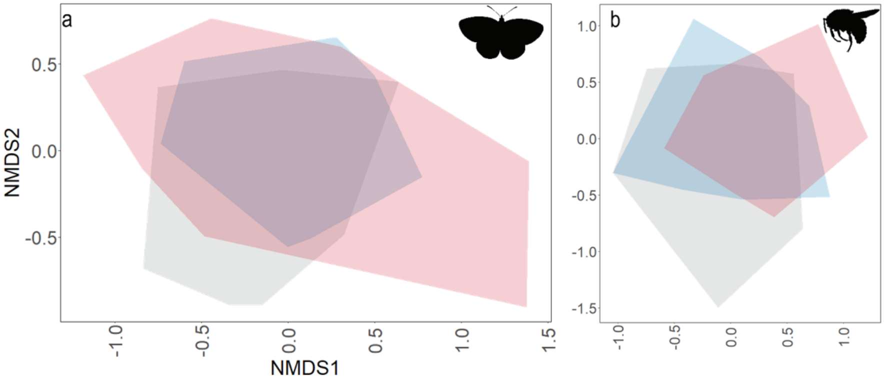

Figure 12. Non-metric multidimensional scaling (NMDS) ordination comparing the community composition of butterflies (left) and bumblebees (right) in semi-natural pastures of high nature value (blue), road verges along small roads (pink) and road verges along big roads (grey).

In contrast to butterflies, bumblebees are generalists in their floral preferences (with a few exceptions such as *B. consobrinus*) and are central place foragers (Goulson et al. 2008). Bumblebees are also capable of flying large distances in search of food (Osborne et al. 2008). These aspects of bumblebee ecology can potentially explain the patterns found in **paper II**. Bumblebees were the only group that had the same number of species in all habitat types, and bumblebee community composition in road verges along big roads did not differ from the composition in semi-natural pastures. Also, despite some differences, there was a big overlap in the composition of bumblebee communities in verges along small roads and semi-natural pastures (Fig. 12b). Most importantly, patterns of beta diversity for bumblebees were mostly driven by nestedness indicating that the species present in road verges are a subset of the species present elsewhere in the landscape, which could explain the lack of effect or road verge density in the landscape on bumblebee gamma diversity (**paper I**). The results presented here pertain mostly to patterns of bumblebee worker occurrence, as the surveys took place between June 1 and August 23. An interesting prospect would be to explore whether the observed patterns for bumblebee workers in **papers I** and **II** are similar for bumblebee queens.

Despite similarities in the community compositions of bumblebees and butterflies among road verges and semi-natural pastures, I did not find any evidence suggesting that road verges contribute to gamma (**paper I**) or beta diversity (**paper II**) of these insect groups. Moreover, there was a marginal (not statistically significant) negative effect of high road verge density in the landscape on the alpha diversity of bumblebees and butterflies, which could suggest that road mortality outweighs the positive effect of the road verges or that road verge management does not benefit pollinators (cf. Kallioniemi et al. 2017). These results suggest that road verges do not increase landscape connectivity nor habitat area, which is a surprising result given their spatial distribution. Indeed, landscapes with a high density of road verges had a different species composition of all species groups than landscapes with a low density (Fig. 13), but such differences were equal among all habitat types, indicating that any differences in the composition of communities in individual habitat types were not due to road verges. However, these results are difficult to interpret without further investigating patterns of functional diversity because most species were present in all habitat types and all landscape types. Further, there were no unique associations between any species of butterflies and road verges or bumblebees and verges along small roads that could help explain the observed patterns.

Roads and road verges have contrasting effects on dispersal, and without further investigating how these landscape elements influence functional connectivity it is difficult to draw conclusions. Thus, a reasonable follow-up to disentangle the effect of road verge density on landscape-scale diversity would be to relate the life-history traits (e.g. dispersal capacity, niche breadth, reproductive capacity) of the species in the different landscape and habitat types. Öckinger et al. (2010) found that considering life-history traits in fragmentation studies can modify the species-area relationships of butterflies, and showed that specialist species and species with low mobility were more affected by habitat loss than generalist butterfly species. In this context, it would be interesting to group the species present in my studies based on their functional traits or phylogenetic relatedness to explore whether road verges support species with specific life-history traits. Another interesting follow-up would be to explore how the differences in the plant communities in the road verges relate to the differences in the insect communities. In connection to this, in **paper III** and **IV** I investigate how differences in flowering plant diversity in road verges influence landscape connectivity for flower-visiting insects.

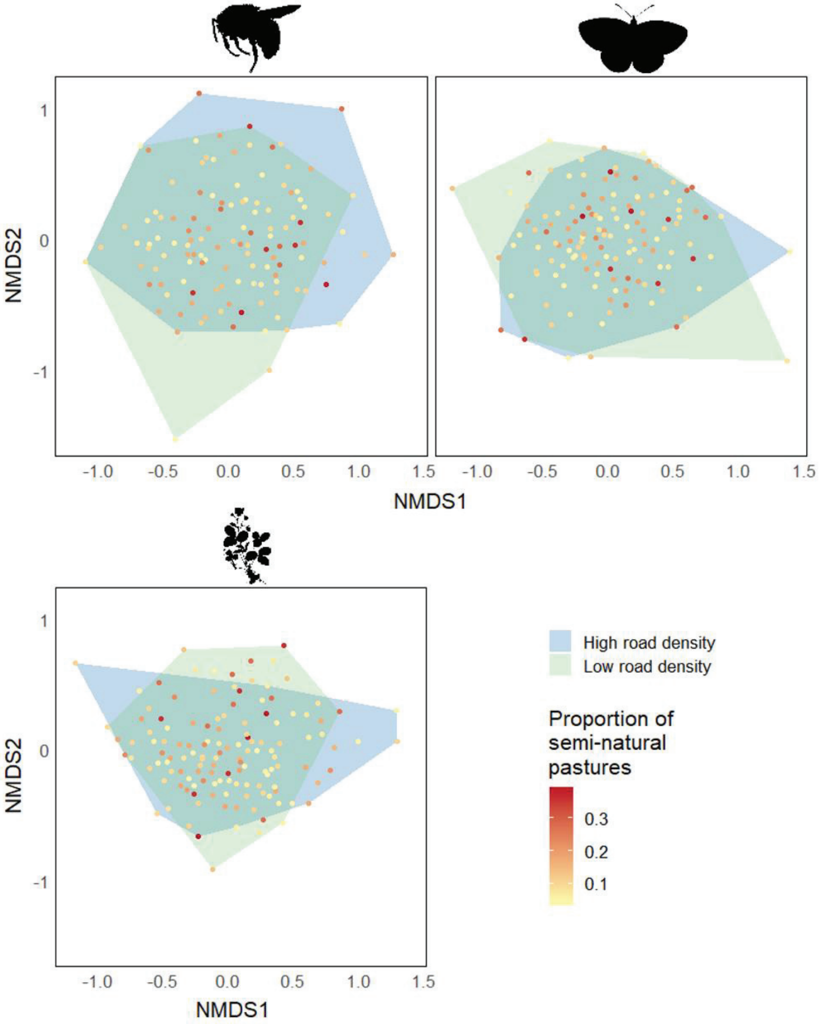

Figure 13. Non-metric multidimensional scaling (NMDS) ordination comparing the community composition of bumblebees, butterflies, and plants in landscapes with high (blue) and low (green) road verge density in the landscape.

4.2.3 The opposite effects of roads and road verges on connectivity

In this thesis, I investigate whether road verges enhance landscape connectivity for flower-visiting insects. In **papers I** and **II**, I concluded that despite an increase in the structural connectivity in landscapes with high road verge density, road verges do not influence landscape-scale diversity for butterflies and bumblebees. This pattern can be better understood by further exploring the functional response of the insects to this habitat type. Measuring functional connectivity involves understanding the behavioural responses of animals to different landscape elements, as well as their relative rates of movement and mortality risk. Therefore, I explored how road verges with differing flowering plant diversity influence behaviour, traffic mortality risk, and the frequency of movements in road environments. In **paper III** and **paper IV**, I found that the most likely reason road verges are not influencing landscape diversity of insects is due to the opposite effects of the roads and road verges on insect movement and survival. In **paper III**, I showed that road verges are corridors irrespective of their habitat quality in terms of floral resources but also that roads, irrespective of traffic intensity, are barriers to insect movement. I also showed that when the quality of the road verge is high, insects are less likely to cross the road, directly reducing their mortality risk and thus increasing landscape connectivity. In **paper IV**, I showed that the mortality of bumblebee queens along roads is positively related to traffic intensity. Further, I found that road verges with high flowering plant diversity neither mitigate nor exacerbate the traffic mortality risk of bumblebee queens. The results in **paper IV** suggest that the mortality risk of bumblebee queens as a result of traffic is associated with their behaviour, and in turn that the frequency of different behaviours is influenced by the flowering plant diversity in the road verges.

Behaviour in road verges and its influence on landscape connectivity

I found that behaviour can be an important constraint on road mortality risk. Behaviour, e.g. whether an individual is searching for food or nesting grounds, can influence the type of movement, which can ultimately determine the traffic mortality risk. For example, migrating individuals are most likely not affected by road mortality because they fly higher than individuals looking for resources near the ground (Phillips et al. 2020b). In **paper III**, I concluded that road verges are most likely increasing connectivity because they promote routine movements (foraging movements over relatively short distances; Van Dyck & Baguette 2005). Further, in **paper IV**, I found that neither the amount of traffic nor the quality of the road verge influenced the number of foraging queens along road verges, but they did influence the number of nest-seeking queens. Both of these findings suggest that the relationship between the road mortality risk of insects and the flowering plant diversity in the road verge can be moderated by their behaviour. More careful behavioural studies are needed to confirm this, as I did not directly study whether the decreasing number of nest-seeking queens with increasing traffic in low quality sites was a result of traffic mortality. Confirming this hypothesis would however require a substantial effort that is very difficult to achieve (finding enough nest-seeking/ foraging bumblebee queens or butterflies looking for a host plant/ foraging to be able to draw statistically significant conclusions, and observe them being killed by traffic while doing so). Yet, understanding the mechanisms that drive traffic mortality is crucial for establishing adequate mitigation measures, and behavioural studies should be combined with complementary explorations. Additional investigations could aim at determining if road verges with high plant diversity along roads with high traffic are acting as ecological traps by measuring birth and mortality rates in landscapes with different contexts. Further, it is important to investigate whether road verges influence genetic exchange and colony success in order to draw more general conclusions that aid managers in deciding where and when conservation efforts along roads are most needed.

The impacts of roads and traffic on functional connectivity

In **papers III** and **IV**, I found that roads have negative impacts on flower-visiting insects through two mechanisms: as behavioural barriers to movement and through traffic mortality. Although these mechanisms are well studied for vertebrates, they have rarely been tested for insects. I investigated the effects of traffic independent of the characteristics of the road by retaining a constant road width and speed limit. Further, I investigated how traffic mortality related to different behavioural constraints that potentially affect the different types of movements presented by an individual (see above). In **paper III**, I found that roads are barriers to the movements of flower-visiting insects. This effect was independent of the traffic intensity, meaning that the barrier effect was mostly due to a behavioural response to the road surface (i.e. road surface avoidance, Jaeger et al. 2005) instead of an effect of the passing vehicles. This result implies that roads decrease the functional connectivity in the landscape for flower-visiting insects, but this is most likely not the case for all species. Road surface avoidance is dependent on the physical characteristics of the road and is also highly dependent on the perceptual range of the species, and on their responses to habitat edges (Tischendorf & Fahrig 2000; Jaeger et al. 2005). For small, less mobile, and more specialised species, even small countryside roads can represent a movement barrier. However, roads might be less of a behavioural barrier for species that are larger, more mobile, and that are less specialised so that their responses to habitat edges are less strong. For these types of species, small roads with low traffic intensity might increase the connectivity in the landscape because they can function as navigational aids (Phillips et al. 2020b), but wider roads with high traffic intensity introduce traffic mortality as an additional threat.

Figure 14. Observed dead bumblebee queens on the road surface (left) and on the road verge (right).

In **paper IV**, I found that the second mechanism by which roads affect pollinator diversity is traffic mortality (Fig.14). In this study, I found that the proportion of dead bumblebee queens along the road verge increased with increasing traffic intensity. Previous evidence based on butterflies showed that the effects of traffic mortality on their populations is low (Munguira & Thomas 1992) and that most often the butterflies killed by traffic belong to more mobile taxa (Phillips et al. 2020b). Bumblebee queens are big and highly mobile, and there are indications that bumblebee workers avoid crossing roads (Bhattacharya et al. 2003). Therefore, this result was somewhat surprising and very concerning. Bumblebee populations are dependent on the success rates of the queens at establishing a nest, and traffic mortality of bumblebee queens can exacerbate population declines. However, the difficulty in locating bumblebee nests has resulted in a limited understanding of the factors that affect their population sizes. Because of this, determining whether the observed mortality rates impact their populations is a difficult task. Future research could attempt to understand how road mortality influences bumblebee populations by exploring whether their genetic structure differs among landscapes with varying amounts of habitat and road verge densities. Overall, my results confirm that roads are detrimental for flower-visiting insect populations but further research is needed to identify which mitigation measures are most appropriate. Based on **paper III**, I conclude that roads are isolating flower-visiting insect populations by reducing connectivity, and increasing the quality of the road verge will not influence the barrier effect for some species. Based on **paper IV**, more appropriate measures to reduce road mortality would be to reduce the speed limit on the road and to take pollinators into account both during road construction planning and maintenance.

5. Conclusions and recommendations

Currently, opportunities to increase habitat area as a means to halt the ongoing population declines of species are increasingly limited due to the growing demand for food, fibre, and housing for the human population (Baguette et al. 2013). Therefore, there is a necessity to utilise the available land in the most effective way to ensure not only adequate ecosystem functioning and ecosystem service provision, but the survival of species that represent millions of years of evolutionary history. My aim with this thesis was to investigate whether linear infrastructure habitats, grassland areas that result as a by-product of human activities, contribute to the conservation of vascular plants and pollinators. My thesis work showed that linear infrastructure habitats can contribute to the biodiversity of plants and insects at several spatial scales, but that in their current state their contribution has not reached its full potential.

My results showed that the presence of a power-line corridor in the landscape is beneficial for the alpha and gamma diversity of vascular plants, but that their contribution to insect diversity is limited and most likely dependent on the context of the surrounding landscape (**papers I** and **II**). Plant and insect composition in power-line corridors is likely influenced by the surrounding amount of available habitat and by the ability of individual species to disperse and establish in a habitat patch. However, the vegetation management in the power-line corridors is a determining factor influencing plant species establishment and thereby the presence of pollinating insects. Based on this, I recommend that future studies should focus on exploring how different management regimes influence the contribution of power-line corridors to biodiversity at several spatial scales. So far, researchers advise that cutting and removing wood debris in productive areas (Lensu et al. 2011; Berg et al. 2013; Steinert et al. 2018), creating patches with low ground vegetation (Berg et al. 2013), and a more frequent clearing interval (Komonen et al. 2013), will enhance plant communities that are beneficial for pollinators. I recommend that land managers apply the suggested improvements to management and that researchers focus on monitoring how these changes at the local community scale influence plants and pollinators over time. Long-term monitoring of the flora and fauna in power-line corridors and in the surrounding landscape is necessary to determine whether changes at the local community scale can also influence the role of power-line corridors for the alpha, beta, and gamma diversity of these groups.

I found that road verges can have a high number of species locally and that the community composition of plants and insects presented some resemblance to the communities in semi-natural pastures of high nature value (**paper II**). While this might indicate that road verges can be important pollinator habitats and that they have the potential to support biodiversity linked with semi-natural pastures (with adequate management), there is still a concern that road verges can act as ecological traps for pollinators. So far research on this subject has been inconclusive, but in this thesis I attempted to fill a few knowledge gaps on this matter. One important question is whether road mortality increases when the road verge is rich in flower resources. My results from **paper IV** suggest that the road mortality risk, at least of bumblebee queens, is neither lower nor higher when the verge provides more floral resources than regular grass-dominated road verges. Whether this is the case for other pollinators needs to be explored further, but there is at least some evidence showing that for butterflies road mortality tends to be higher when the road verge provides few resources and when the traffic intensity is high (Skórka et al. 2013, 2015). Another important question on the role of road verges as ecological traps is whether traffic mortality can affect population persistence. This is an important question because if road verges provide pollinators with otherwise scarce resources, then ultimately they might be supporting an increase in population sizes. But if the traffic mortality is too high such that the death rates are higher than the birth rates, they can be ecological traps. I attempted to shed some light on this question by estimating the total number of bumblebee queens in the landscapes surrounding the roads in **papers III** and **IV** using two estimates of bumblebee nest density in different land-cover types. I found that the variation between the two datasets was too high to draw clear conclusions, but based on my estimations there is a possibility that traffic mortality of bumblebee queens can be an important source of bumblebee population decline and should not be disregarded. Future studies should attempt to estimate whether the mortality rates by traffic outweigh the positive effects of flower-rich road verges at the population level and whether the pattern is the same for all pollinator taxa. I suspect that these effects will be variable and will also depend on the context of the surrounding landscape. Finally, an important question is how the behaviour presented on the road verge influences traffic mortality risk, and how the frequency of different behaviours is affected by the plant diversity in the road verges. I showed that road verges with low flowering plant diversity are attractive for nest-seeking queens. Since I also found that road mortality rates increased with increasing traffic, these results indicate that nest-seeking behaviour can potentially be an important driver of bumblebee queen mortality along roads with high traffic and low flowering plant diversity. If this is indeed the case, a potential mitigation measure to reduce traffic mortality could be to maintain a low vegetation height in verges along roads with high traffic intensity during the period when the queens are establishing a nest. However, more studies are needed to confirm this.

My thesis work showed that roads are barriers to the movements of flower-visiting insects regardless of the traffic intensity (**paper III**), and this result has important repercussions. In the context of climate change, roads can ultimately prevent species from adapting to new environmental conditions by hindering range-shift responses of mobile animals. Further, highly specialised species that are unable to utilise the resources in the road verges and are also unable to cross the roads will be even more vulnerable to reduced habitat area, isolated populations, and overall reduced population sizes. As such, roads and road verges can contribute to the homogenisation of biodiversity if they benefit mostly a specific set of species that share similar life-history traits. Highly specialised species that are less prone to leave their habitat due to e.g. unwillingness to cross edges, will not draw any benefit from quality improvements of the road verge. Further, for species that show road surface avoidance, mitigation measures such as decreasing the speed limit or enhancing plant diversity of the road verge will not affect the barrier effect of roads and the isolation effect of populations. These effects will most likely be exacerbated when the road is wide and when the traffic intensity is high.

The length of roads is expected to increase by >60% globally by 2050 (Ibisch et al. 2016), and currently, 90% of the world's land surface can be reached within 48 hours of travel by road or rail from the nearest city (Selva et al. 2015). I suggest that landscape managers and the road planning community should evaluate the environmental impacts of roads on wildlife populations, including insects and other invertebrates, both before and after establishment. Landscape managers should also critically evaluate whether an existing road that is ecologically damaging can be reclaimed for biodiversity in order to restore landscape-level processes that facilitate species persistence.

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Popular science summary

The agricultural landscape in Europe has undergone considerable changes in the 20th century, with an extensive loss of habitat for organisms that depend on traditionally managed semi-natural grasslands. Traditionally managed semi-natural grasslands are one of the most species-rich habitats in Europe and have been managed with low-intensity grazing or mowing for long periods without the addition of fertilisers. Until the beginning of the 20th century, humans had created an agricultural system that benefitted biodiversity by increasing the diversity of flower-rich habitats in the landscape, supporting plant communities and thereby many wild animals that depend on pollen and nectar for survival. But to meet the increasing demand for food and fibre from a growing human population, small scale farming systems were converted into large monocultures and low productive grasslands were abandoned and have since turned into forests. As a result, plants that depend on nutrient-poor soils and insects that rely on flower-rich areas have declined, and some species have even gone regionally extinct. So how can we ensure the survival of species as we simultaneously require an increasing amount of natural resources to sustain a growing human population?

Opportunities to spare natural areas for biodiversity are increasingly limited as countries worldwide seek economic development, and the demand for agricultural and forestry products increases. To survive and reproduce, organisms need to move across and face increased mortality in intensively managed landscapes devoid of floral resources. In the light of land scarcity for conservation, an alternative employed by conservationists has been to attempt to improve species' persistence by facilitating their movements between remaining habitat patches. This approach does not only ensure the genetic exchange between otherwise isolated populations, but it can also increase the habitat area, allowing larger population sizes and reducing extinction rates. In this regard, unproductive areas that result as a by-product of human land use for the transportation of goods, humans, and energy represent a unique opportunity for biodiversity conservation.

Inadvertently, humans have created grassland habitats that resemble traditionally managed semi-natural grasslands along linear infrastructures such as roads, railways and power-line corridors. However, these areas are usually not managed for biodiversity conservation purposes, but to guarantee the transport of goods and people. For example, power-line corridors are managed with the sole purpose of preventing the vegetation from interfering with the electrical lines. Road verges are regularly cut to ensure visibility and traffic safety. Linear infrastructure habitats cross forests, cities and agricultural land and thus have a unique distribution in our landscapes. In some countries, the area of linear infrastructure habitats surpass the area of remaining semi-natural pastures. In Sweden, the area of grasslands in road verges and in power-line corridors combined is similar to the total area of traditionally managed semi-natural grasslands. Furthermore, linear infrastructure habitats are projected to increase in the next 30 years, but we do not know to what extent these habitats support the persistence and dispersal of plant and insect species. My aim with this thesis was to explore if these habitats along infrastructure support biodiversity linked to semi-natural grassland habitats.

Habitat types can contribute to biodiversity in several ways, for example, by increasing the area so that more species can coexist or by facilitating the movements of species between remaining habitat patches. Habitats can also differ in quality, which can impact the identity of species and the number of individuals that can survive and emigrate into the landscape to colonise other habitat patches. I began by exploring whether linear infrastructure habitats harbour the same number of grassland species as traditionally managed semi-natural grasslands of high nature value. I found that both road verges and power-line corridors were species rich. In particular, power-line corridors can harbour as many species of plants, butterflies and bumblebees as semi-natural grasslands. Road verges can harbour as many species of bumblebees and plants as semi-natural grasslands, but more butterfly species prefer road verges along small gravel roads instead of road verges along big paved roads.

But the number of species in an area is hardly an exhaustive measure of its contribution to landscape-scale biodiversity. I therefore continued by exploring whether the identities of the species in linear infrastructure habitats were similar to those in traditionally managed semi-natural grasslands. Species have habitat preferences where some prefer forested areas, others open areas, and some are generalists and occur in many habitat types. I found that linear infrastructure habitats generally have a high degree of overlap of species compared with semi-natural grasslands, indicating that infrastructure habitats support grassland biodiversity. However, I found differences in the composition of species in power-line corridors, road verges and semi-natural grasslands. Plant and butterfly species that prefer forest habitats were common in power-line corridors, and plant species that prefer dry soils and a high degree of disturbance were often observed along road verges. These dissimilarities can be due to the different managing of each habitat, the neighbouring habitat, or the soil properties. Overall, linear infrastructure habitats supported a subset of grassland biodiversity found in the traditionally managed semi-natural grasslands.

Another open question is whether linear infrastructure habitats can function as corridors, facilitating the dispersal of species across the landscape. Grassland patches that are well connected to similar habitats can have different species composition when compared to isolated patches. Isolated grasslands can have impoverished biodiversity because species have gone locally extinct due to a reduction in the habitat area. Contrastingly, patches that are well connected to similar habitats allow for species persistence and can contain a higher number of species and higher abundances. At first glance, the widespread spatial distribution of power-line corridors and road verges suggest that grassland species should be able to disperse more easily in landscapes with a high amount of linear infrastructure habitats. Thus, I investigated whether the amount of linear infrastructure habitats in the landscape influenced the composition of plant, butterfly and bumblebee species in five types of grassland habitats. I found that the differences in species compositions of these groups in individual grassland habitats were not influenced by the amount of linear infrastructure in the landscape, suggesting that these habitats do not facilitate dispersal. However, there were more plant species in landscapes with power-line corridors than in landscapes without. I also found that all grassland habitat types had on average more plant species when there was a power line crossing the landscape. This indicates that power-line corridors support the populations of grassland species and enrich our landscapes with plant species. Highly specialised plant species that need, for example, nutrient-poor soils can occur in road verges, but to a lesser extent than generalists. While this might limit the use of road verges as habitat for pollinators, it does not necessarily mean that it decreases their utility as movement corridors. I therefore proceeded to investigate whether road verges were utilised as corridors by flower-visiting insects.

A fundamental problem with road verges is that while they might facilitate the movements of insects, the adjacent roads and traffic can have the opposite effect. Roads can be barriers through two mechanisms: as physical or behavioural barriers and by traffic mortality. These effects are difficult to disentangle, as they will largely depend on how individual insect species respond to changes in vegetation structure, their perceptual range, and their behaviour. I investigated this by selecting 20 roads with similar width and speed limits but varying traffic intensity. Ten of these roads were classified as having a high diversity of plant species in the road verge by the Swedish Transport Administration. In these 20 sites, I performed two separate experiments. I explored whether road verges with many flowering plant species increased the frequency of movements of flower-visiting insects along the road verge and whether the traffic intensity influenced the frequency of movements across the road. I also investigated whether the differences in flowering plant diversity in the road verge and traffic intensity influenced the behaviour and mortality risk of bumblebee queens. I found that road verges facilitate the movements of flower-visiting insects and that this does not depend on the number of flowering plant species in the road verge. In other words, all road verges can function as corridors. However, I also found that roads are barriers to the movements of insects regardless of the number of vehicles that cross them. I found a higher probability of observing a dead bumblebee queen with increasing traffic intensity. Interestingly, the number of nest-seeking bumblebee queens dramatically decreased when the traffic intensity was high, but only in road verges with low flowering plant diversity.

I show that linear infrastructure habitats can support grassland biodiversity. Power-line corridors enrich landscapes with plant species, and road verges facilitate the movements of flower-visiting insects across the landscape. However, their contribution to landscape-scale biodiversity does not reach its full potential and can be possibly improved by adjusting management for conservation purposes. Based on my results, I recommend managing road verges along roads with low traffic intensity to enhance plant species richness and flower density. In Sweden, approximately 344 000 km of roads have a traffic intensity ranging from 0 to 2 000 vehicles per day. Still, only 10% of the road verges along these roads are classified as of high nature value. If we managed only one meter width on each side for increasing plant diversity, this would translate to an increase of approximately 69 000 ha of habitat for pollinators. Managing two meters width on each side would translate roughly to a 138 000 ha habitat area increase for pollinators. Along roads with high traffic, I recommend maintaining a low vegetation height during the spring to avoid attracting nest-seeking queens that can be killed by traffic. Finally, my results indicate that the effect of roads as movement barriers for specialised flower-visiting insect species will not be affected by mitigation measures in the road or the road verge. Thus, I recommend that landscape managers carefully evaluate the effect of roads on wildlife populations and whether these roads can be reclaimed for biodiversity to restore the landscape-level processes of populations. Reducing the number of roads and using their area to support biodiversity might also translate into a reduction in the emissions driving climate change. Moreover, reclaiming roads would allow species to adapt to a new climate by facilitating range-shifts hindered by the ever-expanding global road network.

Populärvetenskaplig sammanfattning

Jordbrukslandskapet i Europa har genomgått stora förändringar under 1900-talet som har lett till en omfattande förlust av habitat för organismer som är beroende av traditionellt skötta slåtter- och betesmarker. Gräsmarker som har skötts med lågintensiv bete eller slåtter under långa tidsperioder utan att tillsätta gödningsmedel utgör några av de mest artrika livsmiljöerna i Europa. Fram till början av 1900-talet hade människor skapat ett jordbrukssystem som gynnat den biologiska mångfalden genom att öka diversiteten av blomrika livsmiljöer i landskapet. Men för att möta den ökande efterfrågan på mat och fiber från en växande befolkning omvandlades småskaliga jordbrukssystem till stora monokulturer och lågproduktiva gräsmarker övergavs och har sedan omvandlats till skogar. Till följd av detta har växter som är beroende av näringsfattig jord och insekter som förlitar sig på blomrika habitat minskat, och vissa arter har till och med utrotats i vissa regioner. Så hur kan vi säkerställa arternas överlevnad när vi samtidigt kräver en ökande mängd naturresurser för att upprätthålla en växande mänsklig befolkning?

Möjligheterna att bevara naturområden för att stödja den biologiska mångfalden blir alltmer begränsade när länder över hela världen söker ekonomisk utveckling och efterfrågan på jordbruks- och skogsbruksprodukter ökar. Organismer blir i allt högre utsträckning tvingade att röra sig igenom blomfattiga och intensifierade landskap där mortalitetsrisken är stor. När det inte finns möjligheter att öka arealen av slåtter- och betesmarker, är ett alternativ som använts av naturvårdare att underlätta för arter att röra sig mellan kvarvarande gräsmarksfläckar. Detta säkerställer inte bara det genetiska utbytet mellan annars isolerade populationer, utan kan också öka den arealen av arters habitat, vilket möjliggör större populationer och minskar risken för utdöende. Utifrån detta avseende utgör outnyttjade områden som uppkommit som en biprodukt av mänsklig markanvändning för att transportera varor, människor, och energi en unik möjlighet för bevarande av den biologiska mångfalden.

Oavsiktligt har människor skapat gräsmarkbiotoper som liknar slåtter- och betesmarker längs linjära infrastrukturer som vägar, järnvägar och kraftledningsgator. Dessa områden sköts vanligtvis inte för bevarande av den biologiska mångfalden, utan för att garantera transporten av varor och människor. Exempelvis röjer man regelbundet i kraftledningsgator för att förhindra att vegetationen växer upp i de elektriska ledningarna. Vägkanterna klipps regelbundet för att säkerställa god sikt och därmed säkerhet för trafiken. Linjära infrastrukturmiljöer genomkorsar skogar, städer och jordbruksmark och har därmed en unik fördelning i våra landskap. I vissa länder är arealen i linjära infrastrukturmiljöer större än den av kvarvarande arealen av slåtter- och betesmarker. I Sverige, är arealen av gräsmarker längs kraftledningsgator och vägkanter nästan lika stor som arealen av värdefulla ängs- och betesmarker. Vidare beräknas arealen av linjära infrastrukturmiljöer öka världen över under de närmaste 30 åren, men vi vet inte i vilken utsträckning dessa livsmiljöer stödjer växter- och insekternas överlevnad och spridning. I min avhandling undersökte jag om dessa linjära infrastrukturmiljöer stödjer biologisk mångfald kopplad till slåtter- och betesmarker.

Biotoper med olika kvalitet kan bidra till den biologiska mångfalden på olika sätt, till exempel genom att utöka arealen habitat så att flera arter kan samexistera eller genom att underlätta arternas rörelser mellan kvarvarande habitatfläckar. Livsmiljöer kan också skilja sig åt i kvalitet, vilket kan påverka artsammansättningen och antal individer som kan överleva och emigrera för att kolonisera flera områden i landskapet. Jag började med att undersöka om linjära infrastrukturmiljöer kan hysa samma antal gräsmarksarter som värdefulla ängs- och betesmarker. Både vägkanter och kraftledningsgator var artrika. I synnerhet kraftledningsgator kan hysa lika många arter av växter, fjärilar och humlor som värdefulla ängs- och betesmarker. Vägkanterna hyste lika många arter av humlor och växter som värdefulla ängs- och betesmarker, men det var fler fjärilsarter i vägkanter längs små grusvägar istället för vägkanter längs stora asfalterade vägar.

Att räkna antalet arter i ett område är dock inte ett uttömmande mått på dess bidrag till den biologiska mångfalden i landskapet. Därför undersökte jag om arter som förekommer i linjära infrastrukturmiljöer är samma arter som förekommer i värdefulla ängs- och betesmarker. Arter föredrar olika habitat så att vissa föredrar skogsområden, andra öppna marker, och vissa är generalister och förekommer i många habitater. Jag fann att artsammansättningen i linjära infrastrukturmiljöer i allmänhet har en stor överlapp med den i värdefulla ängs- och betesmarker, vilket indikerar att linjära infrastrukturmiljöer stödjer gräsmarkens biologiska mångfald. Jag fann emellertid skillnader i artsammansättningen mellan kraftledningsgator, vägkanter och värdefulla ängs- och betesmarker. Växt- och fjärilsarter som föredrar skogsmiljöer var vanligare i kraftledningsgator, medan växtarter som föredrar torr jord och en hög störningsgrad förekom ofta längs vägkanter. Dessa skillnader kan bero på skötseln, den angränsande livsmiljön eller jordens egenskaper. Sammantaget stödde linjära infrastrukturmiljöer en fraktion av den biologiska mångfalden i gräsmarker som finns i de värdefulla ängs- och betesmarker.

En annan öppen fråga är om linjära infrastrukturmiljöer fungerar som korridorer som underlättar spridningen av arter i landskapet. Gräsmarker som är väl kopplade till liknande livsmiljöer kan ha olika artsammansättning jämfört med isolerade gräsmarksfläckar. Isolerade gräsmarker kan ha en utarmad biologisk mångfald eftersom arter har utrotats lokalt på grund av en minskning av habitatets areal. Däremot har väl sammankopplade gräsmarksfläckar ett högre antal arter och högre antal individer. Vid första anblicken tyder den utbredda rumsliga fördelningen av kraftledningsgator och vägkanter på att gräsmarksarter lättare skulle kunna sprida sig i landskap med en stor mängd linjära infrastrukturmiljöer. Därför undersökte jag om mängden linjära infrastrukturmiljöer i landskapet påverkade artsammansättningen av växter, fjärilar och humlor i fem typer av gräsmarker. Jag fann att skillnaden i artsammansättning för dessa grupper mellan enskilda gräsmarker inte påverkades av mängden linjär infrastruktur i landskapet, vilket tyder på att de inte underlättar spridning. Det fanns dock flera växtarter i landskap med kraftledningsgator än i landskap utan. Jag fann också att alla typer av gräsmarker i genomsnitt hade fler växtarter när det fanns en kraftledningsgata som korsade landskapet. Detta indikerar att kraftledningsgator stödjer populationerna av gräsmarksarter och samtidigt berikar våra landskap med växtarter. Däremot fann jag att landskap med hög vägkanttäthet i genomsnitt hade samma antal växt-, fjärils- och humlearter som landskap med låg vägkanttäthet. Högspecialiserade växtarter som behöver till exempel näringsfattiga jordar kan förekomma på vägkanter, men i mindre utsträckning än generalister. Även om detta kan begränsa användningen av vägkanter som livsmiljö för pollinatörer, betyder det inte nödvändigtvis att det minskar deras användbarhet som korridorer. Jag fortsatte därför genom att undersöka om vägkanter användes som korridorer av blombesökande insekter.

Ett grundläggande problem med vägkanter är att även om de kan underlätta insekters rörelser, kan närliggande vägar och trafik ha motsatt effekt. Vägar kan vara barriärer genom två mekanismer: som fysiska eller beteendemässiga barriärer och genom trafikdödlighet. Dessa effekter är svåra att urskilja, eftersom de i stor utsträckning kommer att bero på hur enskilda insektsarter reagerar på förändringar i vegetationsstrukturen, deras perceptuella förmåga och deras beteende. Jag undersökte detta genom att välja 20 vägar med liknande bredd- och hastighetsgränser men varierande trafikintensitet. Längs tio av dessa vägar fanns artrika vägkanter. På dessa 20 lokaler utförde jag två olika försök. Jag undersökte om artrika vägkanter ökade frekvensen av rörelser av blombesökande insekter längs vägkanten och om trafikintensiteten påverkade frekvensen av rörelser över vägen. Jag undersökte också om skillnaderna i vägkanten och trafikintensiteten påverkade beteendet och mortalitetsrisken hos humledrottningar. Jag fann att vägkanter underlättar rörelser av blombesökande insekter och att detta inte beror på antal blommande växter i vägkanten. Med andra ord kan vägkanter fungera som korridorer oavsett blomrikedom. Men jag fann också att vägar är barriärer för insekternas rörelser oavsett antalet fordon som passerar dem. Jag hittade en större sannolikhet för att observera en död humledrottning med ökande trafikintensitet. Intressant nog minskade antalet bosökande humledrottningar dramatiskt när trafikintensiteten var hög, men bara så vid artfattiga vägkanter.

Jag visar att linjära infrastrukturmiljöer kan stödja den biologiska mångfalden kopplad till gräsmarker. Kraftledningsgator berikar landskap med växtarter och vägkanter underlättar rörelser av blombesökande insekter i landskapet. Emellertid kan deras bidrag till landskap diversitet potentiellt förbättras genom att anpassa skötseln för naturvård. Baserat på mina resultat rekommenderar jag att sköta vägkanter längs vägar med låg trafikintensitet för att gynna blomrikedom och växtdiversitet. Sverige har cirka 344 000 km vägar med en trafikintensitet mellan 0 till 2 000 fordon per dag. Men bara 10% av dem har artrika vägkanter. Om vi skötte bara en meters bredd på varje sida av vägen för naturvård skulle det leda till en ökning med ca 69 000 ha habitat för pollinatörer. Att sköta två meters bredd på varje sida skulle leda grovt till en 138 000 ha livsmiljöökning för pollinatörer. Längs vägar med hög trafik rekommenderar jag att hålla låg vegetationshöjd under våren för att undvika att locka till bosökande humledrottningar som kan dödas av trafik. Slutligen indikerar mina resultat att effekten av vägar som barriärer för specialiserade blombesökande insekter inte kommer att påverkas av naturvårdsåtgärder på vägen eller vägkanten. Därför rekommenderar jag landskapsplanerare att noggrant utvärdera vägarnas påverkan på biodiversitet och om dessa vägar kan tas bort för att återställa populationsprocesser på landskapsnivå. Att minska antalet vägar och använda arealen för att stödja den biologiska mångfalden kan också leda till en minskning av utsläppen som driver klimatförändringarna. Dessutom skulle detta innebära en ökad möjlighet för arterna att anpassa sig till ett nytt klimat genom att underlätta utbredningsskiften som hindras av det ständigt växande globala vägnätet.

Resumen de divulgación científica

El paisaje agrícola en Europa ha sufrido cambios considerables en el Siglo 20, con una pérdida enorme de hábitat para organismos que dependen de los pastizales seminaturales gestionados de manera tradicional. Éstos pastizales son unos de los hábitats más biodiversos en Europa y han sido gestionados con pastoreo y siega de baja intensidad durante largos periodos y sin el uso de fertilizantes. Hasta el comienzo del siglo 20, los humanos han creado un sistema de agricultura que ha beneficiado a la biodiversidad. Los paisajes eran abundantes en flores, apoyaban comunidades de plantas y por lo tanto los animales que dependen del polen y el néctar para sobrevivir. Sin embargo, para alcanzar la creciente demanda de comida y fibra de una población humana en aumento, los sistemas agrícolas a pequeña escala fueron convertidos en extensos monocultivos y los pastizales de baja producción fueron abandonados y desde entonces se han convertido en bosques. Como resultado de esto, las plantas que necesitan tierras con bajo contenido de nutrientes, e insectos que dependen de áreas con abundantes flores han disminuido, e incluso algunas especies se han extinguido regionalmente ¿Cómo entonces podemos asegurar la supervivencia de las especies a medida que vamos requiriendo de manera simultánea una creciente cantidad de recursos naturales para sostener una población humana en aumento?

Las oportunidades para reservar áreas naturales con el fin de beneficiar a la biodiversidad son cada vez más limitadas a medida que a nivel global los países buscan desarrollo económico y la demanda de productos agrícolas y de silvicultura aumenta. Para sobrevivir y reproducirse, los organismos necesitan desplazarse y se enfrentan con un aumento en la mortalidad en paisajes manejados de manera intensiva y carente de recursos florales. A la luz de la falta de tierra disponible para la conservación, la alternativa empleada por los conservacionistas ha sido intentar aumentar la persistencia de las especies facilitando sus movimientos entre los fragmentos de hábitat restantes. Este enfoque no solo asegura el intercambio genético entre poblaciones que de otra manera estarían aisladas, sino que también aumenta el área de hábitat, permitiendo poblaciones de mayores tamaños y reduciendo las tasas de extinción. A este respecto, las áreas improductivas que resultan como subproducto del uso humano de la tierra para transportar bienes, humanos y energía representan una oportunidad única para la conservación de la biodiversidad.

De manera inadvertida, los humanos han creado hábitats que se asemejan a los pastizales seminaturales gestionados de forma tradicional a lo largo de las infraestructuras lineales tales como carreteras, vías de tren y pasillos de líneas de energía eléctrica. Sin embargo, estas áreas no se utilizan con propósitos de conservación de la biodiversidad, sino para garantizar el transporte de bienes y personas. Por ejemplo, los pasillos de las líneas eléctricas se gestionan con el único propósito de prevenir que la vegetación intervenga con las mismas. Los bordes de la carretera se siegan con frecuencia para asegurar la visibilidad y la seguridad del tráfico.

Los hábitats a lo largo de estas infraestructuras cruzan bosques, ciudades y la tierra agrícola, y por lo tanto tienen una distribución única en nuestros paisajes. En algunos países, el área de los hábitats a lo largo de infraestructura sobrepasa el área de los pastizales seminaturales restantes. En Suecia, el área de los pastizales en los bordes de las carreteras y en los pasillos de líneas de energía eléctrica es similar el área total de los pastizales seminaturales de gestión tradicional. Es más, se proyecta que el área de los hábitats a lo largo de infraestructura aumente en los próximos 30 años, pero no se sabe si estos hábitats contribuyen a la persistencia y la dispersión de especies de plantas e insectos en el paisaje. Mi propósito con esta tesis fue explorar si estos hábitats ubicados a lo largo de las infraestructuras benefician a la biodiversidad asociada con los pastizales seminaturales.

Diferentes tipos de hábitat pueden contribuir a la biodiversidad de varias maneras, por ejemplo, aumentando el área para que más especies puedan coexistir o facilitando los movimientos de especies entre los parches restantes de hábitat. Los hábitats también pueden diferir en calidad, lo que puede impactar la identidad de las especies y el número de individuos que pueden sobrevivir y emigrar hacia el paisaje para colonizar otros fragmentos de hábitat. Comencé explorando si los hábitats a lo largo de infraestructura contenían el mismo número de especies comparado con los pastizales seminaturales de gestión tradicional, considerados de alto valor para la biodiversidad. Encontré que tanto los bordes de la carretera, así como los corredores de las líneas de energía eléctrica eran ricos en especies. En particular, los pasillos de las líneas eléctricas pueden alojar tantas especies de plantas, mariposas y abejorros como los pastizales seminaturales, pero muchas especies de mariposas prefieren los bordes de las carreteras que quedan a lo largo de pequeños caminos de grava en lugar de los bordes de las grandes carreteras pavimentadas.

Sin embargo, el número de especies en un área es difícilmente una medida exhaustiva de su contribución a la biodiversidad de escala del paisaje. Por lo tanto, continué explorando si las identidades de las especies encontradas en los hábitats a lo largo de infraestructuras eran similares a aquellas en los pastizales seminaturales gestionados de manera tradicional. Las especies tienen preferencias por hábitats en áreas boscosas, otras áreas abiertas y algunas son generalistas y ocurren en varios tipos de hábitat. Encontré que los hábitats a lo largo de infraestructura generalmente tienen un alto grado de superposición de especies comparado con los pastizales seminaturales, indicando que los hábitats de infraestructura apoyan la biodiversidad asociada con pastizales. Sin embargo, he encontrado diferencias en la composición de especies entre los pasillos de líneas de energía eléctrica, los bordes de las carreteras y los pastizales seminaturales. Estas disimilitudes pueden deberse a una gestión diferente de cada hábitat, al hábitat vecino, o a las propiedades químicas del suelo. En general, los hábitats a lo largo de infraestructura benefician sólo una parte de la biodiversidad asociada a pastizales en comparación con los pastizales seminaturales de gestión tradicional.

Otra pregunta abierta es si los hábitats a lo largo de infraestructura pueden funcionar como pasillos, facilitando la dispersión de especies a través del paisaje. Los fragmentos de pastizal que están bien conectados a hábitats similares pueden tener una composición de especies diferente en comparación con los fragmentos aislados. Los pastizales aislados tienen una biodiversidad empobrecida debido a que las especies se han extinguido localmente por una reducción del área del hábitat. En contraste, los fragmentos que están bien conectados a hábitats similares permiten la persistencia de las especies y pueden tener un número más alto de especies y en mayor abundancia. A primera vista, la distribución espacial generalizada de los pasillos de líneas eléctricas y de los bordes de las carreteras sugiere que las especies de pastizales deberían ser capaces de dispersarse más fácilmente en paisajes con mayor área de hábitats a lo largo de las infraestructuras. Por lo tanto, investigué si el área de hábitats a lo largo de las infraestructuras en el paisaje influyó la composición de especies de plantas, mariposas y abejorros en cinco tipos de hábitats de pastizales. Encontré que las diferencias en las composiciones de especies de estos grupos en cada tipo de hábitat no estaban influenciadas por el área de hábitats de infraestructura en el paisaje, sugiriendo que estos hábitats no facilitan la dispersión. Sin embargo, se encontró mayor cantidad de especies de plantas en los paisajes con pasillos de líneas de energía eléctrica que en los paisajes sin éstos. También encontré que todos los tipos de hábitats tenían en promedio mayor cantidad de especies de plantas cuando había una línea de energía eléctrica que cruzaba el paisaje. Esto indica que los pasillos de líneas de energía eléctrica apoyan las poblaciones de especies asociadas a pastizales y enriquecen nuestros paisajes con especies de plantas. Las especies de plantas altamente especializadas que necesitan, por ejemplo, suelos pobres en nutrientes pueden darse en los bordes de las carreteras, pero en una proporción menor que las generalistas. Mientras que esto puede limitar el uso de los bordes de las carreteras como hábitats para polinizadores, no significa necesariamente que esto disminuya su utilidad como pasillos que faciliten la movilidad. Por lo tanto, procedí a investigar si los bordes de las carreteras se utilizaban como pasillos por parte de los insectos que visitan flores.

Un problema fundamental con los bordes de las carreteras es que mientras éstos facilitan los movimientos de los insectos, las vías adyacentes y el tráfico pueden tener un efecto contrario. Las carreteras pueden ser barreras a través de dos mecanismos: como barreras físicas o de comportamiento y por mortalidad del tráfico. Estos efectos son difíciles de separar, ya que dependen en gran parte en cómo las especies individuales de insectos responden a los cambios en la estructura de la vegetación, a su rango perceptual, y a su comportamiento. Investigué esto seleccionando 20 carreteras con ancho y límites de velocidad similar, pero con intensidad de tráfico variable. Diez de estas vías fueron clasificadas por la Administración Sueca de Transporte como de alta diversidad. En estos 20 lugares, llevé a cabo dos experimentos. Exploré si los bordes de las vías con muchas especies de plantas con flores aumentaban la frecuencia de movimientos de insectos que visitan flores a lo largo del borde de la carretera y si la intensidad del tráfico influía en la frecuencia de los movimientos a través de la vía. También investigué si las diferencias en la diversidad de plantas con flores en el borde de la vía y la intensidad del tráfico influían en el comportamiento y el riesgo de mortalidad de los abejorros reina. Encontré que los bordes de las vías facilitan los movimientos de los insectos que visitan flores y que esto no depende del número de especies de plantas con flores en el borde de la vía. En otras palabras, todos los bordes de las vías pueden funcionar como pasillos. Sin embargo, también encontré que las carreteras son barreras a los movimientos de los insectos sin importar el número de vehículos que las crucen. Encontré una mayor probabilidad de encontrar un abejorro reina muerta en relación con un aumento en la intensidad del tráfico. De manera interesante, el número de abejorros reina en búsqueda de nido disminuyó dramáticamente cuando la intensidad del tráfico era alta, pero solamente en los bordes de las vías con baja diversidad de plantas con flores.

En conclusión, muestro que los hábitats a lo largo de infraestructura pueden apoyar la biodiversidad asociada con pastizales. Los corredores de líneas de energía eléctrica enriquecen los paisajes con especies de plantas, y los bordes de las vías facilitan los movimientos de los insectos que visitan flores a través del paisaje. Sin embargo, su contribución a la biodiversidad a escala del paisaje es limitada y puede ser potencialmente mejorada ajustando el manejo con propósitos de conservación. Con base en mis resultados, recomiendo gestionar los bordes a lo largo de las vías con baja intensidad de tráfico para mejorar la riqueza de las especies de plantas y la densidad de flores. En Suecia, aproximadamente 344000 kilómetros de vías tienen una intensidad de tráfico que va desde 0 a 2000 vehículos por día. Si solo gestionáramos el ancho de un metro en cada lado para aumentar la diversidad de plantas, esto se vería traducido en un aumento de aproximadamente 69000 hectáreas de hábitat para polinizadores. El manejo de dos metros de ancho en cada lado de la vía puede traducirse aproximadamente en un aumento de 138000 hectáreas de aumento de área de hábitat para polinizadores. A lo largo de vías con alto tráfico, recomiendo mantener una baja altura de vegetación durante la primavera para no atraer a los abejorros reina en búsqueda de nido que puedan ser matadas por el tráfico. Finalmente, mis resultados indican que el efecto de las vías como barreras de movimiento para las especies especializadas de insectos que visitan flores no será afectado por las medidas de mitigación en la vía o en el borde de la vía. Por lo tanto, recomiendo a los administradores del paisaje que evalúen cuidadosamente el efecto de las vías en la biodiversidad y si estas vías pueden ser reclamadas para la biodiversidad para restablecer los procesos a nivel del paisaje de las poblaciones. Reducir el número de vías y utilizar su área para apoyar la biodiversidad también puede traducirse en una reducción de las emisiones que conllevan al cambio climático. Más aún, reclamar las vías para la biodiversidad permitiría que las especies se puedan adaptar al nuevo clima facilitando los cambios en distribución obstaculizados por la red global de carreteras siempre en expansión.

Acknowledgements

Erik, jag kan inte hitta ord för att beskriva hur tacksam och stolt jag är över att ha haft dig som huvudhandledare. Jag skulle aldrig ha klarat mig utan dina kloka ord och råd, ditt tålamod, och dina snabba svar på mina oändliga frågor. Du hjälpte alltid mig att utveckla mina idéer, tänka kritiskt, och att vara kreativ och självständig. Du är verkligen den bästa handledare en doktorand kan ha! **Riccardo,** tack för att du guidade mig under dessa fyra år med dina skarpa kommentarer! **Jörgen,** du var alltid en hjälte! Tack för dina stödjande ord varje gång jag skickade ett manus, under våra handledarmöten, seminarier och pre-disputationer. **Åsa,** tack för alla dina kloka råd och stöd under våra handledarmöten och för att du alltid gick igenom mina manus så noggrant!

Thank you to the amazing F-corridor! **Ineta,** pspsps! I could not have gotten a better office/house neighbour. Thank you for all the times you helped me with R, for all the weird and deep conversations, and all the fun times we had in our trips and in the gym! **Chloë,** thank you for all the academic and all other kinds of support throughout the years. I will always envy your magnificent presentation skills! **Guille,** thank you for your kindness and generosity. We are all very lucky to have you around. **Eirini,** thank you for all the times we laughed together. What will the F-corridor will do without the triplets now? **Tord,** nu kanske vi kan börja springa på riktigt! **Janina,** I am glad you also tried to get Riccardo to be your field assistant. Too bad we failed. **Tarquin,** never change! **Svenja,** I hope you enjoy your PhD years as much as I did!

A special thanks to all of my field and lab assistants. **Camilla,** vilken tur jag hade när jag fick dig att jobba tillsammans med mig i fält. Det skulle inte ha

varit lika roligt utan dig! **Sofie & Maya,** stort tack för all hjälp där ute i fält! **Ged & Carol,** Tack för att ni hjälpte mig identifiera nästan 30 000 insekter. Utan er skulle jag fortfarande sitta på labbet!

Thanks to the various groups that made my life in the Ecology Centre very interesting and rewarding! Thanks to the **Biodiversity Conservation in Managed Landscapes group,** I always looked forward to our Monday meetings! **Tomas & the Landscape Ecology Network,** thanks for all the stimulating discussions. To the **eco-services** group for helping me improve my presentations. Thank you to the **Conservation Biology** unit for the interesting literature seminars and presentations.

Thank you to **all** the PhD students. I hope you can have as much fun as I did these four years.

Special thanks to everyone in the Ecology Department. **Matthieu,** Thank you for making my PhD years so much better! You are indeed my favourite customer **Sirirat,** tack för din hjälp när jag behövde köpa en galen mängd av blommor. **Uffe,** tack för din hjälp med biholkarna. **Katja,** tack för allt ditt stöd!

Mamá, Gonzalo y a toda mi familia: gracias por su apoyo y por siempre hacerme sentir como la favorita. **Fredrik,** tack för att du följde med i fält och för allt ditt stöd.

Acta Universitatis Agriculturae Sueciae

Doctoral Thesis No. 2021:63

The declining area of semi-natural grasslands is threatening the survival of plants and pollinators that depend on them. Road and electricity networks contain vast areas of grassland habitat, which will increase in the future, and constitute an opportunity for biodiversity conservation. My research showed that a considerable proportion of grassland biodiversity can be found in linear infrastructure habitats and that these habitats can contribute to landscape connectivity. However, their contribution to landscape-scale biodiversity is limited by e.g. barrier effects and mortality from traffic.

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Online publication of thesis summary: http://pub.epsilon.slu.se/

ISSN 1652-6880
ISBN (print version) 978-91-7760-803-5
ISBN (electronic version) 978-91-7760-804-2