Roadside habitats and biodiversity conservation

- a literature review with focus on vascular plants and arthropods

Tommy Lennartsson, Weronika Axelsson Linkowski, Jörgen Wissman, Anna Westin, Marcello D'Amico, Johannes Kollmann, Larissa Uhe, Svenja B. Kroeger, Giulia Bastianelli, Eveliina Kallioniemi, Knut Anders Hovstad and Hans Martin Hanslin

Swedish University of Agricultural Sciences
SLU Swedish Biodiversity Centre
CBM:s skriftserie nr 126
2023

Roadside habitats and biodiversity conservation - a literature review with focus on vascular plants and arthropods

Tommy Lennartsson, Weronika Axelsson Linkowski[a], Jörgen Wissman[a], Anna Westin; *SLU Swedish Biodiversity Centre (CBM), Swedish University of Agricultural Sciences, Sweden*

Marcello D'Amico[b]*; CIBIO-InBIO, University of Porto and University of Lisbon, Portugal / Institute of Environmental Assessment and Water Research IDAEA, Spanish National Research Council CSIC, Spain*

Johannes Kollmann, Larissa Uhe; *Technical University of Munich, Germany*

Svenja B. Kroeger, Giulia Bastianelli[b], Eveliina Kallioniemi[c], Knut Anders Hovstad[d], Hans Martin Hanslin; *Norwegian Institute of Bioeconomy Research (NIBIO), Norway*

[a] *Current affiliation: The Swedish Environmental Protection Agency, Sweden*

[b] *Current affiliation: Doñana Biological Station EBD, Spanish National Research Council CSIC, Spain*

[c] *Multiconsult, Natural Resources Trondheim, Norway*

[d] *Current affiliations: Norwegian Biodiversity Information Centre, Norway and Centre of Biodiversity Dynamics, Norwegian University of Science and Technology, Norway*

Publisher:	Swedish University of Agricultural Sciences, SLU Swedish Biodiversity Centre, Department of Urban and Rural Development
Year of publication:	2023
Place of publication:	Uppsala
Cover picture:	Bumblebee on *Knautia arvensis* in a Swedish road verge. Photo Jörgen Wissman.
Copyright:	All featured images are used with permission from the photographer.
Title of series and number:	CBM:s skriftserie 126
ISSN:	1403-6568
ISBN:	978-91-88083-41-8

Table of contents

Summary **5**

1. Introduction **8**

1.1 Why favour biodiversity in roadside habitats? 8

1.2 Aims of the review 10

1.3 Approaches 11

1.3.1 Scope and delimitations 13

2. Knowledge and literature on biodiversity in roadside habitats **15**

2.1 Systematic reviews and other reviews 15

2.1.1 Which aspects of road ecology have been studied in reviews? 16

2.2 Field studies of biodiversity in roadsides 17

2.3 Practical guidelines 19

2.3.1 Which aspects of road ecology are treated in practical guidelines? 20

2.4 Learning from other habitats 24

2.5 Source-critical aspects: Study design, context and definitions 25

2.5.1 Definitions and descriptions 25

2.5.2 Context dependence 27

2.6 How can existing knowledge be used to guide the construction and management of roads for biodiversity? 29

3. How can roadside habitats contribute to biodiversity conservation? **31**

3.1 General importance of roadside habitats for biodiversity conservation 32

3.2 Habitats for reproduction and resources for species of conservation concern 34

3.2.1 Species richness and biodiversity conservation 34

3.2.2 Linking species and habitat 37

3.2.3 Generalist, specialist, and invasive species 38

3.2.4 Plants in roadside habitats 39

3.2.5 Insects and other arthropods in roadside habitats 45

3.3 Effects on habitat fragmentation in the landscape 51

3.3.1 Increased fragmentation 51

3.3.2 Reduced fragmentation 52

3.4 Are roadside habitats ecological traps? 58

4. Key ecological factors for plants and insects in roadside habitats **61**

4.1 General ecological mechanisms for biodiversity in roadside habitats 62

4.2 Ecological conditions 64

4.2.1 Soil properties 64

4.2.2 Light and temperature conditions: Edge effects, slope, and aspect 72

4.2.3 Host plants for insects 79

4.2.4 Road size ... 82
4.3 Disturbance and other ecological processes ... 84
4.3.1 Vegetation cutting ... 86
4.3.2 Burning ... 94
4.3.3 Drought ... 95
4.3.4 Disturbance of the ground and soil ... 96
4.4 Plant competition and vegetation succession ... 99
4.4.1 Patterns and drivers of succession in roadside habitats ... 100
4.4.2 Succession and biodiversity of conservation concern ... 103
4.5 Importance of the landscape ... 104
4.5.1 Effects of adjacent habitats and land use on roadside habitats ... 105
4.5.2 Landscape species pool and ecological similarity ... 107

5. Conclusions ... 115
5.1 Knowledge and literature on biodiversity in roadside habitats ... 115
5.2 Source-critical aspects: Study design, context and definitions ... 115
5.3 How can existing knowledge be used to guide the construction and management of roads for biodiversity? ... 116
5.4 How can roadside habitats contribute to biodiversity conservation? ... 116
5.4.1 Reproduction and resource habitats for species of conservation concern ... 116
5.4.2 Effects on habitat fragmentation in the landscape ... 117
5.4.3 Are roadside habitats ecological traps? ... 118
5.5 Key ecological factors for plants and insects in roadside habitats ... 118
5.5.1 Ecological conditions ... 119
5.5.2 Disturbance and other ecological processes ... 121
5.5.3 Plant competition and vegetation succession ... 124
5.5.4 Importance of the landscape ... 124

6. Implications of the review for road construction and management ... 126
6.1 Construction of roadside habitats for biodiversity of conservation concern ... 127
6.1.1 Key results of the review ... 127
6.1.2 Interpretation of the results ... 128
6.2 Management of ground and vegetation for biodiversity of conservation concern in roadside habitats ... 129
6.2.1 Key results of the review ... 129
6.2.2 Interpretation of the results ... 130
6.3 Construction and management of roadside habitats in a landscape perspective 133
6.3.1 Key results of the review ... 133
6.3.2 Interpretation of the results ... 134

Acknowledgements ... 136

References ... 137

Summary

This review results from reading of 564 articles on biodiversity in road verges, identified using structured search strings for literature between 2008 and 2018. In addition, about 150 older articles were read, based on a large number found through reading the primary articles (‘snowballing’). We focussed on vascular plants and arthropods. These groups represent smaller organisms, which use road verges as habitat during most of their life cycle. Before starting the review, a group of researchers and practitioners compiled the needs for knowledge about biodiversity in road verges, based on a combination of ecological and practical perspectives. That compilation provided an overview of the problems surrounding roadside ecology, which was used as a framework for structuring the information from the literature review.

We summarize our conclusions about the state of knowledge for each topic separately throughout the report, and the conclusions are furthermore assembled in the final chapter of the report.

A large number of studies prove that roadside habitats can host a rich biodiversity, not least of plants and arthropods, and can contribute significantly to biodiversity conservation. The ecological values of roadsides, however, differ considerably across types of road environments, landscapes, and groups of organisms. In order to utilise the potentials of road verges for biodiversity conservation, two essential types of questions need to be answered:

- Which environmental variables make a road verge valuable for biodiversity?
- Which of these variables can be manipulated by activities for construction and maintenance, and how should they be manipulated in order to optimize road verges as habitats for biodiversity?

This review indicates that both questions are frequently addressed in a considerable body of scientific and experience-based knowledge about roadside biodiversity and management. Results found in scientific literature together with management recommendations in practical guidelines thus make a promising knowledge base for developing practices for construction and management of roadside habitats for biodiversity. The knowledge, however, mainly consists of case studies from a wide spectrum of geographical regions, landscapes, habitats, road types and management practices. Case studies therefore need to be evaluated with respect to how results and recommendations can be generalised or translated into other contexts.

Unfortunately, contrary to most other groups of habitats, an ecological framework for describing, analysing and evaluating roadside habitats is lacking. This lack of structured knowledge about roadside ecology hampers generalisation of results and a united analysis of the vast, but scattered, knowledge that exists, as well as the identification of key knowledge gaps for further research. This restricts the possibilities of translating results of roadside studies into recommendations for practical construction and management of roadsides for biodiversity conservation.

This review has generated three main types of results.

First, we have analysed evidence for how roadsides can contribute to biodiversity conservation. Roadsides can constitute species-rich habitats where also demanding and threatened species of plants and invertebrates can establish populations, and the habitats can in addition provide resources, such as nectar and pollen, for species in the landscape. Through species reproducing and foraging in roadside habitats roads can contribute to species' dispersal in the landscape and thereby to reducing habitat fragmentation.

Second, the review has identified a number of interacting ecological variables, which together account for these conservation values by shaping various roadside habitats with their biodiversity. These variables can be grouped into:

- *Ecological conditions* (soil structure, moisture, pH, nutrients, salt and other pollutants; light and temperature in relation to slope, aspect and forest edges; host plants for insects; road size).
- *Ecological processes* (vegetation cutting including frequency, timing and biomass removal; burning; drought episodes; disturbance to the ground surface and soil).
- *Plant competition and vegetation succession* in relation to management.
- *Habitats and species pool of current and historical landscapes*.

The overall literature dealing with all these topics is too voluminous to be treated by a single review like this one, and we conclude that it is necessary to perform more focused reviews of specific topics separately.

Our results thus provide a list of important environmental variables and their biodiversity effects, as well as a brief structure for the relationships between variables. We believe that by taking these results as a starting point, and complementing it by focused knowledge compilations and syntheses of certain topics, it is possible to come considerably further towards a unified framework of roadside ecology, including management.

The focused reviews need to comprise a wider range of literature than roadside studies, by including studies from other habitats as well as studies of single species. Since many basic ecological principles apply to both roadside habitats and other comparable habitats, important information may be found in a wide range of studies, for example studies of grassland ecology, vegetation management, disturbance effects and vegetation change. Studies of single species are among the best sources of information for understanding links between species and their environment, and such links are crucial for describing habitats and for identifying suitable management practices. Systematic approaches, such as meta-analyses, can be used if there are enough studies within a topic that are performed within the same ecological context.

Third, we have interpreted the key results in an applied perspective, in particular their implications for construction and maintenance of road verges.

Figure 1. Flower-rich road verge, Gräsö island, province of Uppland, Sweden. Photo Jörgen Wissman.

1. Introduction

1.1 Why favour biodiversity in roadside habitats?

Roadside habitats and other transportation corridors constitute large areas in most landscapes. For example, about 1% of the land area in the USA is covered by roads and roadsides, and approximately 20% of the land is ecologically affected, either directly or indirectly, by the public road system (Forman 2000). Roads and transport infrastructure impose several types of negative impacts on landscapes and biodiversity, such as habitat destruction and fragmentation, barriers for animals, roadkill mortality, and pollution. The concept of *road ecology* has been developed, in which roads are being evaluated as part of the ecology of entire landscapes, including also indirect effects and other complex ecological impacts of roads (see e.g. Coffin 2007).

Applied road ecology often focus on mitigation of negative impacts of roads on biodiversity (e.g. van der Ree et al. 2015), but road ecology also includes positive effects of roads on biodiversity. Such effects rely on a different set of ecological mechanisms compared to negative effects. For example, road verges may serve as dispersal corridors for some organisms instead of being barriers, and they may provide important habitats and favour populations, instead of causing habitat loss and increased mortality. The positive effects of road verges and other infrastructure habitats for biodiversity have been studied since the 1970's (Way 1977), and have been increasingly acknowledged during the last decades, both in biodiversity conservation and infrastructure management.

If road verges can provide important habitats for biodiversity, they hold a great potential to contribute to biodiversity conservation for both ecological and practical-economic reasons. For example, in New England, USA, sandplain grasslands are of high conservation priority because they support a wealth of vanishing species (Brown and Sawyer 2012). These habitats are expensive to conserve because repeated disturbances are necessary in order to prevent natural succession to woodland. Roadsides in sandplain areas are regularly mowed or otherwise disturbed, with the cost being justified through the importance of human safety. While roadsides will not replace the need for high-quality conservation grasslands, they can supplement sandplain habitats at minimal cost. Even without special efforts to help improving roadsides, the roadside flora in the studied region consisted of up to 45% of native plant species, including rare and specialist species (Brown and Sawyer 2012).

Figure 2. Signage for conservation roadsides in Minnesota, USA. Photo Jan Olof Helldin.

Another example of practical-economic motives for a conservation interest in road verges is provided by Vasconcelos et al. (2014), who studied plant diversity in Brazilian *Cerrado* wooded savanna – a hotspot in biodiversity conservation. They found that the number of species was lower in road corridors through the savanna compared to natural vegetation in reserves, especially the number of forest species and *Cerrado* specialist species. However, 70% of the 108 species found in the savanna also occurred in the roadsides. Considering the continuous pressure on the *Cerrado* biome from different types of land use, which leads to the decline of many species, and considering the large total area of road corridors, the authors concluded that roadside habitats may be important for preserving

Cerrado biodiversity, e.g. as stepping stone and as reservoir for plant genetic diversity.

These, and several more examples show that the large vegetated areas of the world's transport infrastructure has a great potential to be not only constructions for transportation, but also to contribute to biodiversity and thus to multi-functionality of land use.

The conservation of biodiversity follows several national and international agreements but is not only motivated by (inter)national laws and agreements, but also by practical and economic advantages. In Indiana, USA, the use of native grasses and forbs along roads has reduced management costs due to the native species' higher tolerance to heat and other vegetation-damaging factors, compared to the more commonly used imported species (Kraushar 2011).

1.2 Aims of the review

This study, which was a part of the CEDR-funded international project *EPIC-roads*[1], summarises literature on how roads can contribute to biodiversity conservation. It is based on the assumption that even though a road has many negative effects on biodiversity, there are nevertheless several options for favouring certain species groups by designing proper methods for road construction and maintenance. In order to prioritise, plan, design and perform such activities for promoting biodiversity in road verges, it is essential to compile the existing knowledge about how road verges may contribute to biodiversity conservation.

Three questions are particularly important:

1. In what ways can road verges favour biodiversity, i.e. which ecological values for biodiversity can different types of road verges provide?
2. Which ecological factors, e.g. environmental conditions at different scales, natural and anthropogenic processes (such as vegetation management), account for these values?
3. How important are different types of road verges for biodiversity conservation, in relation to other habitats and conservation measures, and for different species groups? The answer to this question is fundamental for conservation policy, for example regarding responsibilities of different actors and cost-benefit considerations.

This study aims to provide an overview of such knowledge based on reviewed literature. We focus on the first two questions, while the third is treated more briefly due to lack of information.

[1] https://www.cedr.eu/peb-research-call-2016-biodiversity

Figure 3. Small blue Cupido minimus. *Photo Eveliina Kallioniemi.*

1.3 Approaches

As a first step in the project, a database[2] of recent ('white' and 'grey') literature was compiled based on structured search strings. The references were evaluated and sorted by relevance for the project (reported in Hanslin et al. 2019). In this review all high-priority publications in the database were read in detail, together with some other important publications cited (thus found through 'snowballing'). Through the snowballing approach we included some of the older literature.

Guidelines and other practical publications and documents were not included in our systematic literature search, mainly because they are, despite a few notable exceptions, not accounting for the knowledge background to conclusions and recommendations. That said, many practical guidelines for roadside management, not the least the ones addressing biodiversity, are impressive works, containing a wealth of information from both published studies and best practice experience, together with creative and thoughtful recommendations for road construction and management. To illustrate briefly how practical guidelines treat roadside biodiversity, we searched for and read some 50 guideline documents in English, Dutch, German, Polish, Romanian and the Scandinavian languages, and discussed them in section 2.3.

Several attempts have been made to compile and synthesize literature on biodiversity in road verges. We found three systematic reviews that have used structured search strings and strict criteria for the quality of the studies reviewed. Such reviews make conclusions based on sufficient numbers of studies, often using meta-analysis methods.

Since all such systematic reviews conclude that there are rarely sufficient numbers of studies for answering specific questions about road ecology, the

[2] Available at https://www.cedr.eu/docs/view/61b9f489603f9-en

EPIC-roads project aimed at complementing the existing systematic reviews with an alternative approach. A stepwise approach (summarised in Fig. x) was used to evaluate knowledge and knowledge gaps regarding the three main questions outlined above.

- **Step 1: Compilation of needs for knowledge**. A list of important types of knowledge, problems and known knowledge gaps was prepared through discussions within the *EPIC-roads* research group as well as with practitioners at the Swedish Transport Administration. The list is thus based on the researchers' knowledge about road and grassland ecology and the state of the art of research, as well as on practitioners' experiences with road construction and management,
- **Step 2: Review structure**. The list of knowledge needs was transformed into specific topics, serving both as a structure for the review (which types of knowledge to search for) and a preliminary outline for a report (report headings).
- **Step 3: Literature review**. All references assigned to the highest priority in the *EPIC-roads* literature database (see above) was read as primary references, and, if being relevant, included in the review. A reasonable number of other important studies, cited by the primary ones, was also read, together with some 'cited by the cited' (i.e. 'snowballing'). No pre-set criteria for type of study, number of replicates etc. were used, but all literature was evaluated and cited using normal source-critical evaluation. The headlines of the report outline were thus filled with relevant pieces of knowledge to various degrees. As the review gradually drew a picture of what knowledge is available, the structure for the review and the report outline (Step 2) was revised, mainly in terms of splitting some topics/headlines and merging others. Search strings and databases used in the literature search are described in Hanslin et al. (2019).
- **Step 4: Synthesis**. The available knowledge, based on the review, was evaluated in relation to the need for knowledge identified in Step 1; we draw conclusions about the state of knowledge separately for each topic in this report.
- **Step 5: Implications for practice.** Based on the synthesis, we interpreted the main findings in an applied perspective. The conclusions are presented in three packages: (1) Construction of roadside habitats for biodiversity of conservation concern; (2) Management of ground and vegetation for biodiversity of conservation concern in roadside habitats; (3) Construction and management of roadside habitats in a landscape perspective.

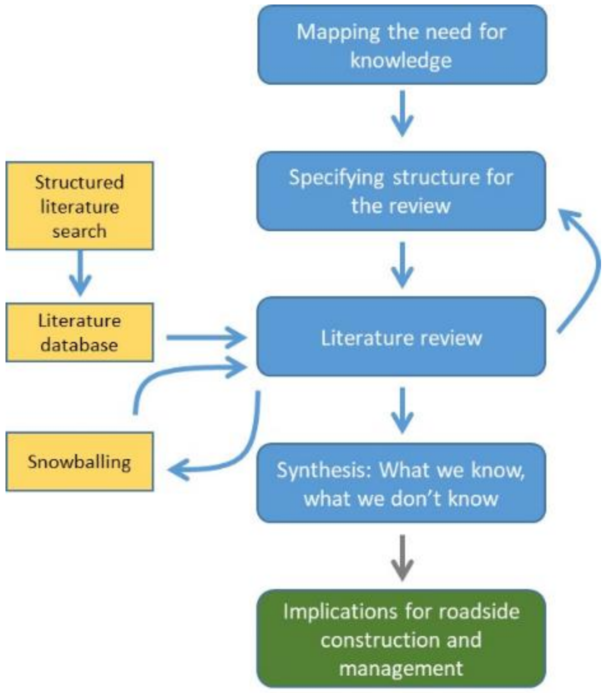

Figure 4. The review procedure

1.3.1 Scope and delimitations

This review thus focuses on how road verges may favour biodiversity, and which ecological key factors account for these values. We did not review literature on negative impacts of roads, such as studies of barrier effects, traffic mortality of vertebrates, sound or light pollution, or literature on mitigation of such effects. We therefore do not attempt to weigh positive and negative effects against each other.

The review focuses on road verges as habitats and resources for biodiversity, where 'road verge' always includes the constructed slopes, ditches and embankments close to the road. In some countries, the road corridor is wider and includes a less disturbed zone further from the road; such areas may be part of the reviewed studies.

The following issues were not reviewed:

- The problem of invasive species was subject to another CEDR-funded project, *ControlinRoad*[3], and is only treated briefly here. It should be noted, however, that the establishment of invasive plant species fundamentally changes conditions for biodiversity and the possibilities to manage roadsides for biodiversity. For example, management costs will increase and in many cases

[3] http://www.controlinroad.org/

species richness and conservation values will be strongly reduced in spite of measures for eradicating invasive species, e.g., modified (intensified) management.

- We excluded the management of trees, avenues (tree rows), and hedgerows along roads, and thus only briefly addressed biodiversity connected to these features.
- We excluded streets and roads in towns and cities.
- We did not analyse how interactions between positive and negative effects of roads on different groups of organisms may be important for biodiversity in roadside habitats, for example whether the absence of some species (such as predators or pollinators) may influence the presence or performance of other species.

2. Knowledge and literature on biodiversity in roadside habitats

2.1 Systematic reviews and other reviews

A systematic review retrieves studies of certain questions that are performed in a way that makes them comparable with each other. The process of retrieval and comparison is carefully planned and documented. Biodiversity in roadside habitats has been subject to some systematic reviews, in which only studies fulfilling certain criteria were included. The reviews of roadside biodiversity found several thousand articles through the use of search strings. Most articles were excluded except for a few hundred, which were judged relevant based on the chosen selection criteria (Bernes et al. 2017; Jakobsson et al. 2018; Villemey et al. 2018). The reviews are often combined with meta-analyses in order to detect patterns and trends among studies. Meta-analyses are only possible for questions that have been subject to a high enough number of similar studies presenting adequate data that allow extraction of effect sizes and variance measures.

A common result of systematic reviews is that the number of studies of any specific question is usually too low to allow secure conclusions using the systematic approach. For example, Villemey et al. (2018) performed a systematic review of the importance of road verges as habitat and dispersal corridors for insects. Based on their systematic review of 91 articles and 104 studies they concluded that a major knowledge gap remains regarding the potential of linear transportation infrastructure verges to serve as corridors for insects, and they encourage more research on this topic. Regarding road verges as habitats, the results were slightly clearer, but the number of studies addressing specific questions, for example the effect of certain management methods or the effect on certain species groups, was low.

Bernes et al. (2017) addressed the question of how biodiversity and dispersal of species in road verges are affected by management. They identified 301 studies in 207 articles and proceeded with a review of the more specific question of how roadside management affects the diversity of vascular plants and invertebrates, using 54 studies (Jakobsson et al. 2018). They found some consistent effects of mowing (vegetation cutting) on plant diversity, but for invertebrates, the number of studies was too low for reliable conclusions.

A number of other reviews have been performed, addressing specific questions or aiming at highlighting the importance of roadside habitats for biodiversity in general (e.g. Forman and Alexander 1998; Spellerberg 1998; Coffin 2007; Fahrig and Rytwinski 2009; Holderegger and di Giulio 2010; Muñoz et al. 2015; Spooner

2015; O'Sullivan et al. 2017; Gardiner et al. 2018). Such reviews interpret evidence from a wider range of studies than the systematic reviews, but with less transparency regarding search strings and selection criteria.

A number of more or less thorough reviews have been performed for applied purposes, often as a background to practical guidelines. Some focus on specific aspects of roadside biodiversity, for example pollinators (e.g. Hopwood 2010; Galea et al. 2016). Other reviews comprise a wide range of ecological and practical aspects on road administration. One example is a review published by the Scottish Natural Heritage (Hambrey Consulting 2013), which, in addition to reviewing a number of practical guidelines and recommendations, covers both ecological values of road verges, a brief ecological background to the values, and Scottish policies for roadside management. Although the review is less thorough regarding ecological literature, it places ecological knowledge in an applied perspective that we find considerably more convincing than most other knowledge compilations.

2.1.1 Which aspects of road ecology have been studied in reviews?

In a review of ecological effects of roads, mainly in Australia and the Netherlands (Forman and Alexander 1998), the authors clustered the studies into five major topics, (a) roadsides and adjacent strips (roadside habitats), (b) road and vehicle effects on populations, (c) water, sediments, chemicals and streams, (d) the road network (landscape ecology), and (e) transportation policy and planning.

A Swedish organisation for evidence-based conservation (*Mistra EviEM*) performed two systematic reviews of how biodiversity and dispersal (Bernes et al. 2017) and the diversity of vascular plants and invertebrates (Jakobsson et al. 2018) are influenced by various forms of roadside management. The 2017 review identified 207 articles, and the 2018 review 54 studies, that met the strict eligibility criteria. A majority of the studies were conducted in North America, and most of the remaining ones were carried out in Europe. Of the 207 articles, more than half were published as grey literature, i.e. reports from agencies and consultants. In the 2017 report, the most studied (defined as >10 studies) types of management activities were herbicide use (86 studies), sowing (86 studies), mowing (85 studies), control of invasive species (61 studies), mulching or compost application (41 studies), fertilisation (39 studies), soil cultivation (23 studies), liming (18 studies), burning (14 studies), and top soiling and erosion control (11 studies each).

Although the current review has focussed on roads and biodiversity, we have come across a number of studies that have included other values of roads than positive effects on biodiversity. Roads may provide a range of overlapping and sometimes competing values, including anthropocentric ones. Spooner (2015) listed the following values associated with minor rural roadsides in Australia:

- Connectivity – prime function of roads for humans, dispersal routes for species, but causing wildlife collisions.
- Cultural heritage – historic roads and routes, historic road heritage such as bridges and memorials, location of old managed trees etc.
- Ecotourism values – routes to explore places and landscapes.
- Environmental values – refuge for threatened species and ecosystems, seed source for revegetation activities, provision of ecosystem services such as pollination.
- Infrastructure corridors – corridor for water supply, electricity, gas and telecommunication.
- Recreational values – sightseeing, hiking, bike and horse riding.
- Resources – source for firewood, gravel, rocks, and stock grazing for fodder,
- Roadside amenity – aesthetic values of roadsides.
- Transport and road safety.

Studies of ecosystem services related to roads are especially common for roads in urbanised areas. For example, roads may provide connectivity between urban greenspaces, and, due to their proximity to human activities, several other ecosystem services (see review by O´Sullivan et al. 2017).

Villemey et al. (2018) carried out a systematic review of the corridor function of road verges and other infrastructure habitats.

2.2 Field studies of biodiversity in roadsides

Since roadsides constitute corridors of habitat that may be more or less ecologically different from the surrounding landscape, they offer opportunities to study the effects of several environmental variables on several response variables of biodiversity. A structured search for literature on road verge ecology in this *EPIC-Roads* project (Hanslin et al. 2019), found 473 recent papers (2008–2018) of high relevance. These studies could be sorted into the categories (a) edge effects, (b) road verges as habitats, (c) dispersal in road verges, (d) road verges and landscape ecology/fragmentation, (e) activities for road construction and maintenance, and (f) indirect effects of roads on biodiversity. Many studies thus focus on the roadside habitats per se, whereas others compare roadside habitats with surrounding landscapes, or focus on the transition zone between roadsides and other habitats. Studies of how roads affect biodiversity in the surrounding landscape have mainly focussed on mobile vertebrates, for example by studying fragmentation effects on larger mammals, and noise effects on birds. There is a pronounced deficit of knowledge about how roads may influence invertebrates in the landscape positively or negatively.

One clear result of this *EPIC-roads* review, as well as of many other reviews, is a scarcity of studies that follow a change over time, for example, the result of a management practice. Of the 91 studies reviewed by Villemey et al. (2018) all but three used experiment-control design, not before-after design (or before-after-control design).

Figure 5. Roadside biodiversity field studies. Photo Anna Westin.

Road constructions and management can be seen as a large-scale ongoing experiment that offers several opportunities to study various applied as well as theoretical questions. Consequently, a number of studies have followed roadside habitats over time or performed single data collection some time after an intervention in the road environment. Also, more controlled experiments have been performed, usually comparing different treatments, among which different types of vegetation management and vegetation establishment are the most common (see, e.g., the systematic reviews by Bernes et al. 2017 and Jakobsson et al. 2018).

Field studies of various groups of organisms in relation to various aspects of road impacts constitute the major body of scientific literature on roadside biodiversity. We discuss such studies in detail in chapters 4 and 5, where we account for both response variables (such as diversity, species richness, and population viability) and the major influencing environmental variables.

We conclude that the collated wealth of examples of biodiversity in roadside habitats provide conclusive evidence that roadside habitats can and currently do contribute to the conservation of several groups of species. However, the studies are scattered over a wide range of organism groups, road verge types, regions, and landscapes, which makes it difficult to find guidance on how to manage specific types of roadside habitats or how to favour specific groups of organisms. This calls for a new direction in roadside habitat research, addressing specific conservation problems (e.g. the conservation of certain groups of threatened species). Such studies are necessary complements to all studies that describe patterns in distribution and abundance of biodiversity in roadsides and surrounding landscapes.

2.3 Practical guidelines

All road administrators build and maintain roads according to certain directives, recommendations and guidelines. Those have been developed by different actors in road administration, and constitute documents that can be found on the internet, having varying publication status and legal status. In recent years, many publications and websites have also been produced that address both road managers and the public, informing about the biodiversity values of roadside habitats (Pro Natura 2015, 2017, see also Czech butterfly highways: www.motylidalnice.cz).

Most practical guidelines and information brochures have in common that they do not account for the sources of knowledge on which their recommendations are based (but see, for example, van Eupen and Knaapen 2000; Hopwood 2010; Galea et al. 2016). This is also the case for many guidelines that clearly contain considerable compilation and synthesis of literature and other existing knowledge (e.g. Heemsbergen et al. 1989; Johnson 2008). This by no means implies that the recommendations are not to be trusted, but it somewhat limits a wider use of the guidelines, for three reasons in particular: (i) it is difficult to evaluate to what extent recommendations developed for one context may be applicable in a wider context, for example in other regions or landscapes; (ii) it is difficult to explain differences and similarities between guidelines, for example whether differences are due to ecological, practical or legal prerequisites for road maintenance; (iii) it is difficult to evaluate recommendations that seem to contradict or have unclear relation to current ecological knowledge. Compare, for example, the text about soil nutrients in 4.2.1 with Trafikverket (2021), Anderson et al. (2011) and Mainroads Western Australia (2016) regarding establishing vegetation on new roadsides by re-using topsoil (with seed bank).

For this reason, we have only occasionally referred to practical guidelines in this knowledge compilation.

It should be noted that also other literature on practical conservation management, especially of grassland habitats, has a great potential to inform roadside management (e.g. van de Poel and Zehm 2014).

We conclude that many of the existing guidelines are based on considerable practical experience of road management and constitute examples of best practice recommendations. This type of experience-based knowledge should make an important complement to the rather restricted scientific support, but since such underlying knowledge is rarely presented, it gains less attention than it deserves. A more thorough compilation and evaluation of recommendations from guidelines than what has been possible here, can be recommended.

2.3.1 Which aspects of road ecology are treated in practical guidelines?

Biodiversity conservation and roadside management

It is common that recommendations for roadside management are for other purposes than favouring biodiversity, and can sometimes be expected to have more or less adverse effects on biodiversity. Examples of such measures are recommendations for intense cutting, mulching, and fertilisation (e.g. Johnson 2008).

There are, however, entire guideline documents that address biodiversity and conservation. In addition, other guidelines may also contain certain recommendations for promoting biodiversity.

The most common focus of research on biodiversity in roadsides seems to be establishment and management of species-rich vegetation, preferably one that reflects the local flora (e.g. Heemsbergen et al. 1989; Sjölund et al. 1999; Cotswolds Conservation Board 2015; Landschap Overijssel undated; Bromley et al. 2019; Parkinson et al. 2019). van Eupen and Knaapen (2000) tries to relate the composition and structure of vegetation to habitat and corridor functions for animals.

Vegetation management

Vegetation management seems to be by far the most common maintenance measure in the guidelines. Such guidelines usually include recommendations for cutting (mowing) time, often for the number of annual cuttings, and sometimes for cutting height or frequency over a number of years.

If biodiversity is mentioned as a goal for adapted cutting regimes, increased flower richness and plant species richness are common targets. Another common target is establishment of native vegetation, e.g. prairie vegetation (Johnson 2008), heathland vegetation (Heemsbergen et al. 1989), or xerothermic habitats (Murariu et al. 2019). Guidelines also address favouring of ground-nesting birds (Johnson 2008) and pollinators (Hopwood 2010; van Rooij et al. 2014; Galea et al. 2016; Fox et al. 2019).

Figure 6. Standard roadside vegetation cutting. Grönbo, province of Västmanland, Sweden. Photo Jan Olof Helldin.

Biodiversity-oriented recommendations always aim at highlighting that cutting for biodiversity purposes differs from “standard” cutting, e.g. for safety purposes. Some guidelines recommend field surveys to identify target vegetation types or native plants, and ways to adapt the timing and frequency of mowing to the phenology and species composition, of the local vegetation (e.g. Heemsbergen et al. 1989; Rijkswaterstaat 2008). For prairie roadsides, prescribed burning is sometimes recommended (Johnson 2008).

Practical guides for vegetation management focus either on roadsides that have already been identified as particularly important for biodiversity, or on all roads, thereby including several more motives for vegetation management. The latter may place biodiversity-oriented management in an integrated program for vegetation management (Walvatne et al. 1997; Johnson 2008; Brandt et al. 2015). Vegetation management for biodiversity always needs to be adapted to the local flora (and sometimes fauna), but integrated management plans may also include other aspects of vegetation management such as safety, economy, aesthetics, drainage, soil control, weed control, wildlife collision risk, and living snow fences. Adaptation may in addition consider local policy, cultural heritage, or public acceptance (Walvatne et al. 1997).

Vegetation establishment

In some guidelines, vegetation establishment is addressed, either specifically or as part of vegetation management in broad sense. Some guidelines present biodiversity motives for vegetation establishment, but many do not.

Most guidelines suggest active establishment of new vegetation, through sowing, planting etc. Such recommendations sometimes stress that the choice of vegetation is the result of both ecology/conservation and more anthropocentric considerations (Völker et al. undated). The use of native species in vegetation establishment is usually recommended, although not necessarily for conservation purposes, but for vegetation hardiness and reduced maintenance costs (Johnson 2008), or aesthetic reasons (Anderson et al. 2011). Guidelines recommending the use of native or local plant material are aware of the difficulties and costs of accessing seeds, and sometimes suggest harvesting from existing plant stands. In the USA there is a commercial interest in producing seeds of native prairie vegetation (Johnson 2008). In some guidelines from snowy landscapes, salt-tolerant species are recommended for vegetation establishment. Chemical mitigation of salt effects has also been proposed (e.g. by spreading gypsum on the ground, Johnson 2008). If the guideline addresses replacement of existing roadside vegetation, for example with native prairie flora, eradication of the vegetation prior to sowing is often recommended, e.g. by using glyphosates or cultivation in combination with burning and cutting (Johnson 2008).

Few practical reports (and research articles) address how native, protected or red-listed plants can be rescued when building a road and promoted in the new roadside habitats. One example of a particularly ambitious project is the building of the A73 road south in the Netherlands (Raemakers and Faasen 2004; van Grinsveen 2016). Such re-establishment of vegetation or target species can be based on sowing or planting. Raemakers and Faasen (2004) discuss briefly these two methods and recommend a combination of both, or planting of perennials and sowing of annuals. Natural revegetation through spontaneous colonisation and succession is sometimes recommended instead of active sowing or planting. Natural colonisation and succession is particularly recommended for creating dry habitats (e.g. Sjölund et al. 1999; Bromley et al. 2019; Murariu et al. 2019).

The reuse of local topsoil is sometimes recommended, in order to take advantage of the seed bank in the vegetation that was present prior to road construction. Some guidelines are explicitly addressing biodiversity in relation to topsoil reuse (e.g. Trafikverket 2021), some are not (e.g. Mainroads Western Australia 2016).

Figure 7. Experimental establishment of meadow flora on recently disturbed ground by sowing collected seeds and by placing hay from the meadow on the roadside. Hällabrottet, province of Närke, Sweden. Photo Tommy Lennartsson.

Roadsides structure and landscape context

With the exception of soil conditions for vegetation establishment, the physical structure of the roadsides (slope inclination, surface structure etc.) is only briefly discussed in most guidelines. However, the potential to create biodiversity-rich habitats such as rock habitats, xerothermic communities, and shrub habitats when making excavations, embankments and terraces, is suggested by Murariu et al. (2019, ch. 4).

Guidelines addressing mobile organisms such as pollinators sometimes stress the importance of preserving habitats and resources adjacent to the road, and of ecologically supporting such core areas in the roadside environment (e.g. Fox et al. 2019).

2.4 Learning from other habitats

Since many types of roadsides can be considered grassland habitats, studies in grassland habitats other than road verges can also contribute to the knowledge of roadside ecology. Runesson (2012) and Svensson (2013) reviewed literature on the relationships between roadside management methods and biodiversity (mainly vascular plants), including studies in a wider range of grasslands, for example Natura 2000 habitats. The focus of both reviews was to inform the management of Swedish road verges, but literature from all countries and regions was reviewed.

Figure 8. Calcareous semi-natural pastures are among the most species-rich grassland types. Knowledge about pasture species' responses to various environmental variables can be used to develop methods for roadside management that favour biodiversity. Byxelkrok, province of Öland, Sweden. Photo Tommy Lennartsson.

Svensson (2013) concluded based on about 400 articles, including studies of pastures and hay-meadows, that removal of mown vegetation is essential for developing and maintaining plant species richness. The vegetation in specific meadows has developed in response to the local mowing regime, e.g. frequency and annual timing of mowing (cf. also Lennartsson and Westin 2019). It is likely that such components of the mowing are important for vegetation composition and for plant species of conservation concern also in mown road verges, and the frequency and timing of roadside mowing was therefore recommended to be adapted to the local vegetation.

Runesson (2012) found similar results, and concluded that it is important to identify different types of road verges based on the vegetation and apply specific mowing regimes on each. She also noted, based on roadside and restoration literature, that more is known about how to remove unwanted species and to improve species-poor vegetation by intense mowing, than about how to preserve species of conservation concern and species-rich vegetation.

2.5 Source-critical aspects: Study design, context and definitions

2.5.1 Definitions and descriptions

All conclusions of a study about the importance of road verges for biodiversity need to be evaluated against the background of the question in focus, the methods and definitions used, the study region etc. We consider the following aspects to be particularly important:

- **The definition of the roadside habitat.** The terms road verge and roadside are both used somewhat differently in different studies. Usually, they refer to a rather narrow strip along the road; comprising disturbed areas that are part of the road construction, from the edge of the road pavement via the slope of the road body and the ditch, to the entire outer slope (see e.g. Chaudron et al. 2016a). Basically, this is the definition of roadside habitat used in our review.

  In some studies, however, the road verge, or roadside, is defined as a wider strip, for example, the corridor of land that is the property of the road owner. For example, in Australia the state road reserve consists of three zones: the road, the disturbed area directly adjacent to the road, and the non-disturbed area further away from the road (Palfi et al. 2017). The Australian road reserves were often surveyed rather widely to allow for, e.g., the extraction of construction material along the stretch (Spooner 2005). Similarly, the network of larger roads in Brazil includes rather wide strips of land along the roads, *faixas de dominio* (Allem 1997).

When the definition includes wider corridors, the roadside may contain woodland vegetation (e.g. Vasconcelos et al. 2014). This is rarely the case when a more narrow definition applies, although narrow road verges may also have avenues (tree rows) or single trees.

- **Description of landscape type.** As discussed under several headings in this report, roads can contribute more to biodiversity conservation in landscapes where a larger proportion of the species pool is adapted to disturbances similar to those occurring in roadsides (see further 4.5.2). Thus, the importance of the roadside habitat will depend on what habitat it is compared with, and which species group is the focus of the study. Through the choice of such comparators, in the majority of cases it is probably possible to prove high values and positive effects of a roadside, as well as negative effects and low values of the same roadside.

- **Description of verge vegetation.** Different groups of organisms, and different types of roadside habitats, depend on different types and combinations of physical disturbances to the ground and to the field layer vegetation. Studies of disturbances that fit the local biodiversity can therefore be expected to show positive results, while studies of other disturbances may show be negative for effects on biodiversity. Typical groups of studied roadside habitats are species-rich, low vegetation (favoured by moderate mowing intensity and not too frequent soil disturbance), bare sand (favoured by frequent topsoil disturbance and low-intense mowing), and nutrient-rich vegetation (favoured by intense mowing that reduces competition).

  The articles reviewed are in many cases surprisingly vague about the type of vegetation and habitat that is studied, which makes generalisation and interpretation difficult. For example, a systematic review of plants and insects in relation to management methods by Jakobsson et al. (2018), found evidence for intense mowing (i.e. mowing twice a year) being more favourable for plant biodiversity than less frequent mowing. Many single studies, however, indicate that for several types of species-rich vegetation, mowing should not be more frequent than once a year (e.g. reviews by Runesson 2012 and Svensson 2013). This suggests a bias towards nutrient-rich vegetation among the studies in the systematic review. Without clear descriptions of the vegetation type however, such biases are difficult to reveal.

Figure 9. A certain mowing regime will show different effects on roadside plant species richness depending on productivity of the vegetation. Upper photo: nutrient-rich roadside with low species richness, Närtuna, province of Uppland, Sweden; lower photo: dry roadside, poor in nutrients but rich in species, Vedum, province of Västergötland, Sweden. Photos Tommy Lennartsson.

2.5.2 Context dependence

Negative and positive effects of roads on biodiversity are due to different ecological mechanisms and often apply to different groups of organisms. It is therefore difficult and conceptually complicated to estimate net effects of roads on biodiversity and to what extent road verges of high ecological quality can compensate for their negative effects. This and most other reviews stress that results regarding positive versus negative effects of roads largely depend on what is studied. The choice of study species and habitat against which the roadside is compared appears to be particularly important.

From this review, we conclude that the results of biodiversity studies in roadside habitats are highly context dependent. Results therefore need to be interpreted considering which organism group, which environmental variable (including management intervention), which type of roadside habitat, and which landscape have been studied. Of these, in particular the importance of the type of roadside habitat may have been overlooked, because of lack of an overall structure for how to classify roadside habitats, and lack of knowledge about their ecology.

Studying positive or negative environmental factors

Studies of positive and negative effects, respectively, of roadside habitats usually investigate different ecological mechanisms. For example, Kollmann et al. (*in press*) found 131 studies reporting negative effects on biodiversity of, in particular, collision mortality, intense traffic, noise, chemical contamination, edge effects and barrier effects. Another 111 studies reported positive effects of different types of roadside habitats, including disturbed ground, managed vegetation, and hedges and other edge habitats, food resources, and corridor function. Only 13 studies considered both positive and negative effects.

The division between types of studies has important implications for how to interpret the overall effect of roadside habitats, for example on population growth or conservation status of species. By studying roadside ecological factors that are usually positive for populations, only the positive effects are discovered. Such effects may however be outweighed by other factors that influence populations negatively. Conversely, if only negative factors are studied, positive effects of other roadside conditions, which may enhance overall population viability, may be overlooked. Furthermore, many examples of negative effects of roads on biodiversity are unrelated to roadside habitats. For example, collision mortality may occur among animals that cross the road independently of the ecological status of road verges.

Comparing roadside habitats to other habitats

As will be discussed in the chapter on landscape effects on roadside biodiversity, the capacity of a road verge to host species from the surrounding habitats largely depends on how similar the roadside disturbance regime is to natural or semi-natural disturbance in the surrounding habitats. Both natural (e.g. fire and flooding) and semi-natural disturbance (e.g. mowing and domestic grazing) are known to have formed numerous species-rich habitats across Europe. Other, more intense human disturbance, such as modern agriculture and forestry often result in species-poor ecosystems, and are often considered threats to biodiversity. This implies that a roadside habitat will show higher or lower species richness than another habitat depending on both the type of other habitat and the choice of target species group.

Clearly, if species that are sensitive to disturbance are chosen, roads will usually have lower biodiversity than surrounding, less disturbed habitats, for example most forest types (e.g. Knapp et al. 2013). If instead species favoured by disturbance are chosen, the roadside habitats can be expected to host a high richness of such species. The importance of the roadside habitat will then depend on whether it is compared with other disturbance-formed habitats, and the quality of those habitats. These types of relationships are noticed by several reviews, for example by Villemey et al. (2018), who found it particularly challenging to analyse the importance of road verges for beetles, which is a heterogeneous group with many species sensitive to and other species favoured by ecological disturbance.

2.6 How can existing knowledge be used to guide the construction and management of roads for biodiversity?

The construction and management of roadsides for biodiversity requires rather specific knowledge about effects of various practices on biodiversity. When performing this review and comparing it with other reviews, we made some conclusions regarding how to best extract such knowledge from literature on biodiversity in roadside habitats.

Systematic reviews, which use strict selection criteria, rarely find enough studies of specific questions to enable reliable answers. For example, Jakobsson et al. (2018) found very few studies that had investigated the same group of invertebrates exposed to the same management intervention. Broader questions and more general relationships between biodiversity and road management are better highlighted by these reviews, but as the question and range of study types widens, the answers become less applicable to the specific questions asked about road construction and management. The same problem applies to meta-analyses. For example, a meta-analysis by Villemey et al. (2018) used 709 cases from 34 primary studies that compared biodiversity in verges with other habitats. Overall, insect species richness did not differ between roadside habitats and compared habitats, a result that contrasts against single studies proving increased or decreased insect diversity, depending on context.

Systematic approaches are, however, the only feasible tool for reviewing and analysing literature on more general aspects of roadside biodiversity. Without the systematic reviews' filtering of studies, the amount of literature rapidly becomes overwhelming.

In conclusion, it seems clear that in order to answer questions about the importance, construction, and management of roadside habitats for biodiversity, it is rarely enough to perform a systematic review or meta-analysis, because too few comparable studies are available. Evidence needs to be retrieved from a more disparate range of studies. This, however, requires the review to be delimitated to highly specific questions, in order to make it possible to find and evaluate all relevant literature on the topic. Since selection criteria cannot be pre-defined as in systematic reviews, the review should include a thorough and transparent (e.g. narrative) source critical appraisal, as well as a self-critical approach when drawing conclusions. Such approaches are commonly used in social sciences, for example when working with historical questions and historical sources. For example, source-pluralistic approaches (Myrdal 2012) can be used in combination with hypothetic-deductive structuring of questions (Westin and Lennartsson 2017).

3. How can roadside habitats contribute to biodiversity conservation?

A majority of the studies reviewed do not address conservation problems, although implications for conservation are often brought up in the articles in the discussion. Therefore, response variables chosen by the studies are often difficult to translate into, for example, effects on conservation status or into indicators typically used in biodiversity conservation. One frequently used response variable is diversity (of species, genes, taxonomic groups or similar). It should be noted that diversity is not equal to biodiversity, although the two terms are often used parallel. While diversity is an index based on some combination of number and abundance of species (or similar), the definition of biodiversity usually also includes interactions between species, relationships between organisms and their environments, and the ecological functions of habitats and landscapes.

The Convention on Biological Diversity defines biodiversity as the variability among living organisms from all sources, including terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part[4]. This definition is operationalized in different ways in national and regional conservation frameworks and legislations. In EU, for example, much of the conservation efforts are performed within the framework of the Habitats Directive. Here, a number of species and habitats are listed, and habitats are protected in the Natura 2000 network of protected areas, covering about 18% of EU’s land area[5]. For each habitat, a number of features and ecological requirements are identified, together with a number of typical species.

Notably, roadside habitats are not included in the Habitats Directive’s list of habitats, which makes it difficult to assess the roadsides’ contribution to conservation in relation to the directive’s framework. Based on this review and our own experience of roadside habitats, we do not believe that it is possible to translate roadside habitats into existing Natura 2000 habitats. However, important groups of roadside habitats could probably be identified using the Habitats Directive’s framework for habitat quality assessment and classification. The framework for roadside habitat ecology outlined in this review could serve as a starting point.

[4] www.cbd.int

[5] www.ec.europa.eu/environment/nature/legislation/habitatsdirective

3.1 General importance of roadside habitats for biodiversity conservation

In order to justify allocation of resources to measures for biodiversity when constructing and maintaining roads, it is important to know to what extent these measures improve the conservation status of biodiversity. Are the measures and the roadsides making significant contributions to biodiversity conservation?

The importance of roadsides for biodiversity conservation is frequently stressed by conservation stakeholders, and has also been highlighted in a number of reviews and conceptual articles (e.g. Way 1977; Thompson 1983; Young 1991; Forman and Alexander 1998; Bellamy et al. 2000; Tanghe and Godefroid 2000; Tikka et al. 2000; Ries et al. 2001; Milton et al. 2015).

In addition, a large number of more specific studies that found high (bio)diversity in roadside habitats claim or suggest that such habitats do contribute significantly to conservation. Consequently, this review provides several examples of biodiversity being favoured by road verges of high ecological quality. Such indications of a conservation value of roadside habitats are of two types, either discussing habitat area and connectivity, including refuge habitats in a deteriorating landscape, or discussing species richness, occurrence of certain species, and viability of populations, mainly in terms of roadsides being reproduction habitats for species. The wealth of examples thus suggests that roadside habitats are indeed important for the conservation of several groups of species and habitats in changing landscapes.

Some of those examples are unequivocal, such as species that nowadays only or almost only occur in roadside habitats and similar infrastructure habitats in a region or country (e.g. Helldin et al. 2015; Ottosson et al. 2012). In a Swedish region, nearly all populations of the former meadow plant *Gentianella amarella* are now to be found along roads (Nilsson 2012). This applies also nationally for Sweden, and roadsides are what keeps this species from being red-listed. Other examples provide more indirect indications of the importance of roadside habitats, for example that a species’ abundance is higher in roadsides than in other habitats.

Figure 10. Gentianella amarella*, province of Härjedalen, Sweden. Photo Tommy Lennartsson.*

It has been suggested that the importance of roadsides for conservation may have been overlooked. Rentch et al. (2013) claim that roadsides have largely been excluded from vegetation studies in the USA because they have been considered as unnatural or wasteland. However, in their study of vascular plants flora of roadside habitats in West Virginia, USA, they documented 467 species of which 325 were natives.

In general, we found very few studies explicitly quantifying or estimating the importance of roadside habitats for conservation in a landscape or in relation to other conservation measures. It can be noted that many studies of plants or insects in roadside environments do not at all discuss how the results relate to conservation policy or conservation problems in general. For example, it is rarely discussed whether higher species richness in roadsides implies a support of the landscape's biodiversity or whether it implies that roads introduce new categories of species in the landscape.

Also regarding the conservation status of roadside habitats, there are very few studies. Just as in other habitats, species may occur in roadsides but with poor conservation status, for example low population growth rate. A ten-year survey of ten butterfly specialists in Wisconsin (USA) bogs and roadside ditches found that most of the specialists had less favourable trends in roadside habitats than in the bogs (Swengel and Swengel 2011). Akbar et al. (2010) classified habitats according to a number of criteria for conservation status, based on a survey of the vegetation in 35 road verges in different types of roads in north England (U.K.). Using criteria selected for conservation evaluation, including verge area, plant diversity, species richness, disturbance, presence of rare species, and structure of hedges, they concluded that 6% of the verges were classified as being of high conservation status, 40% of medium and 54% of moderate conservation status. The lack of studies of conservation status implies that even if many studies show high biodiversity in roadside habitats, it is difficult to evaluate the roadsides' importance in the long run or in comparison with other habitats.

We conclude that roadside habitats can enhance the conservation status of threatened biodiversity, but to varying degrees depending on region, landscape type, species, type of threat etc. For some species in some countries or regions, roadsides may even be the main or the only remaining habitat. There is a need for studies (including specific reviews of literature) of the importance of roadsides for biodiversity conservation in relation to other habitats in the landscape.

3.2 Habitats for reproduction and resources for species of conservation concern

Several studies have reported high numbers of species in roadside habitats. In a Swedish study by Cousins and Eriksson (2001), the most species-rich grassland habitats were dry-mesic semi-natural grasslands (152 species of vascular plants) followed by road verges (92), semi-natural grassland with trees (87), midfield islets (85), and moist-wet semi-natural grasslands (82 plant species). Bratli et al. (2006) assessed vascular plant species richness and composition in different land types (ploughed land, midfield islets, semi-natural open land, and woodland) and transition habitats (including road verges) over agricultural landscapes in Norway. Road verges bordering non-ploughed land stood out as the most species-rich type of patch in this study, representing 83.3% of all species in only 1.3% of the area. Road verges even held more species than semi-natural land (72% of the species in 2.3% of the area). This result is in accordance with other findings in Norway where studied road verges had the same or higher number of species than traditional hay meadows and pastures (Norderhaug et al. 2000).

3.2.1 Species richness and biodiversity conservation

In general, species-rich habitats are not necessarily considered more valuable for conservation than species-poor ones, as the latter may have specialised species not being favoured by the species-rich habitats (e.g. Raemakers et al. 2003).

Norderhaug et al. (2000) found that both road verges and semi-natural grasslands had a number of unique species. The authors conclude that road verges are very species-rich but do not substitute traditional hay meadows. Since high species richness in road verges may thus be caused by high numbers of either non-native species or common generalist species (e.g. species favoured by disturbance), increased species richness is not necessarily implying increased contribution to biodiversity conservation. A more unambiguous indication of high conservation value of road verges than overall species richness may be that roadsides can host large proportions of the surrounding landscape’s species. Noordijk et al. (2009a) found in a study in the Netherlands that up to 68% of all indigenous species of some insect and spider groups could be found utilizing road verges. Another study showed that of 31 selected target species for heathland, drift sand or other nutrient-poor open habitats (all being declining habitats in the Netherlands), 21 species were found in road verges (Noordijk et al. 2011). In such cases, roadsides often contribute considerably to the total populations of species of conservation concern.

In extreme cases, roads may be so similar to the surrounding landscape that their biodiversity does not differ significantly from the surroundings. The road crossing Kheyrud Forest on the northern mountain slope in Iran, had no significant effect on the number of species and diversity when Tehrani et al. (2015) compared plant diversity along a transect from up to 100 m from the road. The road was constructed to be as environmentally friendly as possible, e.g., using local sand and gravel for construction and making the road as narrow as 4 m plus 1 m ditch on each side.

Plant species richness is a common response variable in roadside studies (see further section 3.2.4). High species richness often includes presence of demanding specialist species, many of which are of conservation concern, for example by being protected or red-listed, or by being host plants for specialised insects (e.g. Helldin et al. 2015). Increased, but not necessarily high, species richness may, in contrast, be the result of increased frequency of some common generalist plants. In such cases, species richness is not necessarily associated with presence of species of conservation concern.

Also generalist plant species and moderate species richness may, however, add considerable conservation value to roadside habitats, for example by providing pollen/nectar plants over rather large parts of the road network. Favouring roadside hotspots for plant species richness, versus improving species-poor road verges should probably be seen as two different conservation targets that complement each other.

Figure 11. Habitats in dry regions are characterized by no or low cover of trees and of sparse, seasonal herbaceous vegetation. Here, a road makes little difference in terms of openness and occurrence of bare soil. Upper photo: Tomillar vegetation, Torrevieja in the province of Alicante in coastal south-eastern Spain; lower photo: Alvar vegetation, Jordhamn, province of Öland, Sweden. Photos Tommy Lennartsson.

3.2.2 Linking species and habitat

A large number of studies focused on road verges as reproduction habitat or resource habitat for species, often species of conservation concern. Of the articles found by the initial screening in the *EPIC-roads* project and given Priority 1 (563 articles), 126 articles address species' use of roadside habitats either as reproduction habitat or as resource habitat (Hanslin et al. 2019).

A vast majority of studies analyse abundance, diversity etc. (i.e. these are the response variables) in relation to environmental factors (i.e. explanatory variables) but without discussing the mechanisms or actual causes for species occurring in the habitat. The scarcity of knowledge and information about habitat mechanisms and habitat ecology has been highlighted also by a few other reviews, for example Suarés-Esteban et al. (2016). This knowledge gap is not unique for the study of roadside habitats, but there seems to be a general deficit of frameworks for describing and analysing habitats, or biotopes, nature types etc. (see discussion and examples in Lennartsson 2010 and Lennartsson and Simonsson 2007).

The lack of information about ecological mechanisms in habitats has two consequences for the assessment of roadside values and the management of roadside habitats. First, in many articles it is difficult to discern whether the observed species are using the roadside for reproduction, or if the species visit the roadside for resources but reproduce elsewhere. This difference may be important because in the first case, the roadside habitat constitutes a rather independent ecological unit whose status is controlled by the road manager. In the second case, the roadsides' contribution to populations depends also on habitats controlled by other actors.

Second, in order to optimise the construction and management of roadside habitats, we need to know which features of the habitats make a roadside valuable. Many studies analyse correlations between one or more response variables, e.g. species, and a number of explanatory variables, e.g. habitats features. Significant correlations indicate the importance of certain features, which gives some guidance for roadside management. However, without information about why and how such features favour the study species, the results are difficult to apply to other roads, being slightly different in terms of the roadside environment or species pool. Karim and Mallik (2008) identified different parts of the road construction in Canada, with potentially different microhabitat function for plants. The aim was to provide an ecological basis for selecting desirable native plants based on their autecological attributes in relation to roadside microhabitats. They identified four distinct microhabitats, created by the construction process from the edge of the road to the edge of the forest, namely shoulder, side slope, ditch and back slope. They furthermore found that several native plants that were abundant in side-slopes, possessed autecological attributes such as low stature and drought tolerance, that constitute good adaptations to a dry and regularly mown roadside habitat.

In summary, although many studies of biodiversity in roadsides test correlations between biodiversity and different habitat features, there is a large need for reviews and studies of mechanisms for the relationships between species and their microhabitats. In particular, the importance of basic environmental conditions (climate, soil type, sun exposure, species pool etc.) and different processes (natural and anthropogenic ones, e.g. vegetation management, soil disturbance etc.), needs to be highlighted.

Figure 12. A typical structure in roadsides through rocky terrain is bare bedrock with no or thin soil cover. Many plant species adapted to such microhabitats are spring-flowering, thereby taking advantage of the soil moisture before the summer heat. Viscaria vulgaris, *Gölja, province of Västmanland, Sweden. Photo Tommy Lennartsson.*

3.2.3 Generalist, specialist, and invasive species

Many studies have found that a majority of the species in roadside habitats are generalists that can utilise the heavily disturbed, sometimes nutrient-rich environment (see references in Forman and Alexander 1998; Coffin 2007). The literature, however, also provides a growing list of examples of threatened species which have found rescue habitats in road verges (e.g. Dennis 1992; Spooner and Lunt 2004; Lennartsson 2010; Helldin et al 2015; Ottosson et al. 2012), and threatened species are, in contrast, often specialists that require specific resources and environmental conditions.

The conclusion from such contradicting results is that road verges probably favour a set of functional groups of species, particularly groups adapted to disturbance of vegetation and ground. Among those species, many are indeed generalists, but several also are specialists, some being threatened by the lack of disturbance in the surrounding landscape, in combination with habitat loss (which can in some cases be considered too intense disturbance).

Invasive species constitute a group of generalist species of particular importance because they often alter the environment they colonise more severely than native species. In studies of roadside vegetation, invasive plant species are sometimes referred to, or they are studied together with weed species (e.g. Forcella and Harvey 1983; Sullivan et al. 2009; Buonopane et al. 2013). Several studies have demonstrated a high prevalence of invasive alien species in roadside habitats. For example, Buonopane et al. (2013) characterized the aboveground vegetation and seed bank of mixed conifer forests in central Washington State, and examined the relationships between aboveground vegetation and the distance to roads. They found that roads strongly influenced aboveground vegetative cover and species composition, and that weed populations were largely confined to near-road environments. When examining the difference between plant species that are considered ruderals in Argentina, Chiuffo et al. (2018) found that exotic species were to higher extent confined to roadsides than native species, while native ruderal species were more common in habitats that had traditional types of management, such as burning and grazing. We do not discuss invasive species further since the issue is beyond the scope of this project.

3.2.4 Plants in roadside habitats

Topics studied

Vascular plants are by far the most studied group of organisms in roadside habitats. Of the 563 studies found in the initial screening in this project, and assigned Priority 1, 154 studies included herbs, and 99 graminoids, although sometimes only in terms of vegetation structure. Woody plants and forest structure were subject to 105 studies, and we found 15 studies of lichens and bryophytes. Similar bias towards studies on vascular plants has been found by systematic reviews (e.g. Bernes et al. 2017).

The most commonly recorded feature of vascular plants in roadsides is species composition of the vegetation and the plant community, i.e. roughly the list of species (i.e. the flora) combined with the abundance of different species. Of 167 articles reporting responses of vascular plants to roadside impacts, 67 used community or vegetation composition as response variable; 55 of the studies used species richness (usually measured as number of species), and in 34 articles diversity indices (such as Shannon-Wiener index) had been calculated. Eight articles focussed on specific groups of plants, not the entire flora, and seven studies on single species.

A large number of studies of plants found positive effects of roadside habitats, for example increased plant diversity, species richness, or abundance of endangered species or rare plant communities. Although the proportion of studies with a positive versus negative outcome may largely be an effect of which types of studies have been performed and which response variables and questions have been addressed, there is convincing evidence that roadsides can be favourable for plant species and vegetation types of conservation concern, in several ways.

We conclude that roadside habitats have a great potential to contribute to the conservation of plants, and likely also to several other groups of organisms that depend on plants, mainly different groups of invertebrates.

Species composition, diversity and species richness

Roadsides constitute habitats that are more or less different from the surrounding habitats, and their species composition can usually be expected to differ from the surroundings. Species composition, often referred to as ‘community composition’ or ‘structure’, has been frequently studied and interpreted with various aims, for example, to assess the roads’ contribution to the flora of the landscape or to the abundance of certain species groups, to assess the impact of the road on the surrounding habitats, or to analyse the effects of certain environmental factors, usually variables related to different types of disturbance.

In addition to demonstrating differences in plant communities between roadside habitats and other habitats, studies often find higher diversity and higher species richness in roadside habitats or close to roads, compared to surrounding habitats. For example, Suaréz-Esteban et al. (2016) reviewed literature on ‘linear gap verges’ (roads, power line corridors, railroad tracks etc.), and found that nearly 70% of the reviewed studies showed that verges had significantly higher plant diversity than adjacent surrounding habitats. This also applies to trees and shrubs, usually due to facilitation of recruitment in disturbed road corridors (e.g. Fallahchai et al. 2018).

A few studies follow change over time, and also here, the most common response variables are species richness and vegetation composition. Responses of vegetation composition can in general be expected to be rather slow since the dominating species in the community are often perennials. Many of the more sensitive species are found in too low numbers to influence the estimate of vegetation composition, even if they are influenced by, for example, a management intervention (e.g. Auestad et al. 2011).

Increased diversity through alien species

Higher diversity and species richness are not necessarily indicators of better conservation status, habitat quality, or higher conservation value. Increased diversity and richness may be caused by the road introducing new conditions and microhabitats in the landscape. This creates new niches for other species than those occurring in the undisturbed landscape, including ‘alien’, or ‘exotic’, species of distant origin, some of which may be invasive. For example, in a French oak forest, the roads constituted the least common type of human-made habitat but contributed most (82%) to the diversity of vascular plants, through introducing native non-forest species (Baltzinger et al. 2011). Schultz et al. (2014) found roadsides in Australia to be the habitats contributing most to the diversity of exotic species in a mixed agricultural landscape. In the review by Suaréz-Esteban et al. (2016), much of the enhanced diversity in roadsides was due to colonisation by non-local species, while the authors noted that the studies had a bias towards exotic species.

Figure 13. Daffodils are spreading along roadsides, Mainland Orkney Islands, Scotland. Photo Tommy Lennartsson.

The increased use of salt on roads is one type of niche-forming activity that has gained special attention. Salt accumulation in the soil creates a special niche for salt-tolerant species. Road salt can be deposited in the road verge via run-off and aerial deposition. A review by Tiwari and Rachlin (2018) reported that salt can be deposited on vegetation 40–100 m and even further. It is clear that plants are directly affected by injured tissues and indirectly, via altering of the soil chemistry. However, Tiwari and Rachlin (2018) did not include any literature that demonstrated altered species compositions caused by salt pollution, other than changes due to the addition of a few salt-tolerant species. Fekete et al. (2018) studied the spread of Cochlearia danica, which is native to coastal habitats in several European countries. It does not occur naturally in Hungary but has been established there in four roadside localities with high soil salt content. The spread of C. danica along roads is documented in eight European countries between 1986 and 2016 with an average of ca 62–65 km per year. Willmert et al. (2018) provide an example of salt effects on the vegetation due to reduced abundance of salt-sensitive plants. They studied roadsides along a mountain pass in the USA, comparing the years 1985 and 2005. Chronic exposure to aerially deposited salt can stress plants up to several hundred meters from the road. Near roads, deposition of salt and loss of soil fertility resulted in dieback and prevented regeneration of trees (paper birch, Betula papyrifera), which potentially altered the plant community.

Increased diversity through native species

Many studies, in contrast, show that increased diversity and species richness is frequently the result of more and/or higher abundance of native and local species. When roadsides promote native species, there are good chances of roadside habitats contributing to conservation. A general prerequisite for such patterns is that the roadside habitats resemble other habitats in the landscape in terms of microhabitats and resources for native species (e.g. Noordijk et al. 2008). Arenas et al. (2017a) found that along a 15 km stretch of a road, the verges could act as a habitat for almost all plant species that could be found in natural or semi-natural habitats in the surroundings adjacent to the road. The authors suggest that roadsides may act as reservoirs for biodiversity in agricultural landscapes.

Roadsides may also have preserved biodiversity from habitats that have vanished from the surrounding landscape, see section 4.5.2.

Even native specialists and endangered species are often reported to occur and be favoured in road environments. Irl et al. (2014) found roads on La Palma, Canary Islands, to have a significant positive effect on richness and proportion of endemic species, as well as on overall species richness after correcting for elevation and precipitation. Long-term effects were less clear, however, as roads may disrupt spatial barriers between closely related species, thereby risking hybridization between endemics.

Of course, there are also plant species groups that are disfavoured in roadside habitats. In a study in the USA, Richter and McKnight (2014) grouped mosses into roadside distance specialists, occurring ‘near’ and ‘far’ from the road (0.5 – 8.0 m distance). The differentiation in moss composition along the distance gradient was closely correlated to plot ground cover, and soil physical and chemical attributes.

An estimate of diversity always relates to a certain spatial scale. Schultz et al. (2014) found that roadsides at an Australian farm were relatively species-poor at small spatial scales but were highly variable. The authors compared species diversity at different scales (1-m^2 quadrat, patch of a particular land use, and all patches with the same land use) in native pastures, grazed woodland, un-grazed woodland, crop fields and roadsides. Roadsides had lower quadrat diversity than pastures and woodland but higher variation between patches than most other land uses.

The wild relatives of crop plants are an important source of genetic variation and can be used to introduce new traits into existing crops. Identification and conservation of crop wild relatives (CWR) is, therefore, an important step to safeguard future food security. A study by Jarvis et al. (2015) found that CWR related to forage and fodder crops were most abundant in grassland habitats, while CWR related to food crops were most common in cropped and weedy areas, fertile grassland and lowland woodland, of which linear features including hedgerows, roadsides, field boundaries and field margins were particularly important. The authors argue that roadsides and other disturbed habitats are overlooked conservation targets, especially in site-based conservation measures.

Studies of individual species

There are rather few studies of single species in roadside habitats, but the ones that do exist often reveal important information about the roadside habitat, especially if the studies include responses of different stages of the life cycle or demographic studies. Three factors in the roadside habitat, relating to three major life stage events, seem to be particularly important:

1. establishment opportunities for new plants;
2. survival of established plants (this varies depending on species and road type), and;
3. reproduction/reproductive success (i.e. pollination and seed production).

Auestad et al. (2010) compared the effects of various management regimes in road verges and pastures in an agricultural landscape in Norway. The pasture populations of *Pimpinella saxifraga* had comparatively lower survival but higher reproduction than the road verge populations. Within the roadside environment, different zones were managed differently. Individuals growing in zones receiving survival-lowering management produced seeds that compensated the lack of seeds in zones receiving fertility-lowering management. Fekete et al. (2017) studied three species of endangered orchids of the genus *Himantoglossum* in road verges in eight countries in southern Europe. The species successfully established in road verges which may be an important refugia, resembling the original habitat for the species. The roadsides seemed to provide good opportunities for flowering and seedling establishment, but seed set was lower near the roads. In spite of slightly reduced fecundity most roadside populations were large and viable, and the authors concluded that roads made a significant contribution to the conservation of the species.

The effects of the roadside environment on seed production often seem to be mediated by pollination. Different studies report contradicting results as well as different mechanisms for pollination.

In a Polish study of the orchid *Epipactis helleborine*, Rewicz et al. (2017) found a significantly higher fruit set in road verges compared to the natural habitat of mixed forest. This might be explained by a larger number of pollinator visits, a higher diversity of insects, as well as by a larger size of plants (attracting more insects). In contrast, Geerts and Pauw (2011) studied how pollination of *Erica versicolor* by sunbirds was affected by roads in South Africa. Roads had clear negative effects on pollination as the pollination rates were significantly lower at the roadside edge compared to further away from the road. A Spanish study comparing reproduction of the dominant shrub *Halimium halimifolium* found that there was a lower proportion of fruit set in the verge of unpaved roads compared to the adjacent shrubland (Suárez-Esteban et al. 2014); the plant appeared to be pollen limited, and the study indicated that flowers in road verges receive fewer or poorer quality pollen grains. The lower success in road verges could, however, not be explained by lack of pollinators. The authors suggested that instead, windy conditions, causing the flowers to close, resulted in fewer pollinator visits and that dust deposition negatively affected the pollination efficiency through stigma clogging.

Although some studies indicate a negative effect of road dust on pollination and pollen germination (see references in Suárez-Esteban et al. 2014), dust effects may not be the rule. Jaconis et al. (2017) examined chicory (*Cichorium intybus*) along roadsides in the Cincinnati (Ohio, USA) metropolitan area to assess dust influence on plant pollination through stigmatic clogging. Their results suggest that there was minimal variation of particulate matter found on chicory stigmas among road-types. Furthermore, the deposition of particulates on stigmas based on road type did not show a strong link to variation in pollen deposition and pollen germination. There was also no significant relationship between total particulate levels and pollen germination rates across road types.

3.2.5 Insects and other arthropods in roadside habitats

Topics studied

The initial screening of literature found 113 articles dealing with invertebrates, of which 102 studied arthropods and 85 more specifically insects. In this review, we focus on insects, although some of the reviewed studies also include other arthropods, mainly spiders.

Because of the large number of insect species, total species richness or diversity cannot be recorded, as is frequently done for vascular plants. Instead, most studies of insects in roadside environments focus on specific taxonomic or functional groups of species, and analyse abundance (36 articles), species richness (25 articles), or composition of the species assemblage (26 articles). Seven articles calculated some kind of diversity index. Other studied response variables were behaviour (six articles), dispersal / movement (five articles) and site occupancy (four articles).

We found no other review of overall effects of roadside habitats on insects, but Muñoz et al. (2015) reviewed literature from 1969-2013 on negative effects of roads, including very few studies of roadside habitats though. A systematic literature screening by Bernes et al. (2017) found 17 studies on the effects of certain habitat interventions on insects, of which 12 addressed vegetation cutting (mowing); Jakobsson et al. (2018) reviewed some of these articles.

Abundance, diversity, species richness, and community composition

A number of studies investigated the occurrence of species of groups, and their abundance, in roadside habitats. A common conclusion is that all road verge habitats combined in a region harbour a considerable proportion of species of conservation concern. Noordijk et al. (2009a) claimed that in heavily populated or intensively managed agricultural areas, the role of road verges as a habitat for invertebrates is increasingly important. The authors found that in the Netherlands, up to 68% of all indigenous species of some insect and spider groups could be found in road verges. Another study found that between one third and half of all Dutch species of ground beetles (Carabidae), grasshoppers and bees were found in road verges (Raemakers et al. 2003). In a Czech survey of bees and wasps in an arable landscape, road verges constituted a valuable steppe-like vegetation, hosting a large number of red-listed and rare species (Heneberg et al. 2017). Even if roadside habitats constituted a small area in a landscape context, they were important pockets of species-rich spontaneous vegetation. Roadsides may be the only remaining habitat for certain species or groups in a landscape, region, or even country, and the species today may be regarded as 'roadside specialists' (e.g. Schultz et al. 2014; Helldin et al. 2015).

Figure 14. The role of road verges as a habitat for invertebrates is increasingly important in heavily managed agricultural areas. Road verge with Centaurea scabiosa, *an important plant for many pollinators. Province of Uppland, Sweden. Photo Jörgen Wissman.*

Such an overall pattern indicates the overall importance of road verges, but needs to be split between species groups and habitats in order to answer which types of verges are important in general, and which are important for certain species groups. Roadsides of general importance will favour biodiversity wherever they occur, whereas roadside habitats of more specific importance need to be located where the target species occur. Differences between roadside types as well as between species groups are indicated by contradicting results of similar studies. For example, several studies of bumblebees came to contrasting conclusions regarding the effects of roadside habitats. Kallioniemi et al. (2017) found mainly reduced abundance/species richness of bumblebees in the roadside environment compared to surrounding habitats in Norway. Positive relationships were found with the length of all types of linear elements (e.g. field margins) in the landscape, except for road verges. The authors speculated that the negative influence of roads may be explained by increased mortality due to traffic collisions, sub-optimal timing of mowing, herbicide application, salt spreading at wintertime or pollution. In contrast, Osgathorpe et al. (2012) studied foraging bumblebees in two landscapes in the U.K. and suggested that road verges and track edges are of greater value to long-tongued bumblebees than farmed habitats, particularly in intensively managed agricultural landscapes.

If such discrepancies between studies depend on differences between roadside features, knowledge about those differences would make a valuable contribution to our knowledge about which habitat variables make a roadside favourable, or unfavourable, for invertebrates. Unfortunately, it is rarely possible to trace such potential habitat differences in the articles, mainly because they are not written to be compared with other studies and therefore do not describe the studied systems in a comparable manner. In many cases different results seem to depend on what the roadside species richness (or similar) is compared with. Roadside habitats are always open, sunny and disturbed to some degree, and thus favour species that are adapted to such conditions. If compared with species found in similar habitats, roads may support the studied fauna, but if compared with species in low-disturbance shady habitats, roads are expected to have negative effects on most studied species. In a study in the Czech Republic, Knapp et al. (2013) investigated the effects of highways on assemblages of ground-dwelling arthropods in neighbouring forest and open habitats. Species composition of both spiders and beetles was significantly affected by distance from the highway edge in both open and forest habitats. In general, species richness of forest specialist beetles was negatively affected by highway proximity in forested sites, whereas habitat generalists and open habitat specialists (both spiders and beetles) benefited from proximity to a highway in both forest and open habitats. From a conservation perspective, the impacts of the road on conservation status thus depend on which species group is in focus, forest species or open-land species.

In some landscapes, where the road environment differs a lot from surrounding habitats, the species assemblages in roadside habitats may strongly deviate from the landscape. This is often the case in studies of roads in forest, but may also occur in other landscapes. Kimaro and Kisingo (2017) studied effects of public roads on species richness, abundance, and diversity of ground dwelling insects in Arusha National Park in Tanzania. Counts from pitfall trap data were generally higher in the surrounding ‘core’ habitat than in the road verge; 28 species from the core habitats were absent from the roadside habitat, while nine species were only found in road verges.

Several studies have suggested that roadside habitats mainly favour generalist species, but disfavour specialist species of insects. For example, Palfi et al. (2017) studied the abundance, species richness and species composition, of seed-dispersing ants along roads in Australia. They found that frequent activities that disturb the soil close to the road creates conditions unsuitable to most ant species, whereas the more undisturbed parts of the road corridor hosted a rich ant fauna.

The ant community in frequently disturbed areas mainly consisted of a few generalist species. In a Hungarian study the isopod diversity was highest in the vicinity of road verges, but mainly due to high abundance of many generalist species close to the roads, i.e., at 20–40 m from the road. The diversity of more habitat-specific species was higher further away from the roads (Vona-Túri et al. 2017).

Van Halder et al. (2017) found a higher butterfly species richness in grazed grasslands compared to linear elements such as road verges and grassland strips between arable plots in three agricultural areas of France. Grasslands supported more specialised, more sedentary and less fecund species, which, according to the authors, underlines the more important role of grasslands compared to linear habitats, as habitats for specialist and threatened species. Road verges and other linear habitats supported more generalist species. In another study, diversity of dung-beetles was reduced up to 170 m from forest roads in a rainforest landscape of Borneo, Malaysia, was largely attributed to reduced abundance of specialist species (Edwards et al. 2017).

Figure 15. Bumblebee on Centaurea scabiosa*. Province of Uppland, Sweden. Photo Jörgen Wissman.*

Such results are, however, far from being the rule. In a study of bumblebees in southwest England (U.K.), the abundance along roadsides was over twice that observed on adjacent crop-facing margins, irrespective of crop type. This general pattern was apparent for three of the five most common bumblebee species, including both generalist and specialist foragers (Hanley and Wilkins 2015). A Swedish analysis of literature of 66 red-listed species of plants and invertebrates, subject to special action plans, found that many of them had strong populations and often better conservation status in road verges and other infrastructure habitats than in their populations in the surrounding agricultural landscape (Lennartsson 2010). Most of these species are, like many red-listed species, highly specialised and have a narrow ecological niche width.

Butterflies have been subject to several studies in road environments, and usually show positive responses to the roadside habitat. For example, Munguira and Thomas (1992) carried out a field survey of butterflies as well as a number of environmental variables in road verges in Dorset, U.K. They concluded that road verges support a wide range of butterfly and burnet (Zygaenidae) species, but with large variation between verges. The number of species on the most species-rich road verges were large by British standards, for example 23 and 18 species on the two most species-rich verges, to be compared with an average of 27 species in the ten most species-rich nature reserves for butterflies in Dorset. Also, populations in road verges were large, at least matching those in other habitats in the landscape. The results suggested that many of the species form permanent populations in road verges, rather than being occasionally visiting mobile species. There was, however, a difference between butterfly species regarding to what extent road verges were used permanently or occasionally. This difference was reflected by the proportion of adults killed by traffic. Of the sedentary species studied, 0.6–1.9% of the adults were killed by vehicles. In contrast, around 7% of *Pieris rapae* individuals, which visited the verges for nectar plants and therefore showed a more mobile behaviour in the verges, were killed through vehicle collisions.

In a Swedish agricultural landscape, Berg et al. (2011) found the same butterfly species richness and abundance in forest road verges than in semi-natural pastures. Also clear-cuts had similar values, and, interestingly, power-line corridors even higher. De la Riva et al. (2018) studied various types of 10–15 year-old openings in a boreal forest in Northeast Alberta, Canada: Road verges, 3 m wide corridors, 9 m wide corridors and small clearings (60 x 60 m). All openings except for the 3 m corridors had higher species richness and abundance of butterflies compared to the surrounding forest, and road verges had higher species richness and abundance than all other disturbance types.

Studies of individual insect species

We have found rather few studies of single species in roadside habitats, but roadsides may be part of, or mentioned in, autecological studies. For example, roadside habitats are frequently mentioned as important refuge habitats for endangered species (see Munguira and Thomas 1992; Vermeulen 1993; Eversham and Telfer 1994; Ries et al. 2001; Hopwood 2008; Noordijk 2009a; Lennartsson 2010; Ottosson et al. 2012; Helldin et al. 2015; Homyack et al. 2016 for examples).

In Florida, USA, road verges have been acknowledged as important habitats for Monarch butterflies, because roadsides support populations of the milkweed host plants *Asclepias humistrata* and *Asclepias tuberosa*, provided that there is proper vegetation management (Daniels 2017; Pitman et al. 2018). Similarly, Kasten et al. (2016) investigated the occurrence of milkweed (seven species) and monarchs in roadsides. Milkweeds were found in ~60% of roadside transects. The authors suggested that even if milkweed productivity is lower in roadsides than in other types of sites, the overall contribution of roadsides is large, and has even more potential with more suitable management.

A majority of studies on insects in roadside habitats recorded only the adult life stages. Such data is not always enough to make conclusions about the habitats' importance as reproduction habitat, because adult individuals may only temporarily visit the roadside. More detailed studies looking at more than one life stage, or at the entire life cycle, can provide important information about roadsides as reproduction habitat, and about potential needs for other habitats during different life stages.

In order to assess if road verges are truly important for insects to complete their entire life cycle, Schaffers et al. (2012) studied abundance of overwintering arthropods near Heelsum, the Netherlands, and related it to species composition the following spring and summer. The road verge was used as an overwintering site for a large number of arthropod groups, including both common and declining species. There was a high level of overlap between the overwintering species and the species encountered in summer, especially for the Carabidae, Araneae and Curculionidae, and to a lesser extent Orthoptera. Road verges were used for overwintering both by species that overwinter as adults and by species that overwinter as eggs. This indicated that verges were used for reproduction and that many species can complete their entire life cycle in roadside habitats (see also Munguira and Thomas 1992).

In conclusion, the reviewed studies of insects in roadside habitats show that roadsides may contribute considerably to improving their conservation status. The positive effects, however, differ between types of roadside habitats, landscapes and species groups. Unfortunately, the results of studies also differ depending on study design, choice of comparator etc., which makes it very difficult to disentangle species-habitat relationships in order to identify suitable and non-suitable habitat properties and management methods.

3.3 Effects on habitat fragmentation in the landscape

3.3.1 Increased fragmentation

Roads are known to contribute to the fragmentation of habitats in the landscape, and function as barriers for the movement and dispersal of animals. Barrier effects have mainly been studied for (large) vertebrates, but there are also examples of effects on insects (see review in Muñoz et al. 2015; see also Delgado et al. 2013a and b). These reviews show that several road-related factors contribute to increasing habitat fragmentation, of which the most important seems to be vehicle-caused mortality, barrier effects, edge effects and habitat loss.

Figure 16. A narrow road through a forest hardly constitutes a barrier for birds and flying insects dwelling in the canopy. For ground-living species, on the other hand, the paved road is a very different environment compared to the forest floor. Ferrals-les Montagnes, department of Hérault, France. Photo Tommy Lennartsson.

It should also be noted that for species utilising roadside habitats for reproduction, the proportion of the landscape being urbanised or used for infrastructure may have a negative impact. Cochard et al. (2017) found an overall negative effect of landscape fragmentation through urbanisation on roadside grassland plant diversity. Diversity started to decrease in areas with as low as 10–30% of urbanised land. The authors expressed the decrease of grassland plant diversity as an out-filtering by urbanisation. A specific mechanism is that the road itself may constitute a barrier for movement between the two sides of the road, or across the road to other habitats. Some studies have compared the species diversity or species composition on either side of the road. It has been hypothesized that differences between the two sides indicate that the road acts as a barrier for the studied organisms. Andersson et al. (2017) found that the community of bees and wasps differed between two sides of a highway, a segment of E4 highway in Sweden, with a speed limit of 100 km/h and a traffic volume of c. 90,000 vehicles/day. The number of flowering plants, sun-exposure, area of open sand etc. where similar on both sides. The difference in community was bigger in smaller compared to larger species, which suggests that the highway has stronger barrier effects on poorer dispersers (i.e. smaller species). In high-altitude alpine grasslands in Austria, the mobility of the six butterfly species of the genera *Erebia* (ringlet butterflies) were found to be restricted by resource availability and patch isolation (Polic et al. 2014). A heavily frequented road hindered the mobility between grassland patches on different sides of the road.

Fragmentation and barriers are not addressed in this review, except for a brief overview of trap effects in section 3.4.

3.3.2 Reduced fragmentation

Increased area of grassland habitat

Road verge habitats are usually considered a group of grassland habitats, based on the vegetation and on the fact that most road verges are cut regularly. Road verges constitute a very diverse group of grasslands, in which differences are caused by several environmental factors.

The area of road verge grassland is considerable. Road corridors have been estimated to cover about 1% of the USA, an area of c 84,000 km2, equalling the area of Austria (Forman and Alexander 1998). A Swedish study that used randomised sampling of eight categories of roads found that the Swedish road network of c. 600,000 km contains about 165,000 ha of regularly cut short-grass vegetation, i.e. grassland of drier types (Stenmark 2012). Corresponding figures for the Netherlands are 80,000 km and 50,000 ha (van Eupen and Knaapen 2000). The area of moist grassland types was not estimated. In Sweden, it has therefore been suggested that road verges can considerably contribute to increasing the area of grassland types that, because they have vanished from the agricultural landscape, are of conservation concern. In many European countries, important grasslands for biodiversity are those that were abundant in the pre-industrial agricultural landscape, for example semi-natural pastures and hay meadows, but that have become rare because of the agricultural transformation (Oppermann et al. 2012).

It has not been systematically evaluated to what extent roadverge grasslands mimic and replace grasslands from the pre-industrial agricultural landscape. Species richness and abundance data indicate that similarities may be common. Gardiner et al. (2018) reviewed studies that compare infrastructure habitats with surrounding habitats. Of 28 studies in roadside habitats, only five studies showed lower abundance of invertebrates compared to surrounding habitats, while 23 studies found equal or higher abundance in roadside habitats. Villemey et al. (2018) carried out a systematic review of the corridor function of road verges and other infrastructure habitats. Here, 28 out of 37 articles found infrastructure habitats to be similar in species composition, abundance etc., compared to other habitats.

Arenas et al. (2017a) found that most plant species in various habitats in agricultural landscapes may also occur in road verges. However, the composition of the plant communities differed considerably between road verges and the surrounding natural or semi-natural habitats. Also, several other studies demonstrated differences in species composition between roadside grasslands and other grasslands, but nevertheless stressed that roadside habitat functionally may replace or complement other grasslands for many species (e.g. Jantunen et al. 2006).

In order to truly reduce fragmentation, there should be a connection in terms of individuals or genes (including pollen) moving between road verges and other habitats. The degree of connection can be assumed to be determined by distance (structural connectivity) and ecological similarity. The ecological similarity between roadside habitats and other habitats, may be, for example, the degree of overlap of species composition. There can be assumed a gradient from species living entirely in the road verge and not utilising habitats or resources in the surroundings, to species only occasionally breeding in verges, or using resources in verges, but having their main populations in surrounding landscapes. For example, Munguira and Thomas (1992) found such differences between species of butterflies, as some species showed typical breeding behaviour in verges, whereas others showed foraging behaviour.

Connection between roadsides and semi-natural grassland has been shown for pollinators, which may utilise flower resources in road verges but reproduce elsewhere (see references in Kütt et al. 2016; Cole et al. 2017). Jakobsson and Ågren (2014) showed that the pollination and seed production of *Armeria maritima*, *Lychnis viscaria* and *Lotus corniculatus* tended to decrease with increasing distance to semi-natural pastures and meadows, especially in landscapes with high farming intensity. The results from the study indicate that high quality of semi-natural grasslands may improve not only biodiversity within the actual grassland but also pollination of native plants in the surrounding agricultural landscape.

Roadsides as habitats for grassland species is discussed in detail in section 4.2, where we also provide our conclusions.

Increased connectivity of grassland habitats

Many studies emphasize that road verges constitute an extensive network of corridors with vegetation and habitats of conservation concern, in otherwise biodiversity-poor landscapes. Similar studies of biodiversity have also been performed in other types of linear habitats, for example field margins and hedgerows (Forman and Baudry 1984; Dennis and Fry 1992; Freemark et al 2002; De Blois et al. 2002; Marshall and Moonen 2002), and such studies can contribute to the general understanding of the connectivity function of road corridors. A dispersal corridor is thought to increase the movement of plant and animal individuals between habitat patches, thereby reducing population fluctuations, enabling a balance between local extinctions and re-colonisation, and enhancing genetic exchange. It may be difficult to separate the effects of increased dispersal from the effect of increased area of habitat, provided by the corridor area. Therefore, a dispersal effect of a corridor can be said to be an effect on biodiversity that is larger than expected from the corridor area alone (see Tewksbury et al. 2002).

The roadsides' function as dispersal corridors has been subject to a systematic review by Villemey et al. (2018). From 64,206 identified articles, 91 articles that reported 104 studies were used after critical appraisal. Among the reviewed studies, some showed positive effects of different types of linear landscape structures, others negative effects. The number of studies comparing dispersal along verges with that in habitats away from transport infrastructures was low and showed inconsistent results, and no conclusions could therefore be drawn about road verges' dispersal function. The authors conclude that the function of road verges as a corridor for biodiversity remains controversial. In another systematic review, also Ouédraogo et al. (2020) found inconclusive evidence for corridor or stepping stone functions of roadsides.

Our review confirms the results of Villemey et al. (2018), that the effects of road verges on dispersal differ between studies, and that observations of actual dispersal are few. Similar to other studies of biodiversity in roadsides however, dispersal-related studies are also strongly context dependent. Differences between habitats, species groups and landscapes are considerable, and contradicting results do not necessarily indicate an unclear effect, but rather that the studies investigate different ecological systems. We conclude that it is probably not relevant to ask whether road verges in general function as dispersal corridors. A more relevant question is under which circumstances road verges function as dispersal corridors, and under which ones they do not. With knowledge about those circumstances, roadside habitats can be constructed and managed in order to enhance connectivity of certain habitats, for certain species groups and in certain landscapes.

Thus, even if scientific evidence for a corridor function of road verges is poor, there are many indirect indications of such a function. The indications are of two main types: distribution patterns of species (or other taxonomic units) and species having populations in roadside habitats.

Distribution patterns

One type of indication of connectivity is data on the distribution of species, related to spatial patterns of core habitats and potential dispersal routes.

Skórka et al. (2018) compared grasslands adjacent to roads (including road verges) with reference grasslands surrounded mainly by arable land in southern Poland. Grasslands along roads had a slightly higher number of butterfly species, which could not be explained by differences in plants species richness or plant community composition. The authors suggested that the difference in species number was due to grasslands in arable fields being isolated while grasslands along roads were connected to each other via road verges. Villemey et al. (2016) studied the gene flow of the meadow brown butterfly (*Maniola jurtina*) in three agricultural regions of France. The meadow brown butterfly is an abundant but decreasing butterfly inhabiting grasslands. Road verges and grasslands, enhanced gene flow (through dispersal of individuals), while other landscape features had little effect. A Polish study of parasitoid hymenoptera Pimplinae compared species diversity in shrubs, field borders, roadsides, forest edges and forests (Piekarska-Boniecka 2015). The roadsides were poorer in species than the other habitats but seemed to allow the dispersal of these insects between roadsides and other habitats.

Reproduction habitat as dispersal habitat

Corridor function is often thought of as individuals moving in a corridor from one core habitat to another (cf. Beijer and Noss 1998; Gilbert-Norton et al. 2010). However, also by inhabiting the corridor, i.e. using it as a reproduction habitat, individuals may move and, thus, functionally slowly disperse through the habitat. Such dispersal may occur during the lifespan of an animal individual, or during a number of generations for plants and animals.

In a German study of road verges in an agricultural landscape, Thiele et al. (2018) found that plant species that depend on semi-natural grasslands but lack mechanisms for long-distance dispersal could use road verges for multi-generational migration and reach semi-natural grasslands further away. The road verges were less important dispersal habitats for species confined to semi-natural grasslands, but with the capacity for long-distance dispersal (e.g. wind spread), and for species that also find suitable habitats in the matrix between semi-natural grasslands (in this case nitrophilous tall herbs that can live in fallows of arable fields).

The speed of dispersal through reproduction habitat strongly varies between type of organism and depends on several factors including mode of mobility, behaviour etc.

In the Netherlands, the two butterfly species *Maculinea nausithous* and *M. teleius* were re-introduced in 1990 and their populations studied over nearly a decade (van Langevelde and Wynhoff 2009). The two species typically occur in fragmented habitats and they depend on plots with both host plants and host ant nests as larval resources. The authors found that the spatial arrangement of the habitats limited their dispersal, but in different ways. *M. teleius* only flew shorter distances, and expansion of a population could only occur to high-quality patches in close proximity. In contrast, *M. nausithous* could cover larger distances and therefore had the ability to utilize a network of high-quality habitats further away in the landscape, for example in road verges.

*Figure 17. With suitable vegetation, roadside habitats can serve as reproduction habitats for invertebrates, here larvae of burnet (*Zygaena *sp.). Borås, province of Västergötland, Sweden. Photo Tommy Lennartsson.*

Jansen et al. (2012) provided an example of the importance of behaviour in different habitats. As mentioned above, *M. nausithous* was reintroduced in the Netherlands in 1990, and spontaneously established populations in some road verges around 2001. In road verges, butterflies were found to move significantly shorter distances than in meadows, and the authors suggested that this was caused by differences in the spatial distribution of resources between the two habitat types.

Dispersal by human activities

Many species are or have been dispersed by humans, for example in the preindustrial agricultural landscape (see Auffret 2011). Along roads, some special means of dispersal have been studied, mainly dispersal by vehicles. Vehicles, and the goods they transport, can be assumed to contribute significantly to the mobility of organisms at different scales, even global dispersal (e.g. Taylor et al. 2012). Dispersal by vehicles may be indicated by irregular patterns of distribution of species, deviating from what can be expected based on the natural dispersal capacity of a species in question. Typically, vehicle dispersal causes long-distance jumps, as has been demonstrated for, e.g., the harmful tiger mosquito (*Aedes albopictus*) in Spain (Eritja et al. 2017) and elsewhere (e.g. Medlock et al. 2012, Roche et al. 2015, Egizi et al. 2016). Plant seeds can be dispersed by cars e.g. attached to the underside of the car, on mudguards, cabins, tires, wheel wells and engine bays. Even though each car may transport very few seeds (2–4 per car according to Ansong and Pickering 2013), collectively cars can transport a large number of seeds. Studies have estimated that seeds can be transported several hundreds of kilometres but are more likely to travel between 3–40 km, or shorter distances (Ansong and Pickering 2013). The dispersal is dependent on weather conditions. Taylor et al. (2012) found that seeds attached to vehicles may be transported longer distances under dry conditions than under wet conditions. In Sweden, Auffret and Cousins (2013) collected mud from 48 motor vehicles and germinated 110 different species from 48 motor vehicles, among which eight species were considered grassland specialists and four were invasive alien species. The 110 species represented about 18% of the local species pool. Urban areas in Berlin have a high proportion of non-native species, and in order to study the transport by vehicles, von der Lippe and Kowarik (2008) designed a test based on motorway tunnels leading to and from the urban areas. The results showed that more urban biodiversity seeds were ‘exported’ by traffic, than imported.

Also, the air flow created by cars has been shown to lift seeds and to result in seed transport along roads and to road habitats (Ross 1986; von der Lippe et al. 2013). Seeds that are common in the roadside were more likely to be dispersed along roads, but the probability of transport is higher for seeds with certain traits, e.g. small and wind-spread seeds (von der Lippe and Kowarik 2012).

Another likely important group of dispersal vectors is activities related to the construction and maintenance of roads. Such dispersal mechanisms have been studied rather little, but are increasingly acknowledged in research on invasive species.

Rauschert et al. (2017) studied seed dispersal through grading (evening the surface by scraping) of unpaved roads in an experiment in Pennsylvania (USA). Grading only transported 3.6% of the released seeds. Of the transported seeds, 23.5% moved short distances (0–10 m), 33.1% moved intermediate distances (10–

50 m), and 41.8% moved more than 50 m and up to 273 m. Most of the re-located seeds were transported towards the middle of the road, but a separate experiment evaluating post-grading movement of seeds concluded that 73.9% of the recovered seeds had found their way to the edge of the road and the roadsides.

Chaudron and Isselin-Nondedeu (2017) investigated seed dispersal through cutting machinery. They found that seed dispersal was up to 15 m along and out from the road verge and into the field margin when the verges were cut with heavy machinery. The distance of dispersal of seeds did not differ much between species but to a higher extent on which machine was used. The results suggest a higher focus on examining different machines' effects on spreading of desirable plants but also on the dispersal of invasive species.

3.4 Are roadside habitats ecological traps?

In order to analyse the extent to which road verge habitats contribute positively to the conservation status of species, the abundance and viability of populations in such habitats need to be compared with the performance of the species in the surrounding landscape. As previously mentioned, Gardiner et al. (2018) found only five out of 28 studies in roadside habitats to show lower abundance of invertebrates compared to surrounding habitats. The other studies had found equal or higher abundance of invertebrates in roadside habitats. In the systematic review by Villemey et al. (2018), 28 out of 37 articles found infrastructure habitats to be similar to other habitats, in terms of species composition abundance etc.

Both these examples may indicate that roadside habitats and surrounding habitats have at least comparable ecological quality. However, information about the viability of populations in roadside habitats is rarely given. Therefore, it cannot be excluded that the habitats are ecological traps and function as sinks for biodiversity in the landscape. The potential trap effect of road verges is a key question for evaluating biodiversity effects of roadside habitats. A trap may occur if a habitat attracts species from the surrounding landscape but causes such poor population viability due to collision mortality, chemical contamination or other threats, that the overall viability of the species in an area is reduced. The issue of ecological traps is subject to a separate sub-project of *EPIC-roads* (Kollmann et al. in prep.), and treated only briefly here.

Trap or sink effects are not confined to roadside habitats, but may occur in a variety of habitats, both natural and human-made ones.

This review indicates that very few studies of roadside biodiversity have sampled data that allow analysis of trap effects. This is confirmed by a specific review of trap effects, in which only 14 out of 390 studies explicitly tested trap effects (Kollmann et al. in prep.), as well as by another recent review of trap effects (Hale and Swearer 2016). Thus, our review indicates that the state of the knowledge does not provide any clear evidence either in favour of or against ecological traps. The review also indicates that the issue of ecological traps needs to be developed conceptually in order to evaluate existing studies in terms of trap effects, and to set up new studies. For example, it needs to be discussed whether the trap concept applies to plants as well, for which the place of establishment is not the result of an active choice, but of a passive likelihood of a propagule producing a new plant (see e.g. Fekete et al. 2017 who discussed the potential trap effect on an orchid).

It is likely that a trap effect is more common among species that use the verges as dispersal corridors or nectar resource, because such species have a more active behaviour in the habitat and therefore face a higher risk of collision compared to species that reproduce in the roadside habitat. Baxter-Gilbert et al. (2015) calculated huge numbers of road-killed pollinating insects based on extrapolation of a Canadian highway study (annually around 50 million butterflies, 130 million Hymenoptera and 10 million flies in southern Ontario). A similar study calculated 20 million road-killed butterflies annually in the state of Illinois, USA (McKenna et al. 2001). Baxter-Gilbert et al. (2015) suggested that further studies should be carried out in order to assess whether this mortality factor may contribute to the decline of pollinators worldwide. Other studies have indicated that the mortality rate are rather moderate. For example, in a British study, Munguira and Thomas (1992) found that the collision mortality of adults of the butterfly *Pieris rapae* was around 7%. This species visited the verges for nectar plants and therefore showed a rather mobile behaviour in the verges. In comparison, of all breeding, sedentary butterfly species only 0.6–1.9% of the adults were killed by vehicles. The authors concluded that this mortality factor was insignificant for this group of species.

If viability of populations reproducing in roadsides is lower than in surrounding habitats, there is a risk that the roadside habitat constitutes a trap, or sink, that drain the landscape of individuals (Battin 2004). Sink habitats are by definition habitats in which a population cannot survive without regular influx of individuals from other (source) habitats (Pulliam 1988). A trap is clearly the case if the roadside is more attractive than other neighbouring habitats at the same time as roadside populations are non-viable (population growth rate <1), while populations in the surrounding habitats are viable. Such a situation would draw individuals of animals from a good to a “non-viable” habitat.

Conversely, if viable roadside populations are isolated from other populations, the roadside habitat is clearly *not* a trap, but able to support viable populations. Very few studies of roadside biodiversity assess the viability of the studied populations, but the general impression is that they describe rather persistent occurrences of species, i.e. not sink habitats. This, together with an increasing number of observations of threatened species for which roadsides nowadays constitute either a substantial, major, or the only habitat, suggest that trap effects are definitely not a rule, and may not even be common, among species that utilize road verges as reproduction habitat (see Noordijk 2009a; Lennartsson 2010; Ottosson et al. 2012; Helldin et al. 2015; Homyack et al. 2016 for examples). This is also frequently suggested by studies of larger taxonomic groups of insects reproducing in roadside habitats, for example bees (Hopwood 2008), butterflies (Munguira and Thomas 1992; Ries et al. 2001), and Carabid beetles (Vermuelen 1993; Eversham and Telfer 1994).

Some studies have demonstrated higher abundance together with higher mortality of species in roadside habitats (e.g. Erb et al. 2015 for box tortoises, Meek 2014 for lizards, and Baxter-Gilbert et al. 2015 for pollinating insects). However, such results do not necessarily prove a trap effect. The trap function needs to be assessed by comparing the quality of the surrounding landscape versus the roadside habitat, and the attractiveness of the surrounding landscape versus the roadside habitat. Reduced population viability in roadside habitats compared to alternative habitats does not necessarily imply a trap effect or a sink function. As long as roadside populations are viable, i.e. with a population growth rate >1, roadside habitats may contribute to the conservation of the overall populations of the landscape, especially if alternative habitats are few and threatened, while roadside habitats being abundant (cf. Fekete et al. 2017).

In general, it will probably be difficult to assess trap effects for situations where both roadside habitats and surrounding habitats support viable populations, although roadsides may be less viable.

To conclude based on current knowledge, evidence against trap-effects is scarce. However, also examples of trap effects are few, both in total an in relation to the number of studies indicating roadsides to favour biodiversity of conservation concern. Therefore, there is no reason to refrain from making road verge habitats as useful as possible for biodiversity. However, it should be acknowledged that trap effects have rarely been considered in studies of roadside biodiversity, and may be overlooked. In order to optimise roadside habitats' contribution to biodiversity conservation and avoid unnecessary negative effects, it seems important to identify those circumstances (habitat type, organism group, landscape, road type etc.) that increase the risk of making valuable road verges an ecological trap. It is equally important to identify those habitat variables that reduce the risk of a trap effect, e.g. that reduce roadkill mortality, in a roadside habitat, and to translate those variables into trap mitigation measures in construction and maintenance. We recommend the concept of trap effects to be restricted to situations where roadside populations are non-viable, i.e. where roadside habitats constitute sink habitats by definition.

4. Key ecological factors for plants and insects in roadside habitats

The different studies of plants and insects in road environments together provide a rather long list of habitat conditions and ecological processes that have been shown to influence species abundance, richness, survival, recruitment etc. in different ways. Many of the studied explanatory variables, however, only provide limited information about the relationships between species and their habitats. For example, of 140 articles reporting responses of herbs and graminoids to the roadside environment, the most commonly studied explanatory variable is 'distance to the road' (40 articles); for invertebrates, this concerns 15 out of 69 articles. A similar group of studies are those comparing the roadside habitat with one or more other habitats (24 articles about plants and 18 about invertebrates), often contrasting the human-made road environment with undisturbed natural vegetation (nine articles about plants, four on invertebrates). Some studies relate plant responses to different parts of the road environment (sometimes denoted 'microhabitat'): inner and outer slope, ditch etc. All of these studies demonstrated an effect of the road, but causes of the effects are usually only discussed in the articles, not tested directly.

A number of studies have looked for more specific explanations of plant responses, for example soil conditions (22 articles), soil disturbance and proportion of bare soil (six articles), light availability, aspect and slope (10 articles), mowing and other vegetation management (18 articles), and active alteration of the vegetation through sowing, herbicide application or fertilisation (10 articles). The vegetation structure, including succession processes, was studied as explanatory variable in 12 of the reviewed articles.

Studies of invertebrates have more commonly addressed the significance of local habitat variables, for example by using multiple regression models for testing several variables simultaneously. We found 17 studies of this type. A few studies of invertebrates have addressed more specific habitat factors, such as sun exposure and aspect (two articles), vegetation cover (three articles), mowing and other management practices (six articles), and the occurrence of host plants (five articles).

Several studies (22 articles) related the roadside flora and vegetation to the occurrence of habitats in the surrounding landscape, discussing processes of colonisation of roadside habitats. Some studies emphasize that the roadside flora may also reflect historical landscape conditions (seven articles); 14 studies of invertebrates consider effects of the surrounding landscape, for example proximity to other grasslands.

In conclusion, the potential for favouring plants and insects in roadside habitats is large, but the importance varies considerably across types of roadside habitats, depending on combinations of environmental variables. Several variables can be manipulated when constructing and managing a road. In order to optimise building and management activities for biodiversity, there is an urgent need for better knowledge about how the most important variables influence plants and insects in roadsides.

We encourage in-depth reviews of single or smaller groups of environmental variables. In such knowledge compilations, studies should be evaluated with the aim to extract both theoretical and practical information about species-habitat relationships. Systematic reviews can be used if enough literature is available, such as the review of the effects of mowing practices by Jakobsson et al. (2018). However, in order to build guidelines on as much existing knowledge as possible, in most cases, systematic reviews need to be complemented with traditional reviews of relevant research that do not fill the systematic reviews' selection criteria.

Another important source of information is studies of single species and smaller groups of species. Many such studies and knowledge compilations have been performed for endangered species, and many provide important information about species-habitat relationships, that for several species include roadside habitats. Since the search strings used in this project focussed on roadside studies, publications of this type have only occasionally been found.

This, as well as other reviews, show that the effects of certain environmental variables are highly context-dependent. Depending on species group, 'starting point' and several other factors, the very same environmental variable, e.g. a certain type of vegetation cutting, may give different results. Therefore, each study needs individual contextualisation, together with other source-critical evaluation.

4.1 General ecological mechanisms for biodiversity in roadside habitats

This review of species' responses to the roadside environment, and of key ecological factors for roadside biodiversity, indicate that the key factors largely belong to three main categories that are interacting with each other:

- *Ecological conditions*, being consistently present at a location, and making the foundation for the plant communities; examples are regional and local climate, topography, and soil and bedrock type.
- *Ecological processes*, imposing comparatively rapid changes of the environment, either frequently and more or less regularly, more randomly, or

as a slow process over a few decades; processes may be both natural and anthropogenic, such as drought, vegetation succession, soil disturbance, and vegetation management.

- *Species pool* for colonising roadside habitats, mainly a function of the habitats in the surrounding landscape, today and historically, sometimes in combination with active sowing and planting of vegetation.

The categories are defined here for convenience. We do not attempt to problematize the categories in relation to other ecological concepts used for describing habitats and plant communities. For example, the terms 'conditions' and 'processes' overlap with the commonly used categories of abiotic and biotic interactions (see e.g. Crawley 1997a). The categories relate to the construction and maintenance of roads in four main ways:

1. In order to favour biodiversity when constructing a road and a roadside habitat, it is important to build upon and make the best out of those ecological conditions that are given by the location of the road and cannot be changed. For example, south-facing embankments will provide different ecological conditions compared to north-facing ones, and roads at higher altitudes have different conditions than lowland roads.

2. Some basic ecological conditions can be influenced when constructing roadsides, for example the type of material that makes up the road body, the topsoil on outer slopes, if topsoil is added, the inclination and shape of slopes, and some light conditions through planting of trees. How such conditions are created at construction largely determines which species that can colonise the roadside habitats, which communities that can establish, and which subsequent management activities the habitats will require.

3. The (micro)habitat for species, in roadsides and other habitats, can be considered as being created by the interaction between ecological conditions and ecological processes. Therefore, it is important to adapt the management methods to the basic conditions of each major type of roadside habitat, for example to adapt frequency of mowing and soil disturbance to the productivity of the soil.

4. The species pool in the surrounding landscape can be seen as another site-specific condition, which determines which species can potentially colonise those habitats. Furthermore, even if the vegetation in new roadside habitats may be constructed by sowing and planting, the ecological value of the habitat largely lies in its interaction with the surrounding landscape, through exchange of genes and individuals, provisioning of complementary resources etc. Thus, in order to favour biodiversity, the new habitat should relate to the surrounding habitats and species pool as much as possible.

4.2 Ecological conditions

Here, we define ecological conditions as conditions related to the region (climate, altitude, large-scale topography, biogeographic region etc.), and the local landscape and site (local topography, soil, bedrock, aspect and light conditions). Most of these conditions cannot easily be influenced by road maintenance, with the exception of soil, in particular the topsoil and the material in the road body.

4.2.1 Soil properties

The type of soil and bedrock is of fundamental importance in determining which plants can survive at a site, and thus the resulting type of plant community at the site. At large scale, the vegetation on Earth varies with climatic conditions, often referred to as climatic or zonal variation. At smaller scale, the vegetation varies depending on the site conditions, often referred to as edaphic variation (e.g. the Council of Europe 1987). Of the edaphic factors, soil type is usually the main explanatory variable for the vegetation since the soil is the principal source of water and nutrients for plants. In most systems for classification of vegetation within an ecoregion, the vegetation on different major types of soil falls into different major vegetation categories. In classic phytosociology, the most important gradients of variation of soil properties are moisture, nutrient level, and contents of limestone or similar minerals (Nilsson 1902; Påhlsson 1994).

This review shows that studies of roadside vegetation frequently identify soil properties as an important explanatory variable for the vegetation. More detailed information on which soil type supports which vegetation is, however, rare. Most studies that link plant responses to specific soil properties focus on soil chemistry related to deposition of salt, nitrogen and metals.

Moisture

When relating plants to soil chemistry, the water content of the soil is always a covariate, since it influences the uptake in the roots. Soil moisture is determined by a combination of water availability (rain, overflow water, and groundwater), the soil's capacity of keeping the water, and the evapotranspiration (e.g. Holdridge et al. 1971). Roads are typically constructed to be well drained, but soil moisture may still vary within a range that creates large variation in roadside vegetation, through variation in local topography (water availability), soil texture (water-holding capacity), aspect (evapotranspiration) etc. Further, the microtopography of the road construction itself contributes to this variation, since road embankments and slopes may be drier but ditches wetter than the surrounding habitats.

Ditch habitats have been shown to be important refuges in the landscape for certain plant groups. For example, Zielinska et al. (2013) found high abundance of locally rare species in roadside ditches in Poland, 46% of which only occurred in these roadside habitats. Swengel and Swengel (2011) showed that bog butterflies in Wisconsin, USA, frequently visited lowland ditches along roadsides, and that they utilized a variety of nectar sources.

Figure 18. Roadside ditches can occasionally develop certain types of fen vegetation which, together with openness, favour wetland plants, e.g. the orchid Dactylorhiza maculata*. Norberg, province of Västmanland, Sweden. Photo Tommy Lennartsson.*

Since many roadside habitats are dry, soil moisture and drought are likely to be particularly important factors in roadside habitat ecology. Soil moisture interacts with soil nutrients as nutrient uptake is constrained by water deficit, and therefore also strongly interacts with vegetation succession. Severe drought may also be seen as a process that kills vegetation and restarts succession. In this report, nutrients, succession and drought are treated in other sections. Our systematic literature search did not find any scientific studies explicitly addressing the dry conditions of roadside habitats. In some practical guidelines, however, the potential to create dry habitats is mentioned (e.g. Murariu et al. 2019).

Calcium and pH

Botanists have long recognised that the flora on limestone, chalk, and similar soils and bedrocks, is more species-rich than that on acidic soils, and a large number of basiphytic plant species are known. This is valid also for the roadside flora. Lime content is mainly determined by the mineral soil particles, although other factors are also involved in the rate of calcium uptake in plants.

Both pH and calcium are found to influence plant species richness in some studies. For example, in 35 road verges in north England (U.K.), Akbar et al. (2009) registered 212 vascular plant species. When relating species composition to environmental variables (in a multivariate CCA ordination), the most important factors identified were altitude, pH, exchangeable sodium and calcium, verge age and macronutrients. Other likely important (but not measured) factors were management activities such as mowing, and trampling. Neher et al. (2013) found that concentrations of Pb, Cd, Cu, and Zn were elevated near the road compared to further away, and along large roads compared to smaller roads. Additionally, roads of all sizes increased soil alkalinity. In the study, the pH in soil next to the road was 7.7 compared to 5.6 in the forest nearby. Also Müllerová et al. (2011) detected an increased pH in soils near roads due to the use of alkaline road materials. In this case, the pH went from 3.9 to 7.6 in an alpine tundra vegetation, which resulted in a changed species composition near the road, replacing the tundra species with meso- and nitrophilous species.

Figure 19. Road verge on lime soil and bedrock, and with the road embankment in a different phase after disturbance. Byxelkrok, province of Öland, Sweden. Photo Tommy Lennartsson.

A study by Jaźwa et al. (2016) assessed the effects of road-related alteration of substrate, including increased salinity, on vegetation along a meridional gradient in Fennoscandia. Substrate pH was found to be a factor limiting growth of plants. The analysis indicated that vegetation composition was affected by the meridional gradient and by the substrate salinity and pH, which both varied independently of meridian.

The mechanisms for the effects of pH and calcium on plants are complex and by no means a straightforward relationship between plants and pH or lime content (Crawley 1997b). This implies that many of the studies finding significant effects of, for example, pH on plants, do not necessarily demonstrate a functional relationship.

Nutrients

The level of soil nutrients accessible to plants is determined by the type of mineral particles, the content of organic matter, and the soil moisture. In general, low nutrient levels promote high species richness in grasslands because tall and fast-growing species cannot utilise their competitive potential (Clark and Tilman 2008; Hautier et al. 2009). Several studies also indicate or explicitly demonstrate such relationships in road verge vegetation.

In most practical guidelines that recommend measures for biodiversity, the need for nutrient-poor conditions is highlighted. Examples include the establishment of native prairie vegetation (Johnson 2008) or forest vegetation (Anderson et al. 2011), or the maintenance of existing species-rich vegetation (Bromley et al. 2019; Parkinson et al. 2019; Provincie Zuid-Holland 2019).

However, guidelines that recommend the reuse of stockpiled topsoil as a way to (re)establish local vegetation do not seem to consider the risk that added topsoil is nutrient rich, for example through decomposition of roots and other organic matter (Mainroads Western Australia 2016, Trafikverket 2021).

Explicit studies of nutrient–vegetation relationships include measuring the nutrient content of the soil. Most studies on this topic also measure a number of other environmental variables and analyse the importance of all variables combined. Significant effects of soil nutrients were sometimes found; for example, a Scottish study suggested that pollution from vehicle traffic has a significant impact on plant diversity in some road verges (Truscott et al. 2005). The study found gradients in the cover of salt tolerant species, aerial nitrogen concentrations (NH_3 and NO_2) and in the Ellenberg fertility indices of the vegetation, which were all higher closest to the roads and decreased with increasing distance from the roads. The gradients in Ellenberg fertility indices were especially evident in upland sites with a low background nitrogen concentration, and in general increased with increasing traffic pressure. The cover of salt-tolerant species also differed between areas with different background-nitrogen deposition. Garcia-Palacios et al. (2011) studied the vegetation succession over 20 years in Spanish road verges, and found the succession towards a ‘climax vegetation’ to be accompanied by an increase in soil nitrogen and carbon due to a gradual increase of organic matter in the soil.

Figure 20. The topsoil may contain a species-rich seed bank, but, due to decomposition of organic matter, often becomes too nutritious for high species-richness. Vittinge, province of Västmanland, Sweden. Photo Tommy Lennartsson.

A considerably larger number of studies investigated the effects of nutrient levels on vegetation more indirectly, through vegetation height-species richness relationships, or litter thickness-vegetation height-species richness relationships (see the section about vegetation cutting). Other reviews, such as Svensson (2013) and Jakobsson et al. (2018), concluded that vegetation management which depletes nutrient levels in the soil, increases plant species richness.

Soil nutrient levels may also have strong effects on insect communities, through effects on vegetation structure and host plant abundance. Wrzesień and Denisow (2016) found railway embankments to be more important refuge habitats for bee forage flora in Polish agricultural landscapes than roadsides. The species richness and abundance of bee forage plants was reduced in road verges due to dominance of tall graminoids.

Soil nutrients have been studied from the perspective of vegetating road constructions. Since such studies usually deal with the establishment of a few introduced species and not with rich biodiversity, we have not included them in this review. To establish vegetation on new soils in road constructions rapidly, fertilisation and spreading of nutrient-rich topsoil is often used, sometimes in combination with sowing (e.g. Johnson 2008). It has been questioned how efficient such measures are in roadside conditions where drought and high temperatures may disfavour those fast-growing species that are favoured by high nutrient levels. Hillhouse et al. (2018) evaluated the effects of nitrogen and phosphorus fertilization on the foliar cover of species planted into two roadside sites in eastern Nebraska, USA. They found no effect of fertilisation on foliar cover or erosion because the fertilisation protocols were developed for fast-growing cool-season plant species.

Figure 21. Sun-exposed road verge with sparse vegetation and a large proportion of bare soil. Mariefred, province of Södermanland, Sweden. Photo Jan Olof Helldin.

In contrast to targets for rapid vegetation establishment on new road constructions, high species richness and biodiversity of conservation concern are usually associated with sparse vegetation, early successional phases, and slow establishment of vegetation on bare soil, which conditions are especially associated with nutrient-poor, well-drained soils. (Andersson and Askling 2005; Thylen 2007; Helldin et al. 2019). Such relationships are frequently demonstrated by biodiversity inventories (e.g. Bjørndalen 1972; Saure 1996; Karlsson 2008; Larsson and Knöppel 2009), but have not been subject to any substantial research in roadside environments. In a Dutch project aiming at relocating a number of target plant species in a new road, monitoring showed that 3-5 years after establishment, eight out of 19 attempts had resulted in establishment, of which three seemed to be fairly viable. It was concluded that the roadside vegetation was too dense and productive for most of the target plants, but that, hopefully, some years of cutting with biomass removal would create more favourable habitats with less competitive vegetation (van Grinsveen 2016).

Salt and other pollutants

The accumulation of salt in roadside soils has attracted considerable attention and been subject to several specific studies, many of which demonstrating significant effects of soil salinity on, e.g. plant diversity (e.g. Truscott et al. 2005; Jaźwa et al. 2016). The spread of salt-tolerant plant species is, however, not necessarily entirely an effect of increasing soil salt levels, but may also be caused by other factors, such as the origin of road building materials. Fekete et al (2018) studied the salt specialist and seashore plant *Cochlearia danica* in its new habitat along roads in Hungary. They found it likely that roadside conditions, such as high soil salt content and open vegetation structure, provide optimal conditions for the establishment of *C. danica*, but also that other factors, such as interactions between local precipitation and soil type, may have large effects on the population. Where roads stretch through naturally salty soils, runoff from the roads may, in contrast, reduce soil salinity and thus favour less salt tolerant plants. One such example is provided by Zeng et al. (2012) from roads in a Chinese delta with halophytic vegetation.

Some studies have investigated effects of runoff of 'road chemicals' on biodiversity in adjacent ponds. Such ponds may be part of the road construction (storm water retention ponds), or being natural or created for other purposes, but influenced by runoff water from roads. A study of snails in Polish ponds (Krodkiewska et al. 2019) found reduced density of snails in ponds closer to roads, due to higher concentrations of nitrates. Le Viol et al. (2009) found the fauna of Coleoptera, Heteroptera, Odonata and Gastropoda in water retention ponds along a highway in France to be very similar to that in other types of ponds, in spite of differences in water chemistry. The similar community compositions and structures suggest that highway ponds contribute to the biodiversity of the pond network at a regional scale.

Increased concentrations of metals have been found in roadside plants (e.g. references in Trombulak and Frissell 2000), and Phillips et al. (2021) found effects of metals and dust on pollinator behaviour in roadsides. However, population effects of pollutants on terrestrial plants and arthropods are poorly studied.

The effects of herbicides in road verges was studied both in designated chemical weeding in roadsides, and with respect to unintentional spread in agricultural landscapes. Many of the latter type of studies addressed differences between organic and conventional farming. Henriksen and Langer (2013) found a 1.9-fold higher density of flowering plants for wild bees in road verges bordering organic arable fields than in those bordering conventional fields. This was mainly due to the absence of herbicides. On the other hand, in conventional farming, road verges may be better protected from agrochemicals than many other, otherwise similar, field margins. In a study in U.K., bumblebee abundance along roadsides was over twice that observed on adjacent crop-facing margins (Hanley and Wilkins 2015). However, the total number of flowering plant species and the floral abundance of three of the five most visited plants was also higher on roadsides, which the authors partly attributed to reduced impact from agrochemicals. They concluded that road verges should be utilised more as a conservation tool to promote pollinator biodiversity.

Further discussion of the spread of biocides in road verges is beyond the scope of this review.

Soil structure

The structure of the soil, such as coarse or fine, lose or compact etc., influences plants through several mechanisms, e.g. soil moisture, frost movement and recruitment conditions. Invertebrates are influenced by the vegetation, but also directly, e.g. through temperature and suitability for digging.

Road construction often removes the topsoil and exposes subsoil surfaces for colonisation. Therefore, it is important to understand the relationships between plants and soil properties in a situation of primary colonisation and succession. If topsoil is added, the soil is often nutrient-rich (Hillhouse et al. 2018). Experiments have also been conducted with stockpiling the original topsoil during the construction process and re-spreading it on the new surfaces. Some such studies focus on vegetation cover without considering biodiversity aspects (e.g. Huxtable et al. 2005). A few studies have also addressed the question of how this procedure may facilitate the establishment of native vegetation from propagules in the topsoil. Skrindo and Pedersen (2004) showed a considerable establishment of local species. Many of the early colonisers were pioneer weeds that decreased in abundance over time, and the authors concluded that the re-distribution of local topsoil founded for a succession towards indigenous vegetation.

Most studies that measure several soil properties have found that the relationships between plants and soil structure may be complex. For example, Cousins and Eriksson (2001) showed that subsoil affected species occurrence more than top soil (24 and 14 species, respectively, were positively associated), but the directions of the effects were different for different species.

Vegetation cover

The vegetation cover, or its opposite, the extent of bare soil or sparsely vegetated ground, is the result of a combination of several environmental conditions, mainly soil nutrient level, moisture and structure, evapotranspiration, aspect, ground disturbance, vegetation management and successional stage. For plants, the vegetation cover is particularly important during the establishment phase (establishment success of most vascular plant species from seeds is favoured by bare soil), but vegetation cover is also a component of competition for light and space among adult plants. For insects, bare soil is important for several groups such as digging bees and wasps, dung beetles, and carabid beetles.

In conclusion, considering that road construction includes considerable manipulation of the soil, and creates escarpments and embankments with new and often designed soil surfaces, better knowledge of relationships between soil properties and roadside vegetation and invertebrate fauna is crucial in order to favour roadside biodiversity. We encourage specific reviews of literature on soil–vegetation and soil–invertebrate relationships, as well as new research, preferably with a focus on biodiversity conservation issues.

Although poorly supported by scientific evidence, a number of soil-related positive effects on biodiversity are well established in practice. Examples are higher plant-species richness on lime-rich soils, and the importance of certain types of sand for wild bees and other digging insects. The use of such soils, and the avoidance of nutrient-rich topsoil, can probably be recommended as general biodiversity-promoting measures, especially when motivated by specific conservation goals.

4.2.2 Light and temperature conditions: Edge effects, slope, and aspect

Light and temperature

Roads are generally open environments, and in forested regions, they constitute open-land corridors through the landscape. In the absence of trees, the field layer vegetation is favoured, which is one mechanism for increased species richness and diversity of herbs and graminoids (and invertebrates) in many studies. For example, in a Japanese study, roadsides were compared with natural vegetation along an altitudinal gradient (Takahashi and Miyajima 2010). The species composition was clearly affected by light conditions. At altitudes below the timberline, roadsides constituted canopy openings compared to the adjacent forest canopy. Light-demanding plant species dominated in the roadsides irrespective of altitude, and in the natural vegetation they increased with altitude as canopy cover decreased.

Figure 22. Dry, sun-exposed slope along motorway. Bålsta, province of Uppland, Sweden. Photo Tommy Lennartsson.

Insects (as ectotherm animals) are influenced by sun exposure both through increased abundance of plant resources in light environments and directly through temperature. Sydenham et al. (2014) studied the phenological dispersion of solitary bees in Southern Norway with the focus on field edges. The bees were divided in three groups based on seasonal presence (spring, mid-summer, late summer), and a general result was that sun-exposed field edges, including road verges, had more species and individuals of bees than shady field edges. Dai el al. (2013) studied leaf miners and leaf gallers, which both preferred leaves in the sun to those in the shade. In addition, branches in the sun were longer and had more leaves, also leading to more mines and galls. Raemakers et al. (2003) found vegetation height and moisture to be the best predictors of ground beetle communities in the Netherlands, and such an importance of vegetation height was also found by Lenoir and Lennartsson (2010) in Sweden. This effect is probably a combination of temperature and food requirements of different species.

Furthermore, in slopes and disturbed dry soils in various parts of the road construction, the light influx to the ground should be particularly high, which can be expected to create low-competition, light, warm and dry microhabitats, favouring low-growing and thermophilic and xerophilic (drought-tolerant) species, as well as species connected to slow vegetation succession. In many European countries, these species groups contain several endangered species, and roadside habitats may therefore be important for their conservation. A Swedish compilation of literature on 66 red-listed species of plants and invertebrates, subject to special action plans, found that many of them had viable populations, and often better conservation status in road verges and other infrastructure habitats than populations in the surrounding agricultural landscape (Lennartsson 2010). A large proportion of those species were associated with dry, warm conditions and bare soil, and therefore particularly favoured by south-facing slopes on well-drained soil. In general, however, these types of relationships between plants or insects and roadside structures have been studied rather little.

Edges

Several studies have focussed on the linear edge that is formed by the road, either a forest edge or an edge between the roadside habitat and other open habitats. In the case of forest edges, gradients in light and temperature are important, whereas edges in open environments may depend more on gradients in disturbance. Many studies have demonstrated higher species richness or species diversity in the edge than in surrounding habitats (e.g. Čepelová and Münzbergová 2012; Rotholz and Mandelik 2013; Dymitryszyn 2014). However, the effects of edges on biodiversity differ depending on which species group is studied, and also depending on whether only the edge habitat was studies, or also edge effects on the surrounding habitat. In a Japanese study, forest specialist carabid beetles were negatively influenced by roads through forest habitats, while open-habitat species showed the opposite response and used the roadside habitat as reproduction habitat and as a dispersal corridor (Yoshiki et al. 2010).

Avon et al. (2011) studied the effect of forest road distance on plant understory diversity at 20 sites in young and adult oak stands in a French lowland forest with a long history of management and road construction. The plant response varied with stand age, and the results suggest a colonisation from road to forest interior for non-forest and forest-edge species in the early stages of the forest cycle, and the reverse phenomenon for forest species in the later stages of the cycle. Batáry et al. (2009) studied how road edge versus tree edge affected the distribution of two sympatric butterfly species within meadow fragments (*Maculinea teleius* and *M. nausithous*). They showed that edge type had contrasting effects on the two species: *M. teleius* favoured both interiors and road edges, while *M. nausithou*s preferred tree edges, and showed a strong positive response to the edge. The authors thought this kind of within-habitat niche segregation to be related to the different microenvironmental conditions at the edges.

A study by Jacot et al. (2012) examined whether meadow edges in the Swiss Alps have higher plant species richness and evenness than the centre of meadows. Vascular plant species were recorded using a paired meadow-edge sampling approach, and three types of meadow edges were considered: roadsides and north- and south-facing forest borders. Almost 50% of all recorded plant species were found exclusively in the edges, whereas a few species were detected exclusively in the meadow centres. Most relevant for plant conservation is the result that richness of endangered species (regionally protected or red-listed species) was significantly higher in almost all edge structures than in the adjacent meadows. Also Rotholz and Mandelik (2013) found that the effects of edges along roads (in Israel) were mostly positive or neutral across species groups, and they concluded that several species-rich groups (plants, beetles and spiders) developed distinct species-rich road edge communities. In Spain, unpaved road verges have been found to receive higher densities of fleshy-fruit shrubs that are dispersed by birds or small mammals than the surrounding shrubland (Suárez-Esteban et al. 2013a, b). The reason is that small mammals choose these edge habitats for defecation (rabbit and fox) and that birds use shrubs for perching, feeding and defecation. Narrow tree strips along roads can thus favour plant diversity in fragmented landscapes, and dispersers can promote roadside colonisation and restoration through spreading seeds of conservation interest. The authors noted, however, that dispersers may also spread unwanted species.

Figure 23. Old pollards are light-demanding and can survive in tree rows and forest edges along roads. Saint-Léons, department of Aveyron, France. Photo Anna Westin.

One aspect of forest edges with high conservation relevance is that forest edges may support several structures of key importance for biodiversity, for example shrubs, old-growth 'light trees', layered shrub–tree vegetation, and herbs that are light-demanding but disturbance-sensitive. The spontaneous occurrence of old trees and shrubs is sometimes complemented with old planted tree rows and hedges, respectively. These types of values of forest edges have been studied in road contexts and have also been subject to several reviews and guidelines regarding other types of forest edges (for example in Sweden: Gerhardt et al. 2018). The importance of ancient roadside trees for insect populations has been acknowledged in some studies (e.g. Oleksa et al. 2009; 2013; Kadej et al. 2016). In Northern Poland, Oleksa et al. (2009) found the rare jewel beetle *Ovalisia rutilans* (Buprestidae) to occur only on old lime trees along roads.

Åström et al. (2013) stressed the importance of warm and sunny conditions for the red-listed marbled jewel beetle *Poecilonota variolosa* (Buprestidae) in Sweden. The species is monophagus on aspen (*Populus tremula*) and a study showed that sunny habitats like road verges, clear cuts and pastures had significantly more exit holes than aspen in dense forest.

Hedgerows, which are common features along roads in several regions of Europe, are a special case of edge habitat. For example, in the six counties of Northern Ireland, there are ca 5.3 million hedgerow tree standards (Spaans et al. 2018), constituting a hedgerow network of about 113,650 km in length, at an average density of 8.0 km hedgerow per km^2 (McCann 2012). Hedgerows, together with avenues and other long standing plantations of trees and shrubs, represent a group of semi-natural habitats, which, through management and suitable light conditions, provide a number of important woody micro-habitats for biodiversity outside of forests (see, e.g., references in Natural England 2015). In addition, such habitats may constitute an important biological cultural heritage. Their importance for biodiversity increases as intensive agriculture leads to ecological impoverishment of agricultural landscapes (Matson 1997). For example, hedgerows may increase the connectivity of several habitat types, such as semi-natural grassland and wooded habitats (Dennis 1992, Saville et al. 1997; Svensson et al. 2000). In practical guidelines, the importance of hedgerows for pollinators has been stressed (e.g. Fox et al. 2019). Hedgerows and trees in road environments are not treated further in this review, but doubtlessly deserve particular attention in road ecology.

Figure 24. Upper photo: In many European landscapes, roads and field margins are bordered by hedges with or without tall trees. Uxeau, department of Saône-et-Loire, France. Lower photo: If the cutting of hedges stops, the hedges can develop diverse screens of trees and shrubs. Gilly-sur-Loire, department of Saône-et-Loire, France. Photos Tommy Lennartsson and Anna Westin.

Slope and aspect

The effect of the direction of a slope (aspect) on the vegetation can easily be seen along roads, as north-facing and south-facing slopes have very different cover and composition of the vegetation. Bochet and García-Fayos (2004) found 5% mean cover of vegetation in south-facing slopes, compared to 78% in north-facing slopes. Several studies from ecosystems other than road environments indicated that evapotranspiration is one of the main mechanisms for the effect of slope angle and aspect on vegetation (Cerdà 1998; Kuitel and Lavee 1999; Bennie et al. 2006). The ecological effects of slope properties are therefore linked to and interacting with effects of sun, temperature, drought, and ground disturbance by erosion. Due to erosion risks, the benefits of creating slopes for biodiversity are often seen as problematic in practical road administration, and the flattest possible slopes are therefore recommended (Johnson 2008). There are rather few studies on aspect effects on roadside vegetation; only seven articles were found in our screening. Some of these studies failed to prove significant aspect effects when testing for effects of several environmental variables simultaneously (e.g. Cousins and Eriksson 2001; Akbar et al. 2010). Such results cannot, however, be interpreted without knowledge about which type of slopes were studied.

Figure 25. North- and south-facing slopes experience very different climatic conditions, which is reflected in the vegetation. Here, the north-facing slope (to the right) is dominated by few species of mosses while the south-facing slope has a rather species-rich flora of vascular plants, especially species adapted to sun and drought. The sun exposed slope has sparse vegetation cover, which favours wild bees and other digging insects. Arlanda, province of Uppland, Sweden. Photo Tommy Lennartsson.

Some studies found effects of the slope angle, without relating it to aspect. For example, Bouchet et al. (2017) found earlier onset of flowering on steep slopes, which the authors attributed to dryer conditions in steeper slopes. In another study, Bochet and García-Fayos (2015) also addressed slope aspect and tested the hypothesis that the distribution of successful roadslope colonizers results from a filtering process which is primarily controlled by seed availability and dispersal and then by plant competition on north-facing slopes, and by environmental harshness on south-facing slopes. The authors provide an ecological basis for selecting suitable species based on morphological and functional plant traits (Bochet et al. 2010).

In addition to making the aspect more pronounced, steeper slope angle may influence the vegetation through erosion. Tsuyuzaki and Titus (2010) studied vegetation cover in roadsides in relation to various factors in a mountainous oak forest, Oak Creek Wildlife Area, USA. They found that steeper slopes had less vegetation cover, but this did not affect plant species composition, only the frequency of species.

Munguira and Thomas (1992) showed that topographic variation of road verges, in terms of presence of ditches, banks, slopes or uneven terrain, increased the diversity of breeding habitats for butterflies in Dorset, U.K., thereby increasing species richness of butterflies.

In conclusion, several microhabitats in roadside environments can be expected to be extremely warm and light, depending on, e.g., the soil type, slope angle and aspect. Although such conditions are known to be important for various specialised organism groups, they have rarely been studied in roadside habitats. Also, the potential biodiversity values of forest edges along roads are probably overlooked in conservation and road management.

4.2.3 Host plants for insects

Insects feeding on nectar, pollen, seeds or other plant tissue, are depending on sufficient availability of their host plants during the insects' active season. For plant-eating insects, comprising most butterflies, grasshoppers, bugs (Hemiptera) and many groups of beetles, the breeding habitat requires host plants and microenvironments of a quality that suits the species.

Insects can be more or less specialised, from monophagous species (feeding only on one host plant species), to oligophagous (feeding on a few) to polyphagous generalist insect species. Specialisation implies that insects may be influenced by changes of the composition of the vegetation, such as the establishment of alien species. Several studies have shown that road verges dominated by native species host greater abundance and species richness of wild bees (Hopwood 2008) and butterflies (e.g. Ries et al. 2001), compared to road verges with invasive species. The reasons seem to be both invasive grasses that reduce plant species richness, and the fact that few insects utilize non-native flowering herbs.

Figure 26. The road corridor has become a rescue for the important host plant Inula salicina *and accordingly also for its insects.* Inula *cannot stand high grazing pressure. Province of Öland, Sweden. Photo Tommy Lennartsson.*

In addition, the insects' demands on their environment are often considerably higher than those of their host plants, and there are many examples of insects with very narrow distribution ranges in spite of their host plants being common. Specific demands may be related to, e.g. the microhabitat of the plant, the food quality of different plant individuals, or the combination of host plant availability and other resources that are used during other stages in the life cycle. These types of specialisation imply that insects may be strongly influenced by the physical structure of the vegetation and habitat, irrespective of the abundance of host plants *per se*.

Raemakers et al. (2003) found an interesting correlation between occurrence of endangered insects and rarity of plant communities in the Netherlands. Across all studied insect groups, endangered species were significantly more common in rare plant communities (having a characteristic species composition) than in common ones. This indicates both specialisation among the insects on certain vegetation types and habitats, and that deficit of these particular habitats may be a cause of threat.

It has long been acknowledged that roadside habitats may be richer in host plants for invertebrates than the surrounding landscape, both in forest (Baltzinger et al. 2011; Knapp et al. 2013) and agricultural landscapes (Munguira and Thomas 1992; Bratli et al. 2006; Cole et al. 2017). This has been studied particularly in relation to flower richness and pollinators, probably inspired by the at times extraordinary flower richness along roads. Other insect-host plant relationships have been subject to considerably fewer studies.

Several studies have shown that host plant abundance, and sometimes also their suitability as host plant, explains patterns of insect abundance and distribution in roadside habitats (e.g. Kasten et al. 2016 and Daniels 2017 in USA, Riva et al. 2018 in Canada). The dependence of host plants links insects to a number of habitat conditions and processes that influence plants. In a Dutch study of several insect groups in relation to plant species richness the diversity of weevils, but not of other groups, was significantly correlated with plant species richness (Raemakers et al. 2003). Weevils is a plant eating group with several species being specialised on single or a few plant species.

Figure 27. Silver-washed fritillary Argynnis paphia*. Photo Jan Olof Helldin.*

One common result is that higher plant species richness provides a higher diversity of habitats and resources. Munguira and Thomas (1992) found that the variation in number of butterfly and burnet species between road verges in Dorset, U.K., was mainly explained by the variety of breeding habitats, largely the variety of host plants, together with the co-varying factor abundance of nectar plants. Noordijk et al. (2010) showed in an experiment of different management regimes in roadside vegetation that plant species richness and richness of flowers were correlated to flower visiting insects and the species richness of arthropods. Itzak (2013) studied ground-nesting ants in a Mediterranean region of Israel. Here, the diversity and seed production of seed-producing plants was correlated with the abundance of seed-harvester ants. Sydenham et al. (2014) found road verges to contribute to the phenological dispersion of species assemblages because verges increased landscape diversity. Cole et al. (2017) found that the late summer flowering lasted longer in road verges than in many other grassland habitats, which was suggested to be important for pollinators in agricultural landscapes, especially late in the season.

We conclude that roadside habitats may be very important sources of host plants for several groups of insects, and of high conservation value in many landscape types. The literature we reviewed indicates that relationships between insects and their host plants are well known with respect to which insect species uses which plant species, but that considerably fewer studies address the insects' needs for specific 'ecological qualities' of the plants, for example requirements for certain microsites. Furthermore, relationships between the insects' seasonal rhythm (phenology) and the seasonal variation of plant resources are surprisingly poorly studied, for example in relation to timing of vegetation management.

In order to better utilise the roadsides' potentials, knowledge about their function as sources of host plants, including host plants in favourable microsites, seem crucial. We recommend extended knowledge compilations on this topic, including also studies not primarily dealing with roadside environments. In particular, studies of endangered and other demanding species would provide important additional knowledge.

4.2.4 Road size

The size of the road may influence both plants and insects through providing a larger habitat area along larger roads (positive effects). Insects are in addition influenced through larger traffic volume on larger roads (negative effects).

The habitat area effect has been shown in a few studies of insects. Munguira and Thomas (1992) found that the road verge width explained 88% of the adult density of butterflies and burnets in Dorset, U.K. Species richness was uncorrelated with verge width, but instead with diversity of breeding habitats and abundance of nectar plants, both in turn correlated with plant species richness. Also Skórka et al. (2013) found that the abundance of butterflies was positively affected by the width of road verges in south Poland. They partly attributed the effect to a larger grassland area, which reduced butterfly migration and the proportion of individuals being killed on the road.

Noordijk et al. (2008) showed that the area of suitable habitat in road verges may be a problem for ground-dwelling beetles. Many of these species occur in open, short and nutrient-poor vegetation. Although such microhabitats were frequent along studied roads in the Netherlands, their distribution in road verges was too patchy for several species of ground beetles. Species preferring taller vegetation were therefore more common in verges. Although not directly addressed in the study, the results indicate that both larger roadside habitats and more suitable management would favour these habitat-specific species.

Since the zone closest to the road is usually mown frequently for safety reasons, a management-related advantage of wide verges is that they offer a wider zone that does not need frequent mowing.The relationship between roadside biodiversity and traffic volume is treated in the ecological traps sub-projects of *EPIC-roads*.

In conclusion, most studies of road effects on biodiversity have focussed on the road as a linear element, or corridor, through the landscape, containing habitats that are more or less different compared to the surrounding habitats. Biodiversity responses have been studied either along the verges, mainly addressing dispersal, or transversal to the road, addressing road effects on the landscape. We have found no studies that explicitly analyse road verge width in terms of habitat area, and thus, no studies of the potential importance of larger habitat areas that are common in highway construction. Such areas constitute habitat patches of considerable size, rather than a habitat corridor, and can be expected to have great potential to contribute to biodiversity conservation.

We encourage more explicit studies of wide road verges and other constructed areas in the road environment, which have the largest potential to support viable populations of species.

4.3 Disturbance and other ecological processes

We define ecological processes as factors that cause changes to the habitat. Many of the processes affecting roadside habitats cause rather rapid changes and can be regarded as disturbances.

In many contexts disturbance is something negative that should be avoided. In plant ecology, however, it is not. On the contrary, a wide range of habitats are formed and maintained by certain types of disturbance, and, consequently, a large number of species are adapted to and dependent on disturbance. A key task in biodiversity conservation is often to restore disturbance regimes, either natural, such as fire regime in boreal forest or flooding regime in a river, or semi-natural, such as traditional grazing and mowing regimes in pastures and hay meadows. Disturbances may be frequent and regular, such as annual mowing, or less frequent, such as grading of embankment and ditches, or drought episodes. Roadside management is a disturbance regime that influences both ground and vegetation, and is a prerequisite for roadside habitats and their biodiversity.

Figure 28. Recently graded road embankment. Province of Bohuslän, Sweden. Photo Jörgen Wissman.

Disturbance is a concept that has been used to link species functional groups and plant evolution to the habitat, for example in the classical identification of plant growth forms by Raunkiaer (1907). In botanical-ecological literature, disturbance is often discussed in the context of exogenous and endogenous processes (see e.g. White 1979). For example, vegetation die-off may be caused by frost, drought or mechanical impact (exogenous disturbance agents) or by plant senescence or interspecific competition (endogenous).

Ecological processes also include slower changes such as vegetation succession, erosion, and accumulation of organic matter in the soil or litter on the ground. Different processes interact with each other and to some extent with the basal ecological conditions at a site: for example, dry soil and high evapotranspiration create fundamental conditions for the vegetation, but also increase the risk of drought episodes, which can be seen as a process that rapidly changes the vegetation.

Species in road verges thus need to cope with the disturbance (i.e. mowing, ground disturbance, or both). The disturbance regime constitutes a ‘filter’ through which some of the species of the local species pool are favoured by the roadside habitat. This implies that the importance of road verges for biodiversity differs both across functional groups of species and across landscapes depending on which habitats and species pools the road passes through. The relationship between the disturbance regimes in roadside habitats and different species’ responses to such disturbance, often mentioned in roadside studies as an important explanatory variable for road verge biodiversity. Hence, one type of result reported for studies of roadside biodiversity is either negative effects on species groups that are sensitive to disturbance, or positive effects on groups that are adapted to disturbance.

In vegetation management such as roadside cutting, meadow mowing, and pasture grazing, such positive and negative effects on different species groups together usually lead to higher plant species richness. A few competitive species are disfavoured or suppressed by the disturbance, thereby favouring several other, less competitive but more disturbance-tolerant species. Disturbance thus counteracts the slower ecological process of succession towards taller vegetation dominated by competitive species, initially competitive grasses and herbs, later shrubs and finally trees.

From a management perspective, it may be useful to distinguish between disturbance of the field layer vegetation and the ground. Disturbance of the ground always affects the aboveground vegetation, but disturbance of aboveground vegetation, such as mowing, does not necessarily affect the ground and soil.

One of the most important effects of ground disturbance is that it initiates a vegetation succession. We discuss the process of succession in 4.4.

4.3.1 Vegetation cutting

The most common type of disturbance to the field layer vegetation is cutting in order to reduce the vegetation height for visibility reasons, and to prevent establishment of woody vegetation. The cutting of vegetation on road verges is often denoted ‘mowing’, although this term in most other contexts refers to cutting for the purpose of hay harvesting. When mowing for biodiversity conservation or cultural heritage reasons, the actual use of the cut grass for hay is often obsolete, but the mowing still includes removal of the cut material. Removal is not necessarily done in roadside cutting, even if the cutting is termed mowing.

Vegetation cutting reduces competition through damage to competitive plants and, if biomass is removed, through reduced nutrient levels. In general, both these factors increase plant species richness, which also favours several groups of invertebrates. The cutting also strongly influences plants and sessile insect life stages through direct damage. In plants, several adaptations to the damage have evolved, and been subject to considerable theoretical and empirical research.

Similar studies of insects’ responses to damage are rare. While many studies of insects focus on the benefits of increased plant species richness in mown vegetation, some have instead addressed the disadvantages of the mechanical damage. Many species of which the eggs, larvae or pupae are attached to the host plants, are as sensitive to the cutting as are the plants themselves. Van Halder et al. (2017) suggested that biomass removal and management intensity were the most important local factors determining butterfly species richness in grasslands, road verges and other linear habitats in three agricultural areas of France. The disturbance affected the butterflies either directly or indirectly through effects on vegetation structure and composition. Habitats with taller vegetation, less bare soil and lower biomass removal supported relatively more species with a slow larval development. Species with a faster larval development or more generations per year were less sensitive to biomass removal and grazing since they can escape or compensate temporary unfavourable habitat conditions. Skórka et al. (2013) found vegetation cutting to be a disturbance that induced butterfly migration and therefore increased the risk of collisions with vehicles.

On the other hand, many insects are mobile and may therefore escape the mechanical damage and, if available, find alternative plant individuals nearby. Szentesi et al. (2017) studied bruchids (Coleoptera: Chrysomelidae: Bruchinae) that feed on members of the Fabaceae, in relation to cutting regime in road verges along Hungarian highways. Cutting twice a year reduced the abundance of host plants in half of the studied area, but this did not significantly affect the bruchids.

The timing and frequency of cutting

Vegetation cutting has been subject to several studies and a few reviews. Jakobsson et al. (2018) reviewed 48 studies, of which 38 compared effects of cutting versus no cutting, 28 compared different cutting frequencies, and 16 compared different timing of cutting. 41 of the studies were experimental, and 22 of them studied cutting for biodiversity conservation purposes, either in general or in order to restore native vegetation. Seven studies examined vegetation cutting for control of invasive species. The review analysed 22 data sets quantitatively and found that plant species richness and diversity (measured as 'Shannon index') were influenced by the interaction between cutting frequency and removal of the cut grass, and that no significant effects of the single tested cutting regimes could be found. There were, however, indications of higher species richness in cut verges with removal of the cut material, compared to uncut verges.

The review by Jakobsson et al. (2018) thus indicates that there are not enough experimental studies of vegetation cutting to allow the drawing of overall conclusions, because the studies show highly varying results. This is also seen in our review, which, in addition, indicates a strong context-dependence of the results. In particular, the productivity of the road verge can be assumed to influence the results, yet very few articles discuss their results in a productivity context. Also presence of a some certain dominant species may strongly influence the results, but this is rarely discussed. Interestingly, however, single studies often provide clear evidence for advantages of one cutting regime compared to another, e.g. in terms of flower diversity (Noordijk et al. 2009b), which further supports the assumption that patterns of vegetation response are habitat-specific, and that general patterns across studies can not be expected.

Practical guidelines for biodiversity-promoting vegetation management in general recommend late-season cutting and warn against too many cuttings per season (e.g. Heemsbergen et al. 1989; Rijkswaterstaat 2008; Parkinson et al. 2019). 'Too many' here refers to a cutting frequency that not only reduces competition through suppressing dominant plants, but also disfavours many plant species that would be favoured by reduced competition. In contrast, cutting for safety and access often includes both early cutting and frequent cutting.

Timing of cutting

Regarding timing of cutting, later cutting has frequently been suggested to favour biodiversity, because it allows reproduction of plants and insects beforehand. Chaudron et al. (2016a) found significantly increased seed production and diversity of the seed rain in late cut compared to early cut road verges in France. These effects had not yet significantly impacted species richness after four years, however, increased species richness following late-season cutting was found in another study in central western France by the same authors (Chaudron et al. 2016b). Haaland (2017) studied the butterfly scarce copper (*Lycaena virgaureae*) in urbanised areas in Sweden. This species was not present at all in grasslands with continuous management, such as urban parks or pastures with continuous grazing, but it could utilise grasslands with late onset of management.

In contrast, some studies have found more positive effects of early cutting. For example, Chaudron et al. (2018a) showed that a single early cutting of road verges promoted higher species richness in agricultural landscapes in mid-western France compared to late cutting practices. Late cutting mostly favoured nitrophilous and competitive species that were also present in the field margins. Baum and Sharber (2012) noticed that summer cutting of road verges in the Great Plains of Oklahoma, USA, made milkweed (*Asclepias viridis*) produce a new burst of shoots in August–September, at a time when undisturbed milkweed plants had senesced. Such late appearance of milkweed was identified as a benefit to monarch butterflies (*Danaus plexippus*), which uses different milkweed species as their sole host plant. This positive effect of cutting for monarch butterflies has also been demonstrated by cutting experiments in habitats other than road verges (Fischer et al. 2015), as well as by experimental summer burning. Re-flowering after early cutting was shown also by Noordijk et al. (2009b) in the Netherlands. In that study, pollinators responded positively to cutting twice a year (with removal of the cut vegetation) in productive road verges, because that type of cutting regime promotes the highest flowering. The early cutting triggered reflowering later in the season.

Figure 29. Early cutting next to the road has reduced flower abundance and (most likely) plant species richness compared with later cutting. Province of Öland, Sweden. Photo Tommy Lennartsson.

These examples show that the timing of cutting may have contrasting effects on plants in different types of roadside habitats and different landscapes, and that timing of cutting should be adapted to the habitat and its species in order to favour biodiversity. For example, early cutting in Portuguese road verges has been shown not to influence the seed production of Mediterranean plant species negatively (Simões et al. 2013). This is largely because early cutting resembles the traditional grazing that has formed the surrounding habitats and their flora.

Figure 30. In this case, early cutting next to the road has increased plant species richness by suppressing competitive grasses, here Arrenatherum elatius, *compared with later cutting. Södvik, province of Öland, Sweden. Photo Tommy Lennartsson.*

Interpretation of studies of meadow mowing with a roadside perspective would no doubt contribute considerably to a conceptual framework for roadside vegetation management, as well as to practical guidelines. For example, grassland literature highlights that the effects of different timing of cutting include several interacting mechanisms that influence different species and life stages of species. The common recommendation for late cutting is based on the aim to increase seed production and insect reproduction before cutting, especially for early-flowering plants. This advantage of late mowing for seed production, however, comes with the disadvantage of increased light competition during the early or mid season, which affects seedlings and other smaller life stages negatively, as well as smaller plant species and ground-dwelling invertebrates (see references in Lennartsson and Westin 2019). Such a disadvantage is more pronounced in taller and denser (more productive) vegetation, and can thus be expected to increase due to management that enhances nutrient status of the soil, as well as due to atmospheric nitrogen deposition. A trade-off between seed production and competition is indicated by a meta-analysis of effects of delayed cutting in meadows on biodiversity (Humbert et al. 2012). Delayed cutting from spring to summer had positive effects on biodiversity, whereas delay from spring to autumn or from early summer to autumn had predominantly negative effects. Another drawback of late cutting that needs to be taken into account is that it reduces flower resources for pollinators late in the season. Possible mechanisms may be that re-flowering after cutting is higher following early cutting (longer period for re-flowering before the autumn), and that the conditions for establishment from seeds should be higher in late cutting due to limited regrowth of the vegetation (see references in Svensson 2013 and Lennartsson and Westin 2019).

Since both cutting in the autumn and cutting in the spring may have disadvantages, a moderately late cutting may be recommended, adapted to the reproduction phenology of the local biodiversity (Heemsbergen et al. 1989). Another alternative is mosaic cutting; for example, a Dutch practical guideline recommends leaving 15-30% of the vegetation each year in a rotating scheme (Provincie Zuid-Holland 2019). In a review of land management impacts on European butterflies, Bubova et al. (2015) stated that vegetation succession is a major threat to butterfly populations, and that extensive grazing and rotational mowing, which imitate the traditional way of meadow use appear to be the most suitable management. Cutting and grazing should optimally be of low intensity and in a mosaic design. Cole et al. (2017) and Skórka et al. (2013) suggested mosaic cutting: For example, only one side of the road should be cut at a time.

Frequency of cutting

The frequency of cutting (the number of cuttings per season) has been subject to several studies. The quantitative analysis of 22 data sets in the systematic review by Jakobsson et al. (2018) showed that grasses decreased and forbs increased when verges were cut twice a year instead of once a year, and that cutting twice enhanced species richness. However, both their review and our examination of single studies indicate that effects of cutting frequency on plants are also highly context-dependent, and that several studies have demonstrated negative effects of increased cutting frequency on biodiversity.

A review of urban road verges in the U.K. (O'Sullivan et al. 2017) found that reduced cutting frequency enhances biodiversity. This is due to the very high cutting frequency in urban areas in the U.K. Similarly, Entsminger et al. (2017) concluded that native grass and forb species richness, in right-of-way plant communities in Mississippi, USA, were positively influenced by a reduced cutting frequency compared to the conventional cutting regime (four times per year). Frequent cutting mainly favoured non-native grasses of agricultural origin. The authors recommended a one-cut-per-year regime and to increase the width of the cut area in order to control the otherwise encroaching trees and bushes. A change in management practice from several cuttings to one late-season cutting in 27 road verges in the region of Picardie, France, increased the abundance of short-lived plant species (Lanciaux 2013). Auestad et al. (2010) found that cutting twice a year reduced the population growth rate of the herb *Pimpinella saxifraga* in Norway, compared to a single cutting, mainly because of reduced seed production.

These examples show that the effects of increasing versus reducing the frequency of cutting may depend on the starting conditions. If the original frequency is high, then reduced frequency may lead to increased species richness. As discussed earlier, the actual optimal number of cuttings per season probably depends predominantly on vegetation productivity and presence of strong competitors.

The effects of cutting frequency can also be expected to differ according to productivity, with larger effects in more productive habitats, having taller vegetation and more litter production. This was shown in a Dutch study by Noordijk et al. (2010), who found that ground arthropod abundance and species richness was favoured by cutting twice a year (with hay removal) in high and medium productive road verges. In low productivity road verges no such effect was found. Similar effects of an interaction between productivity and cutting frequency, but on flower diversity and richness, is brought up in the discussion in a study by Noordijk et al. (2009b). It is likely that many low-productive roadside habitats can be maintained using even less frequent cutting than once a year (cf. the *Pimpinella saxifraga* study cited above, Auestad et al. 2010). Presence of certain competitive plant species may have the same competition effect as high productivity, and such species may thus motivate more frequent cutting. For example, cutting twice per year in Portuguese road verges reduced the dominance of the shrub *Dittrichia viscosa*, which otherwise reduced the floristic diversity (Simões et al. 2013).

Related to cutting frequency is the length of the interval between the cutting occasions. For example, the effect of mowing frequency on floral density, floral richness, butterfly abundance and butterfly mortality was tested in three highway sites in Florida, USA (Halbritter et al. 2015). The treatment with the shortest mowing interval (i.e. three weeks, corresponding to the typical road management frequency in this region) resulted in the lowest floral species richness and densities, compared to six weeks cutting interval and no cutting, respectively. There were also detectable but unclear effects of cutting frequency on butterflies.

Practical guidelines often recommend reduced frequency of cutting, and one cutting per season in nutrient-poor habitats (e.g. Rijkswaterstaat 2008). Some guidelines also propose cutting only every few years (cf. Hopwood 2010), or outside of the growing season (Bromley et al. 2019).

We conclude that frequent cutting as well as early cutting, probably favour plant species richness in nutrient-rich road verges in which species richness is inhibited by a few competitive plant species. Under such conditions, early and frequent cutting in combination with removal of the cut material can be expected to deplete the nutrient contents and reduce competition, thereby favouring species richness. From a conservation perspective, however, these types of road verges may be less prioritised since they are species-poor, dominated by grasses, and, even when being improved, may be species-poor compared to many other roadside habitats. In species-rich verges, usually having poorer nutrient status and less grass dominance, a single cutting per year, performed after most plants have finished their reproduction, is highly likely to favour plant species richness through enhanced flowering and seed production.

Reviews of studies of cutting regime effects on flora and vegetation have failed to identify clear consistent patterns that could support general recommendations for vegetation management. Single studies may provide clear evidence for advantages of one cutting regime compared to another, but different studies show disparate results. This is not surprising considering the great ecological variation across roadside habitats. We conclude that lack of consistent patterns across studies are not due to lack of consistent vegetation responses to cutting, but that overall patterns are hidden by ecological variation. A key to extracting guidelines for vegetation management from existing studies and knowledge should be to better understand why certain types of vegetation respond in certain ways to certain management regimes. It should be possible to establish a solid ecological foundation for cutting regimes with rather limited efforts by combining knowledge from road verges (including practical guidelines) and from meadows and pastures. Such an analysis should aim at guiding both the choice of road verges to cut for biodiversity, and suitable cutting regimes (timing, frequency, biomass removal etc.) for those prioritised roadside habitats.

Removal of the cut vegetation

The systematic review by Jakobsson et al. (2018) found six studies that explicitly studied effects of removal versus no removal of the cut vegetation, but some additional studies of mowing regimes also included removal. As previously mentioned, in their qualitative analysis, removal interacts with cutting frequency, and the authors conclude that there are not enough studies to analyse the effects of removal alone on plant species diversity. One exception was that positive effects of cutting compared to no cutting, were found only in combination with removal of the cut material.

Svensson (2013) conducted a review of literature on both roadside cutting and other grassland management in order to evaluate the possibilities of promoting a species-rich hay meadow vegetation in roadside habitats. She concluded that in order to favour plant species richness the cut vegetation should be removed irrespective of mowing regime, and that the effect of removal is larger in nutrient-rich road verges.

There appear to be two main mechanisms for the effects of vegetation removal on plants, i.e. nutrient depletion and litter removal. If the cut vegetation is not removed, it will contribute to building a topsoil that is rich in nutrients and organic matter. Litter obstructs germination and establishment of early life stages and small plants (e.g. rosettes), which can be regarded as a type of competition. Auestad et al. (2013) performed a management experiment in western Norway including different types of management in semi-natural pastures and road verges. Biomass (litter) removal in the early spring changed species composition in both the seed bank and the established vegetation in the direction of semi-natural pastures. The litter is dependent on the type of vegetation and the nutrient content in the habitat. In a study of roadside vegetation in China, He and Monaco (2017) showed that plants that were categorized as the rarest were also the species that were most sensitive to litter. Thus, preventing litter accumulation may be an important management task for conservation in these areas.

Very few studies argues against the removal of cut material. One exception is a study of the spider *Urocoras longispinus* that seemed to be favoured by warm, humid microclimate in the grass that was left on the ground (Szmatona-Túri et al. 2017).

In some practical guidelines that have been adopting an ecological and biodiversity conservation perspective, removal of the cut vegetation is strongly recommended (e.g. Heemsbergen et al. 1989; Sjölund et al. 1999; Parkinson et al. 2019). Other guidelines, however, mainly base their vegetation management recommendations on targets other than biodiversity, and argue in favour of mulching instead, which leaves the cut material. It is suggested that mulching may protect the soil against erosion and that it increases the nutrient levels in the topsoil, making it easier to maintain a lush green, dense grass vegetation. Spreading of new mulched material has also been recommended for those same reasons (e.g. Johnson 2008).

In conclusion, removal of the cut material seems to generally favour plant species richness in road verges and other grasslands. In order to translate this general conclusion into management recommendations, it is, however, necessary to consider the cost efficiency of this rather expensive and complicated procedure. This calls for more specific studies of the magnitude of the effect of removal in different types of road verges. From a conservation perspective, it may not be cost-efficient spending resources on removal of nutrient-rich species-poor vegetation, because even improved vegetation may be rather species-poor. Similarly, removal may not be cost-efficient for low-productive species-rich vegetation, where the removal of the small amount of litter would only marginally increase species richness.

4.3.2 Burning

Burning is sometimes used in roadsides, e.g. for controlling invasive alien plants (Barker and Prostak 2009) or for restoring roadside vegetation for biodiversity (Persson 1998). The effects of burning vary largely, and different studies reported either positive or negative effects on plant species diversity, richness and abundance of native or alien species; see e.g. the systematic review of effects of management practices on vascular plants and invertebrates by Jakobsson et al. (2018), which also included seven studies of burning in roadsides.

In general, positive effects of burning are most common in landscapes that are characterised by natural fires. For example, Palfi et al. (2017) noted that in Australia, many species are adapted to fires, and may be favoured by the burning of roadsides. Milberg and Lamont (1995), however, found that such positive effects are not the rule in Australian landscapes, but burning may instead enhance the invasion of invasive alien weeds. Positive effects have also been shown for single species that are today threatened by reduced fire frequencies in the landscape, either natural fires or traditional burning in agricultural landscapes. In Sweden, *Pulsatilla vernalis* and species of *Cytisus* have been favoured by roadside burning (Ottosson 2014).

We conclude that the number of studies of burning in roadside habitats are too few and scattered to allow any secure assessment of burning and roadside biodiversity. It seems that burning may be favourable if performed in a way that imitates fire regimes – natural or anthropogenic – that the local species are adapted to. The evidence is more ambiguous regarding burning as an alternative to cutting, i.e. as management method for grasslands; this is not specific for roadside grasslands but applies for grasslands in general.

4.3.3 Drought

Dry conditions are caused by the combination of low water supply (from rain and/or ground water), low water content in the soil (by coarse material causing low water retention capacity, or thin soil that rapidly dries), and high evapotranspiration (through warm climate and/or microclimate). As discussed earlier, the soil moisture can be considered a fundamental condition for determining the vegetation and can be regarded as a stress factor. In addition, dry conditions increase the risk of shorter periods of drought, here defined as periods much drier than the average, which kills some of the vegetation. Drought is thus a process that could open the sward and cause rapid changes of the habitat similar to physical disturbance to the ground.

Figure 31. Large slope with local nutrient-poor soil, good potential for slow succession and species-rich dry vegetation. Överfors, province of Södermanland, Sweden. Photo Tommy Lennartsson.

The disturbance effect of drought was studied in several types of grasslands, especially in large natural grassland biomes (see e.g. Archbold 1995). One often cited example is the effects of the so-called Great drought 1933–1938 in the Great Plains of the USA. Drought in combination with grazing reduced the vegetation cover and opened for establishment of ruderal weeds, and thus, the more drought-tolerant shortgrass prairie expanded eastwards as much as 240 km (Weaver 1968).

Dry conditions are in general slowing down vegetation succession (e.g. Berry et al. 2016) due to reduced productivity. It is also likely that drought-generation dieback of the vegetation contributes to such succession patterns.

In conclusion, road constructions are generally well drained, and frequently include sun-exposed slopes, with both factors potentially contributing to episodes of drought-induced vegetation die-off. We have, however, not found any literature reporting studies of such drought-induced disturbance. It is likely that specific reviews of literature on the ecology of drought may suggest drought to be an important ecological process in some specific types of roadside habitats.

4.3.4 Disturbance of the ground and soil

The environment next to a new road is characterised by intense disturbance, i.e. surfaces without vegetation, mostly of well-drained soil types. Subsequently, many roadside habitats are subject to regular and sometimes frequent disturbances of the ground and soil, for example by regular grading and digging or by other activities for maintenance or reconstruction. Ground disturbance may also be caused by erosion in roadside slopes (Tsuyuzaki and Titus 2010) and ditches, and by frost movement of the soil.

In spite of the huge importance of ground and soil disturbance, the initial screening of literature in the *EPIC-roads* project found very few studies that explicitly studied these types of disturbance; three articles each for the study of plants and invertebrates, respectively. Some other studies, however, implicitly deal with ground and soil disturbance, for example by studying or detecting effects of bare soil and vegetation cover.

The importance of reducing competition in the vegetation for many species has been discussed above under mowing. Several species of plants and invertebrates, many of which are endangered, in addition require bare soil or at least a sparse vegetation cover (see Lennartsson 2010 for Swedish examples). In a Polish study, the high frequency of disturbance of forest roadsides resulted in survival of relict populations of the mountain plant *Pulsatilla vernalis* in lowland Poland (Zielinska et al. 2016). The specific mechanisms that favoured the occurrence of said species were lighter conditions in roadsides compared to the forest interior, and a lower cover of bryophyte carpets as a result of disturbance. The authors claim that roadside habitats will be increasingly important under warmer, future climate conditions.

In general, reduced vegetation cover and bare soil promote the establishment of many species. For example, Tsuyuzaki and Titus (2010) showed that slopes had lower vegetation cover than flatter ground, and that more of the occurring species more frequently colonised new patches in slopes.

Disturbance may to some extent also apply to the creation of new rock surfaces for specialised plants. Irl et a. (2014) found roads on La Palma, the Canary islands, Spain, to have a significant positive effect on species richness of endemic plants, and the same tendency for overall plant species richness. The result was surprising as endemic plants on isolated islands are usually considered to be disfavoured by human presence. The authors interpreted the effects as the result of new cliff surfaces in the road construction, in combination with the protection from negative disturbances such as fire and grazing by introduced herbivores, mainly rabbits and goats.

Figure 32. Pulsatilla vulgaris *in road verge. Uppsala, province of Uppland, Sweden. Photo Jan Olof Helldin.*

Several studies of insects in roadside habitats found a positive correlation between increased abundance and the degree of disturbance. For example, in Hungary the spider *Urocoras longispinus* was found in semi-natural and disturbed areas, including in road verges, forest openings, shrubland and hay meadows (Szmatona-Túri et al. 2017). Ground disturbance in roadside habitats is particularly important in landscapes with many species adapted to disturbed habitats. One example is roads through heathland, drift sand or other nutrient-poor open habitats. Noordijk et al. (2011) found that of the 31 selected target species living in such declining habitats in the Netherlands, 21 were found in road verges. The authors stressed the need for proper management that keeps verges open and nutrient-poor.

Some species groups may need sites with sparse vegetation cover, i.e. habitats typically formed by ground disturbance, but are also sensitive to the disturbance events. For such species, the frequency of disturbance may be particularly important. A study comparing abandoned fields and road verges in China found that seed dispersing ant communities inhabiting road verges were of smaller body sizes than ants inhabiting abandoned fields (Zhu and Wang 2018); this is likely partly a result of the disturbance frequency in road verges. Palfi et al. (2017) showed similar results in a study of seed-dispersing ants along roads in Australia. Frequent activities that disturb the soil close to the road create conditions unsuitable to most ant species, except for a few generalist species. King and Tschinkel (2016) found disturbed roadside plots in Florida to attract queens of most of the occurring ant species, trying to establish new colonies. However, successful colony establishment was primarily achieved by the exotic fire ant *Solenopsis invicta*, whereas native species commonly failed to establish colonies.

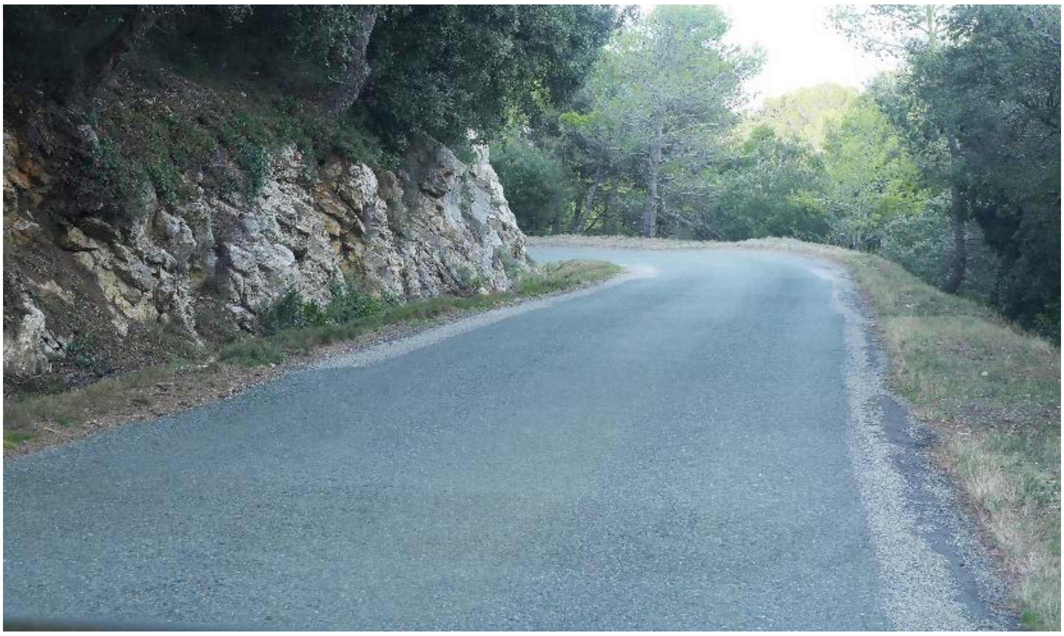

Figure 33. In Mediterranean vegetation many species of vascular plants, lichens and bryophytes are adapted to bare rock surfaces. Carcassonne, department of Aude, France. Photo Anna Westin.

Disturbance of the ground and of the field layer vegetation

There are more studies of roadside vegetation management than of relationships between ground disturbance and biodiversity, which may reflect that roadside habitats are often viewed as a type of meadow grassland, formed by cutting (mowing). Although meadow-like habitats no doubt occur in roadsides, it is likely that many roadside habitats are instead formed by ground disturbance, while the cutting regime is of lesser importance. Such a grouping of roadside habitats in disturbance-induced and cutting-induced habitats is indicated by the review of Svensson (2013), who explicitly addressed mowing-induced habitats.

Also in roadside habitats resembling semi-natural meadow and pasture, succession after ground disturbance is often a characteristic process. Comparisons between roadside habitats and mown or grazed grasslands (see references in

Jakobsson et al. 2018) have found both similarities and differences in plant species composition. Jantunen et al. (2006) found a large habitat variation within road stretches, and that the species composition of the vegetation was rarely comparable with adjacent semi-natural grasslands. They attributed the difference between grasslands and verges mainly to the young age of roadside habitats, and to too high nutrient levels. Larger similarities, and more grassland indicator species, were found in older verges and in nutrient-poor sandy soils, thus indicating the importance of ongoing succession. Auestad et al. (2011) conducted a management experiment including both semi-natural pastures and road verges in the same area of Norway. They found similarities in plant species composition between pastures and road verges, but pastures had a higher content of traditional grassland species. Road verges thus resemble - but are not identical to - semi-natural pastures.

In conclusion, this review has found several studies that implicitly, but rarely explicitly, indicate that mechanical disturbance of the ground is an important ecological process in roadside environments, and that many species-rich roadside habitats are formed and maintained by such disturbance. A systematic approach to research on ground disturbance in roadside habitats is however lacking, which we believe constitutes a critical deficit in the knowledge about roadside ecology.

We recommend specific reviews of and research on the importance of ground and soil disturbance in roadside habitats. The reviews should preferably also include studies from other disturbance-induced habitats. The role of ground disturbance also needs to be considered in the classification of roadside habitats (see e.g. Sjölund et al. 1999). Classification is treated in a separate sub-project of EPIC-roads *and is not discussed any further here.*

4.4 Plant competition and vegetation succession

Roadside habitats, especially those closest to the road, are subject to different types of disturbances to the soil and ground. Therefore, roadside vegetation is usually characterised by succession from recently disturbed ground to more closed vegetation, and, where disturbances are frequent, by rather early successional stages. Ecological succession refers to the change of species composition over time, often following a more or less severe disturbance, but also due to other changes of environmental conditions, such as changed nutrient or water conditions of the soil, or the establishment of competitive species.

4.4.1 Patterns and drivers of succession in roadside habitats

The succession of vegetation and soil is subject to a wealth of studies in various fields of ecology, vegetation history, soil science etc. There are both theoretical and empirical studies, dealing with various time spans. For an overview of studies and literature see for example Walker and Reddell (2007) or Walker et al. (2010), which provide more detailed information about the following general notes on succession.

Succession of vegetation may be caused by several interacting changes of the environment. For example, competition patterns between plant species may change due to the colonisation and establishment of new species, changes in soil structure or soil nutrient levels, increasing biomass and the accumulation of plant litter – all these factors often occur simultaneously. If the disturbance removes all or most of the vegetation, a primary succession starts, initially driven by the influx of diaspores to the area. If the disturbance leaves a considerable amount of propagules (seeds, roots, whole plants), the succession will be secondary and more influenced by the biological legacy dating prior to the disturbance.

In spite of all research on ecological succession, very few studies deal with road verges or other infrastructure habitats. Applying the general knowledge about succession on road verge habitats, it can be assumed that most habitats of that type are subject to both rather short-term vegetation succession initiated repeatedly by disturbances caused by the road maintenance, and more long-term succession following road construction or major re-construction. Long-term succession includes ongoing colonisation by species and gradual changes of the soil, for example through the incorporation of organic matter. This implies that cycles of short-term change, for example between grading events, may follow somewhat different successional trajectories depending on the stage of the long-term succession, for example the nutrient status of the soil. Furthermore, if a new road is built of mostly new subsoil material, the initial succession will be primary and with opportunities for short-lived and ruderal specialists to establish. The subsequent cycles of short-term succession may be of more secondary nature due to increasing dominance of competitive plants, e.g. deep-rooted species that survive grading and other topsoil disturbance and therefore rapidly become dominant in early-successional stages.

Another likely conclusion of general succession theory applied to road verges is that ecological key factors for plants may differ depending on successional stages. For example, Ross (1986) identified three key factors for the initial establishment of vascular plants in primary succession in road verges: (1) levels of salt and lead in the soil, selecting for tolerant pioneers, (2) the occurrence of species on adjacent land, including competitive weeds and woody plants, and (3) wind turbulence promoting species dispersal. The relative importance of those factors varied during the course of succession.

Figure 34. Recently constructed road, with good potential for slow succession both in the slope and flat area. Överfors, province of Södermanland, Sweden. Photo Tommy Lennartsson.

The study by Ross (1986) of primary succession in Scottish road verges illustrates how the number of species first increases through establishment of new species, and then decreases due to vegetation management (e.g. mowing and herbicides), and through competition. The studied highway was constructed in 1969 and the species composition was recorded 10 and 20 years after construction. Four species of grasses together with white clover were sown at construction. After 10 years, 84 vascular plant species were found, and after 20 years 68 species; 71 new dicots established during the first ten years, but in 1984, only 44 dicots remained. During the last 10 years, the number of grass species increased from nine to 13 species and the number of bryophytes from none to nine. The study also indicates that many of the species that entered the verge habitats during the first 10 years, continued to spread along the road to new verge microsites during the following 10 years. A similar result was found in a study of plant diversity in a Chinese delta area (Zeng et al. 2010, 2011). The vegetation in this highly dynamic area is characterised by primary succession, and the disturbance along the roads favoured plant diversity, of which about 75% of the plant species in the roadside habitats were native plants. The native plant species richness peaked at the road age of 20 years and then decreased, while the abundance of alien species increased.

Garcia-Palacios et al. (2011) demonstrated a succession from bare soil at road construction towards a more natural vegetation in two regions in Spain. Roads of different age since construction (0–2, 7–9 and <20 years, respectively) were compared with natural reference habitats in the surrounding landscape. The results suggested that ecosystem development along successional gradients was mainly caused by vegetation succession, including both colonisation and competitive exclusion, together with increased microbial activity and nutrient levels in the soil (due to accumulation of organic matter). The longer the time since road construction, the more similar plant community composition became to the reference ecosystems. Jakobsson et al. (2016) investigated small-scale plant species richness in linear grassland elements in a Japanese agricultural landscape. They found that age of the levee was the strongest predictor of plot species richness, as older levees supported higher species richness than younger ones.

At late-successional stages, species richness may be reduced both by competition among present species and by reduced colonisation of new species in dense swards. The importance of competition for establishment of new species in road verges was shown in a study by Vasconcelos et al. (2014) in Brazilian savanna woodland (‘Cerrado’). Many species from the savanna, for example woody species, were rare or absent from the verges of the road network in the savanna. This seemed to be due to higher cover of competitive grasses (many of which are invasive), which inhibited the establishment of other species. Furthermore, these grasses produce biomass that fuels fires, which, in turn, kills the saplings of woody species.

The direction and rate of vegetation succession are influenced by a number of environmental variables, including management. One is vegetation cutting, but to our knowledge, the interaction between cutting and succession has not been systematically studied in roadside habitats and very little in other grasslands. Since both early-successional species (i.e. ruderals) and late-successional competitive species are disfavoured by regular cutting, it may be expected that cutting preserves mid-succession species richness by counteracting the later, species-poor stages. Bouchet et al. (2017) compared the species composition in road verges that were cut with those that were left without management for 40 years. Although successional change of the vegetation composition was slower in cut verges, cutting did not prevent vegetation changes.

Active sowing can strongly influence succession, especially if competitive species are introduced, for example in order to rapidly establish a closed vegetation cover. Rentch et al. (2013) documented the vegetation along highways in West Virginia, USA, and found roadsides to have relatively similar species composition despite initial variability of landform, parent material, forest cover types, and climate. The authors attributed this homogenisation of vegetation partly to postconstruction seeding and vegetation management. Auestad et al. (2016) found that the standard revegetation method in Norway, using hydroseeding of species-poor commercial seed mixtures, prevented subsequent establishment of semi-natural grassland vegetation, because the initial seed-mixture hindered the establishment of local species. Skousen and Venable (2008) concluded that introducing or increasing the cover of native species in West Virginia, USA, required reducing the competition of non-native species such as *Festuca arundinacea, Festuca rubra, Lolium multiflorum* and *Lotus corniculatus*.

Succession is also influenced by the productivity of the vegetation, i.e. by soil nutrients and water. Dominance of competitive species appears faster and more pronounced in the succession where site nutrients are not limiting (Martin-Sanz et al. 2015). Berry et al. (2016) studied the vegetation in a road corridor through the Mojave Desert, USA, 36 years after the road was built. They concluded that under desert conditions, it may take centuries for the vegetation to recover after a severe ground disturbance. The study illustrated how the role of pioneer, nursing, and competitive species differed between different stages of succession. Bochet and García-Fayos (2015) studied plant colonisation and succession in roadside slopes having different productivity. Species' abundance in the neighbouring vegetation, ability of diaspores to long-distance dispersal, and traits associated with stress and competition, all influenced slope community composition. At the most productive end, species success was associated with a competitive-ruderal strategy and, at the harshest end, species success was related to seed resistance, removal by runoff, and to drought resistance. In a population study of *Pimpinella saxifraga* in Norway, populations in unmanaged roadside habitats performed as well as populations in mown road verges (Auestad et al. 2010). This was most likely due to conditions being too xeric for rapid succession.

4.4.2 Succession and biodiversity of conservation concern

Early-successional plants, e.g. ruderal species, are common in many ecosystems characterised by natural or anthropogenic disturbances. If such disturbances become rare, for example due to ceased traditional land use, roadside habitats may constitute important refuges. In Belgium, the herb *Centaurium erythraea* occurs as an early-successional species after forest clear cuttings (van Rossum 2009). The species is often found in forest paths and road verges, and the author suggests that road verges constitute refuge habitats for these and similar forest species.

Early successional stages are clearly linked to several important conditions in roadside habitats, discussed earlier in this review. Examples are bare soil, good establishment conditions for plants, low competition, high sun influx, low nutrient levels, and pronounced contact edges towards other habitats that provide seeds for establishment (sometimes in combination with remaining seed bank from earlier vegetation). Therefore, it is likely that many of the conservation benefits of roadside habitats are associated with early successional stages, and thus also by conditions that promote slow succession and extended early successional stages. Such relationships between succession and biodiversity values have, however, not been explicitly studied, and hardly even discussed, for roadside environments. In contrast, in practical management guidelines it is common to recommend measures for speeding up the trajectory towards a closed and dense vegetation to counteract erosion (e.g. dense early seeding, Johnson 2008).

The potential of natural succession to form biodiversity-rich roadside habitats have been acknowledged in some practical guidelines (e.g. Sjölund et al. 1999; Bromley et al. 2019). Fox et al. (2019) recommend not to reuse topsoil, in order to favour pollinators through natural succession. Many other guidelines, however, also recommend dense seeding when establishing native vegetation (e.g. Brandt et al. 2015).

In conclusion, one of the most conspicuous effects of ground disturbance is that it initiates a vegetation succession. This implies that disturbance-induced roadside habitats may be regarded as successional habitats. As discussed above, the importance of ground disturbance, and thus of succession, in roadside habitats, may have been overlooked in roadside research.

Succession can be slowed down by vegetation management, and eventually reach a more or less stable stage that is maintained by the cutting. Under many conditions, such as nutrient-rich soils, or conditions favourable for establishment of a dense cover of mosses or creeping woody vegetation, however, the vegetation becomes rather species poor compared to earlier successional stages. This, together with the potential importance of disturbance and succession raises the question of whether species richness in some roadside habitats cannot actually be preserved by cutting or other frequent management, because it is linked to a certain successional stage that will inevitably pass. In such habitats, it is important to identify a suitable frequency of ground disturbance, and suitable disturbance regimes, in order to restart the succession. Probably, in many cases the normal frequency of grading and ditching is sufficient, but this remains to be studied.

4.5 Importance of the landscape

Roadside biodiversity is not only the result of local environmental conditions in the roadside habitat, but also influenced by the surrounding landscape. Thus, a large number of studies of roadside biodiversity have explicitly addressed, or found effects of, the surrounding landscape. Of 167 studies of plants identified through our literature screening, 24 revealed different landscape effects. In arthropods specifically, 15 of 70 articles included investigations of landscape effects. The landscape is also discussed in several of the studies that compare roadsides with other habitats.

The reviewed literature indicates that the surrounding landscape influences road verge biodiversity in three major ways: Through (a) direct effects of the adjacent habitats on the roadside environment, (b) colonisation from the surrounding species pool during the succession of roadside habitats, and (c) subsequent exchange of individuals between roadsides and other habitats.

Some practical guidelines bring up the landscape as a part of the roads' aesthetic properties, and then usually recommend to visually align the road to the landscape as much as possible (e.g. Anderson et al. 2011). Recommended measures include adapting roadside vegetation to the surrounding habitats. Since biodiversity conservation is not an explicit aim of such recommendations, we do not further consider this type of literature, even though such measures may favour biodiversity in the landscape.

4.5.1 Effects of adjacent habitats and land use on roadside habitats

The type of habitat and land use next to the roadside may in some cases have large influence on roadside habitat conditions. One effect is the colonisation of nearby species, which we discuss in the next section. Adjacent habitats may also directly influence the ecological conditions and processes in road verges.

Several studies have shown that roadsides in forested areas differ from those in agricultural landscapes (Cousins 2006; Knapp et al. 2013; Dymitryszyn 2014 and references therein). These differences can be assumed to be caused by a combination of species pool effects and ecological effects of the forest and arable habitats, respectively.

Roads through forests

While many studies have investigated the effects of a road corridor on forest and forest edge habitats, almost no studies have discussed the reverse influence, i.e. how proximity to forest may influence the roadside habitat. This is also the case for studies of light and temperature at forest edges, which is otherwise a topic that has been subject to several investigations (section 4.2.2).

In addition to shade effects of forest on roadsides, the forest trees can be expected to influence the roadside habitat through deposition of leaf and needle litter (Le Coeur et al. 1997). Since this type of litter cannot be controlled by vegetation cutting, it may have substantial effects on the roadside habitat.

Figure 35. Road at forest edge; the shading ends the species-rich vegetation. Province of Öland, Sweden. Photo Tommy Lennartsson.

Roads through arable fields

A systematic review by Villemey et al. (2018) indicated that urbanisation and agriculture in the surroundings tended to lower biodiversity hosted by verges, while natural and forested areas seemed to promote it. Possible explanations for reduced biodiversity in agricultural landscapes are lower species pool in intense farmland landscapes, and effects of fertilisers and biocides. In these landscapes, the effects of the surrounding landscape was mainly studied in the context of field boundaries, in which the road verge is seen as one of several types of boundaries (see Grashof-Bokdam and Langevelde 2005 for a review; see also Freemark et al. 2002; Aavik et al. 2008; Aavik and Liira 2010).

Field boundaries, including road verges, adjacent to arable fields, are often strongly influenced by fertiliser and herbicides used in the fields, which reduces species richness (Kleijn and Snoeijing 1997; Snoo and van der Poll 1999; Aavik et al. 2008). Consequently, some studies have found that species richness is higher in field boundaries in organic farms compared to conventional farms due to the latters’ use of pesticides and mineral fertilizers (Aavik and Liira 2010). Woch and Hawryluk (2014) found 18 species of rare or protected plant species in xerothermic roadside slopes, but the number of such demanding species was strongly reduced towards the upper parts of the slopes, which were influenced by fertilisers and herbicides from arable fields above the slopes.

Changes of the flora and vegetation lead to changes of the invertebrate communities, as has been demonstrated in a number of studies of pollinators (e.g. Noordijk 2009b; Hanley and Wilkins 2015; Cole et al. 2017). Invertebrates can also be expected to be directly influenced by pesticides, but we have not found any studies of impacts of agrochemicals on terrestrial invertebrates in road verges.

Considering the mechanisms for the effects of agriculture on roadside habitats, we might expect that some conditions may bolster the negative effects, for example particularly well-drained soils (reduce fertilisation effects), and high road embankments in which the upper parts can escape the spread of agrochemicals. We found, however, no studies of such differentiation between types of road verges.

In conclusion, land use in arable fields often has a negative impact on the biodiversity in roadside habitats, mainly through fertilisation and use of pesticides. Thus, from a management perspective, roadsides in agricultural land have lower priority if the aim is to promote high species richness or species of conservation concern in road verges. There might, however, be differences between types of roads regarding effects of agrochemicals, which should be investigated further. Even if roadsides in arable land may be species-poor, they can still constitute an important source, e.g. of flower resources in an otherwise ecologically deteriorated landscape.

Further, adjacent forest can be expected to contribute to forming the roadside habitat, but very few studies have investigated effects of tree shade and litter on roadside habitats. Proximity to forest (or presence of trees in general), as well as the type of forest and trees, are probably important criteria for roadside habitat classification, and thus need further investigation. This mainly requires new research, since there seems to be very little published information.

4.5.2 Landscape species pool and ecological similarity

The ecological similarities and differences between the roadside habitats and the landscape are of great importance for the roadsides’ contribution to biodiversity conservation. If roadsides offer similar habitat conditions as the surrounding habitats, then roadsides may support some of the landscape’s indigenous biodiversity (e.g. Jantunen et al. 2006; Lennartsson 2010; Noordijk et al. 2011). In general, road verges are characterized by openness, ground disturbance, vegetation management and succession. Roadsides can therefore favour species from pastures, dry meadows and arable fields, e.g. through providing complementary habitats for these species groups. This is of conservation importance especially if the area of important surrounding habitats is declining. In forest landscapes, in contrast, the roadsides constitute a different set of habitats than the surrounding landscape, and they may mainly have negative effects on the indigenous biodiversity, through reducing the area of (forest) habitats and favouring non-local species, including species that threaten local biodiversity (cf. sections 3.1 and 3.2).

Figure 36. In this case, the roadside habitat can be seen as an extension of the grazed pasture, but better for mowing-adapted early-flowering species. Orust, province of Bohuslän, Sweden. Photo Tommy Lennartsson.

Several studies demonstrated similarity between biodiversity in road verges and surrounding habitats, indicating that road verges were colonised from the surrounding habitats, and indicating subsequent exchange of individuals between habitats. Some of these studies compared habitat types in landscapes. For example, a Swedish study compared species composition in road verges and semi-natural grasslands using Jaccard similarity index and found 38–42% similarity. This can be compared with 57% overlap between mid-field islets and grasslands in the same two landscapes (Cousins 2006).

Other studies have also included spatial patterns of habitats in the analysis, for example the distance between the road and other habitat patches. Van Halder et al. (2017) showed that the proximity to grasslands as well as woodlands increased species richness and host plant specialisation in butterfly communities of linear habitats in France. Their interpretation of the results was that linear habitats may function as sinks and depend on immigration from nearby grasslands. The possibility that proximity to surrounding species pools influenced species richness through initial colonisation in the new habitats, was not discussed. In a study of 150 road verges along 51 km of a highway in central Spain, Arenas et al. (2017b) found that the establishment of native tree species along roads depended largely on the proximity to natural vegetation, and the occurrence of vectors in the form of birds or other animals, which help with the seed dispersal.

Additionally, landscape diversity has been suggested to constitute an important component of the spatial patterns of roadside habitats. Boháč et al. (2004) found a higher number of carabid beetles along smaller roads in the Czech Republic compared to highways. The authors explained the difference mainly as a higher plant diversity and higher patchiness in the landscape along the smaller roads compared to landscapes around the studied highways, which were more uniform and had lower plant diversity. The effect of landscape structure on butterfly species richness had a strongest effect on a spatial scale of 250 m in a Canadian study in Ontario (Flick et al. 2012). The authors postulate that the mechanisms behind these responses may have to do with the movement between complementary resources in the landscape.

Although the diversity of surrounding habitats, as well as the distance to them, can be assumed to influence roadside biodiversity through a continuous exchange of individuals (or a source-sink relationship), some studies did not find such impacts. For example, Munguira and Thomas (1992) reported no differences in abundance and diversity of butterflies between road verges in Dorset, U.K., depending on whether the verges stretched through intensive agricultural land, urban areas, or semi-natural grassland, heath or woodland. They explained the lack of landscape influence as being the result of most of the studied species being sedentary and having entire viable populations in the roadside habitats. Of course, the landscape may also influence populations of single species.

Mimicking of important habitats in roadsides is suggested in several practical guidelines as well as in scientific literature. For example, in Southern Britain, abandoned quarries and defence constructions are among the most important habitats for butterflies (Warren and Stephens 1989). Learning from those habitats, Thomas (1991) has suggested a design of larger slopes and cuttings along roads (see Munguira and Thomas 1992). He suggests that by making slopes descend in a series of steps rather than uniformly, and by excavating indentations in large slopes, roadsides may provide some of the most important features of these butterfly habitats. This would increase the diversity of food plants as well as create shelter and result in a more favourable microclimate for butterflies.

Several studies of vegetation establishment are performed in order to establish vegetation that is similar to other habitats of conservation concern in the landscape, such as semi-natural pastures and meadows (Rydgren et al. 2010; Auestad et al. 2016). A common type of studies is within projects for replacing

North American road verges dominated by non-native grasses or weeds with vegetation that resembles native prairie vegetation (see www.tallgrassprairiecentre.org). In the Iowa state, USA, such measures have resulted in a two-fold increase in species richness of habitat-sensitive butterflies, and a five-fold increase of their abundance (Ries et al. 2001). Although it seems logical that the local butterfly fauna should be favoured by local vegetation types compared to vegetation with invasive species, it is difficult to disentangle this mechanism from the effect of higher plant species richness in a prairie road verge compared to a grass road verge.

Origin of roadside biodiversity

Based on which species roadsides host from the surrounding landscape, habitats might be grouped into landscape-related categories. Such grouping would be useful for evaluating the conservation potential of different roadsides (different types and in different landscapes). In the Swedish road verge flora (Sjölund et al. 1999), such a grouping is suggested, combining a local perspective (considering, e.g., soil type and sun exposure) and a landscape perspective (considering the adjacent species pool).

In many countries, for example in those in Scandinavia, road verges are often associated with habitats and species assemblages belonging to the agricultural landscape (Lennartsson 2010; see also Helldin et al. 2019 for rail habitats). Cousins and Eriksson (2001) found that of the 152 species of vascular plants found in dry–mesic semi-natural grasslands in a Swedish region, 60% also occurred in road verges, which constituted the most common alternative habitat for those grassland species. For the 82 species found in moist–wet semi-natural grasslands, road verges were the second most common alternative habitat (62% of the grassland species). In addition, road verges had 11 habitat specialists (species occurring only in road verges). In total dry–mesic semi-natural grassland was the most species rich habitat in this landscape, followed by road verges and mid-field islets.

For species and habitats connected to such agricultural landscapes, disturbances and management regimes in road verges that resemble traditional management regimes can be expected to be favourable for biodiversity conservation.

In several other regions, road verges represent various types of near-natural grasslands or woodlands. In Australia, many species are adapted to fires, and may be favoured by the burning of roadsides (Palfi et al. 2017). Also, natural disturbances to the soil are common in many types of Australian habitats, and roadside habitats may possess similar conditions (Spooner et al. 2004). In Australia, ‘grassy woodland’ and similar grassland types have been heavily reduced and fragmented, and road verges today constitute an important refuge for species of these habitats (Forman and Alexander 1998; Lunt and Bennett 2000; Spooner 2015). On the other hand, other types of roadside management that are less similar to natural disturbance regimes may have negative impact on biodiversity. One example is mowing, which has been shown to have negative impacts on plant species richness in some Australian landscapes (see review by Forman and Alexander 1998). In Brazil, road verges harbour 70% of the plant species found in *Cerrado* wooded savanna (Vasconcelos et al. 2014).

Figure 37. Roads running through active semi-natural pastures may harbour a large proportion of the pasture biodiversity. Province of Belluno, Italy. Photo Tommy Lennartsson.

Importance of the historical landscape

As discussed earlier in this review, one of the major conservation values of roadsides is that they may preserve species originating from declining habitats. This implies that several of the species in roadsides may be the legacy of past landscapes, and, in the case of semi-natural habitats, also a biological cultural heritage from earlier land use. An analysis of 66 Swedish red-listed species in the agricultural landscape indicated that roadsides and other infrastructure habitats today contribute to preserving species from at least 17 habitats that were common in pre-industrial Swedish agriculture. These habitats are nowadays extremely rare or even completely lost (Lennartsson 2010).

Spooner and Lunt (2004) found that the conservation ranking of road corridors in south-eastern Australia was correlated with the age of the corridor, i.e. time since the corridor was set off as a reserve for a future road. In contrast, there was no correlation with time since a road was actually constructed in the reserve. The proposed explanation was that the oldest reserves, from the 1870s, were cleared and reserved at a time when human disturbance was small. The ecosystems in later reserves, on the other hand, were already to a larger extent degraded by anthropogenic disturbance. Land-use history before road reserve age was thus more important for the conservation values than later road-use activities. Some roads were even older than the oldest road reserves, i.e. they existed already before 1870. Interestingly, these roads had lower conservation ranking than those that were constructed later, which also could be explained by land-use history. These oldest roads usually originated as stock routes, used by farmers to transport livestock to the market. Since grazing is known to have deleterious effect on Australian native flora, low conservation values (associated with naturalness) could be expected in areas that have long been affected by intense grazing. The oldest roads, however, had the highest density of old hollow eucalyptus trees, whereas roads constructed after 1900 were dominated by *Callitris glaucophylla* trees (Spooner and Smallbone 2009). The eucalyptus trees were interpreted as a remnant of the original eucalyptus-rich, fire-characterised landscape. The fact that *Callitris* trees, not eucalyptus, established in younger roads, can be explained by an increasing abundance of *Callitris* in the landscape from the 1870s, caused by anthropogenic activities such as disturbance and fire prevention.

Figure 38. This road verge contains almost all species from rotational cultivation in semi-steppe. Babadag, County of Tulcea, Romania. Photo Tommy Lennartsson.

Koyanagi et al. (2009) compared road verges situated at the edges of open *Pinus densiflora* forests with different land use history in Japan, having plant species composition similar to semi-natural grasslands. The species richness in edges of forests was positively correlated with the availability of suitable grassland habitats around 1950 in the surrounding landscape at a 500x500 m scale. This suggests that species composition today is a legacy of changes that happened more than 50 years ago. The grassland species richness was also correlated to current habitat conditions (forest type, edge direction, road width and steepness). Also, Chaudron et al. (2018b) showed that species richness and composition in road verges in mid-western France depended to a higher extent on the local landscape history than the present landscape.

In a study by Cousins (2006) in two Swedish landscapes, current land use had significant effects on plant species richness in both landscapes. In one of the landscapes, the presence of semi-natural grassland 150 years ago also showed significant effects. Gustavsson et al. (2006) performed a similar study in semi-natural grassland and showed that land-use history 200 years ago, but not the current land use, had significant effects on plant species richness and diversity.

Landscape versus local habitat

One important applied question is the relative importance of landscape versus local conditions in roadside habitats. While the latter can be manipulated by measures for construction and maintenance, the former cannot. Therefore, in order to motivate measures for favouring biodiversity in road verges, it is important to know whether these measures favour colonisation from the landscape and enhance roadside biodiversity, or whether the landscape and species pool constrain the ecological efficiency of the effort. Very few studies, however, have addressed this question.

Van Halder et al. (2017) compared grassland butterflies in road verges and other linear habitats with grazed grasslands in three agricultural areas in France. The local variables were more important determinants for species richness and composition than landscape variables. Landscape variability also contributed more to explaining butterfly species composition in road verges than in grazed grasslands. The overall implication of the results was that populations in linear habitats depend on populations in the surrounding landscape as sources of colonisation, and probably also on resources in the surroundings. Furthermore, when a species pool is present in the landscape, measures for improving the roadside habitat are of crucial importance. Arenas et al. (2017b) found an effect of distance to natural vegetation on the establishment of trees along a Spanish highway. However, for wind-dispersed tree species the site characteristics on road verges was the most important factor for successful establishment.

From an applied perspective the adjacent species pool has been considered in recommendations for vegetation establishment in some practical guidelines. Methods based on spontaneous colonisation (Sjölund et al. 1999), seeding of local plant material (Johnson 2008), and on reuse of local topsoil (Trafikverket 2021) have been considered.

In conclusion, the reviewed literature provides many examples of the significance of the surrounding landscape for colonisation of roadside habitats and for subsequent exchange via dispersal. Effects have been found of both the current and the historical landscape, and on species composition estimates of both single species and species groups. The results vary between studies, depending on the landscape context and the system studied, and it is not possible or relevant to try to give an overall estimate of landscape effects.

Landscape effects on local roadside biodiversity, however, have large implications for roadside construction and management, in two ways in particular. First, the roadsides' potential to form habitats harbouring species of conservation concern is not entirely a question of how the roadsides are constructed and managed. In landscapes with large potential for colonisation of species of conservation concern, measures for improving the roadside habitat are more likely to give the desired results. Therefore, it might be more cost-efficient to assess the landscape regarding colonisation potential before costly measures are taken. Such assessment will also give guidance for how the roadside should be constructed and managed. On the other hand, if roadside habitats have a great potential to favour the landscape's biodiversity, but this potential is unlikely to be realised due to dispersal (colonisation) limitations, facilitated dispersal, i.e. sowing, planting and other introduction, may be a cost-efficient measure.

Second, if the current roadside biodiversity is largely a legacy of landscapes from the past, biodiversity cannot be expected to return if lost through, e.g., major reconstruction of the road. It is possible that even grading or ditching that removes the topsoil may irreversibly destroy roadside biodiversity. This calls for development of methods that enable maintenance and reconstruction without removing the roadsides' biodiversity.

Species of conservation concern often represent vanishing habitats. The fact that roadside habitats may harbour species from past landscapes implies that roadsides may be considerably different from the surrounding landscape and still be important for conservation of the landscape's biodiversity.

5. Conclusions

In this section we have collected all conclusions presented under different headlines throughout this report.

5.1 Knowledge and literature on biodiversity in roadside habitats

The collated wealth of examples of biodiversity in roadside habitats provide conclusive evidence that roadside habitats can and currently do contribute to the conservation of several groups of species. However, the studies are scattered over a wide range of organism groups, road verge types, regions, and landscapes, which makes it difficult to find guidance on how to manage specific types of roadside habitats or how to favour specific groups of organisms. This calls for a new direction in roadside habitat research, addressing specific conservation problems (e.g. the conservation of certain groups of threatened species). Such studies are a necessary complement to all studies that describe patterns in distribution and abundance of biodiversity in roadsides and surrounding landscapes. Much information can also be derived from studies in other habitats than roadsides, for example various types of grassland.

Most practical guidelines are based on considerable practical experience of road management and constitute examples of best practice recommendations. This type of experience-based knowledge should make an important complement to the rather restricted scientific support, but since such underlying knowledge is rarely presented, it gains less attention than it deserves. A more thorough compilation and evaluation of recommendations from guidelines than what has been possible here, can be recommended.

5.2 Source-critical aspects: Study design, context and definitions

The results of biodiversity studies in roadside habitats are highly context dependent. Results therefore need to be interpreted considering which organism group, which environmental variable (including management intervention), which type of roadside habitat, and which landscape have been studied. Of these in particular, the importance of the type of roadside habitat may have been overlooked, because of lack of an overall structure for how to classify roadside habitats, and lack of knowledge about their ecology.

5.3 How can existing knowledge be used to guide the construction and management of roads for biodiversity?

It seems clear that in order to answer questions about the importance, construction, and management of roadside habitats for biodiversity, it is rarely enough to perform a systematic review or meta-analysis, because too few comparable studies are available. Evidence needs to be retrieved from a more disparate range of studies. This, however, requires the review to be delimitated to highly specific questions, in order to make it possible to find and evaluate all relevant literature on the topic. Since selection criteria cannot be pre-defined as in systematic reviews, the review should include a thorough and transparent (e.g. narrative) source critical appraisal, as well as a self-critical approach when drawing conclusions.

Such approaches are commonly used in social sciences, for example when working with historical questions and historical sources. For example, source-pluralistic approaches can be used in combination with hypothetic-deductive structuring of questions.

5.4 How can roadside habitats contribute to biodiversity conservation?

Roadside habitats can enhance the conservation status of threatened biodiversity, but to varying degrees depending on region, landscape type, species, type of threat etc. There is a need for studies (including specific reviews of literature) of the importance of roadsides for biodiversity conservation in relation to other habitats in the landscape.

Notably, roadside habitats are not included in the directive’s list of habitats, which makes it difficult to assess the roadsides’ contribution to conservation in relation to the Habitats Directive’s framework. Based on this review and our own experience of roadside habitats, we do not believe that it is possible to translate roadside habitats into existing Natura 2000 habitats. However, important groups of roadside habitats could probably be identified using the Habitats Directive’s framework for habitat quality assessment and classification. The framework for roadside habitat ecology outlined in this review could serve as a starting point.

5.4.1 Reproduction and resource habitats for species of conservation concern

Although many studies of biodiversity in roadsides test correlations between biodiversity and different habitat features, there is a large need for reviews and studies of mechanisms for the relationships between species and their microhabitats. In particular, the importance of basic environmental conditions (climate, soil type, sun exposure, species pool etc.) and different processes (natural and anthropogenic ones, e.g. vegetation management, soil disturbance etc.) needs to be highlighted. Road verges probably favour a set of functional groups of species, particularly groups adapted to disturbance of vegetation and ground. Among those species, many are indeed generalists, but several also are specialists, some being threatened by the lack of disturbance in the surrounding landscape, in combination with habitat loss (which can in some cases be considered too intense disturbance).

Roadside habitats have a great potential to contribute to the conservation of plants, and likely to several other groups of organisms that depend on plants, mainly different types of invertebrates.

The reviewed studies of insects in roadside habitats show that roadsides may contribute considerably to improving their conservation status. The positive effects, however, differ between types of roadside habitats, landscapes and species groups. Unfortunately, the results of studies also differ depending on study design, choice of comparator etc., which makes it very difficult to disentangle species-habitat relationships in order to identify suitable and non-suitable habitat properties and management methods.

5.4.2 Effects on habitat fragmentation in the landscape

Our review confirms the results of Villemey et al. (2018), that the effects of road verges on dispersal differ between studies, and that observations of actual dispersal are few. Similar to other studies of biodiversity in roadsides however, dispersal-related studies are also strongly context dependent. Differences between habitats, species groups and landscapes are considerable, and contradicting results do not necessarily indicate an unclear effect, but rather that the studies investigate different ecological systems. We conclude that it is probably not relevant to ask whether road verges in general function as dispersal corridors. A more relevant question is under which circumstances road verges function as dispersal corridors, and under which ones they do not. With knowledge about those circumstances, roadside habitats can be constructed and managed in order to enhance connectivity of certain habitats, for certain species groups and in certain landscapes.

Thus, even if scientific evidence for a corridor function of road verges is poor, there are many indirect indications of such a function. The indications are of two main types: distribution patterns of species (or genes) and species having populations in roadside habitats.

5.4.3 Are roadside habitats ecological traps?

Examples of trap effects are few, both in total and in relation to the number of studies indicating that roadsides favour biodiversity of conservation concern. Therefore, the lack of evidence against trap effects should not motivate refraining from making road verge habitats as useful as possible for biodiversity. However, it should be acknowledged that trap effects have rarely been considered in studies of roadside biodiversity, and may be overlooked. In order to optimise roadside habitats' contribution to biodiversity conservation and avoid unnecessary negative effects, it seems important to identify the circumstances (habitat type, organism group, landscape, road type etc.) that increase the risk of making valuable road verges an ecological trap. It is equally important to identify the habitat variables that reduce the risk of a trap effect, e.g. reduced roadkill mortality, in a roadside habitat, and to translate those variables into trap mitigation measures in construction and maintenance. We recommend the concept of trap effects to be restricted to situations where roadside populations are non-viable, i.e. where roadside habitats constitute sink habitats by definition.

5.5 Key ecological factors for plants and insects in roadside habitats

The potential for favouring plants and insects in roadside habitats is large, but the importance varies considerably across types of roadside habitats, depending on combinations of environmental variables. Several variables can be manipulated when constructing and managing a road. In order to optimise building and management activities for biodiversity, there is an urgent need for better knowledge about how the most important variables influence plants and insects in roadsides.

We encourage in-depth reviews of single or smaller groups of environmental variables. In such knowledge compilations, studies should be evaluated with the aim to extract both theoretical and practical information about species-habitat relationships. Systematic reviews can be used if enough literature is available, such as the review of the effects of mowing practices by Jakobsson et al. (2018). However, in order to build guidelines on as much existing knowledge as possible, in most cases, systematic reviews need to be complemented with traditional reviews of relevant research that do not fill the systematic reviews' selection criteria.

Another important source of information is studies of single species and smaller groups of species. Many such studies and knowledge compilations have been performed for endangered species, and many provide important information about species-habitat relationships, that for several species include roadside habitats. Since the search strings used in this project focussed on roadside studies, publications of this type have only occasionally been found.

This, as well as other reviews, show that the effects of certain environmental variables are highly context-dependent. Depending on species group, ‘starting point’ and several other factors, the very same environmental variable, e.g. a certain type of vegetation cutting, may give different results. Therefore, each study needs individual contextualisation, together with other source-critical evaluation.

5.5.1 Ecological conditions

Soil properties

Considering that road construction includes considerable manipulation of the soil, and creates escarpments and embankments with new and often designed soil surfaces, better knowledge of relationships between soil properties and roadside vegetation and invertebrate fauna is crucial in order to favour roadside biodiversity. We encourage specific reviews of literature on soil–vegetation and soil–invertebrate relationships, as well as new research, preferably with a focus on biodiversity conservation issues.

Figure 39. Sandy roadside slope with frequent nest cavities for digging insects. Lindesberg, province of Västmanland, Sweden. Photo Jan Olof Helldin.

Although poorly supported by scientific evidence, a number of soil-related positive effects on biodiversity are well established in practice. Examples are higher plant-species richness on lime-rich soils, and the importance of certain types of sand for wild bees and other digging insects. The use of such soils, and the avoidance of nutrient-rich topsoil, can probably be recommended as general biodiversity-promoting measures, especially when motivated by specific conservation goals.

Light and temperature conditions: Edge effects, slope, and aspect

Several microhabitats in roadside environments can be expected to be extremely warm and light, depending on, e.g. the soil type and slope aspect. Although such conditions are known to be important for various specialised organism groups, they have rarely been studied in roadside habitats. Also, the potential biodiversity values of forest edges along roads are probably overlooked in conservation and road management.

Host plants for insects

Roadside habitats may be very important sources of host plants for several groups of insects, and of high conservation value in many landscape types. The literature we reviewed indicates that relationships between insects and their host plants are well known with respect to which insect species uses which plant species, but that considerably fewer studies address the insects' needs for specific 'ecological qualities' of the plants, for example requirements for certain microsites. Furthermore, relationships between the insects' seasonal rhythm (phenology) and the seasonal variation of plant resources are surprisingly poorly studied, for example in relation to timing of vegetation management.

In order to better utilise the roadsides' potentials, knowledge about their function as sources of host plants, including host plants in favourable microsites, seem crucial. We recommend extended knowledge compilations on this topic, including also studies not primarily dealing with roadside environments. In particular, studies of endangered and other demanding species would provide important additional knowledge.

Road size

Most studies of road effects on biodiversity have focussed on the road as a linear element, or corridor, through the landscape, containing habitats that are more or less different compared to the surrounding habitats. Biodiversity responses have been studied either along the verges, mainly addressing dispersal, or transversal to the road, addressing road effects on the landscape. We have found no studies that explicitly analyse road verge width in terms of habitat area, and, thus no studies of the potential importance of larger habitat areas that are common in highway construction. Such areas constitute habitat patches of considerable size, rather than a habitat corridor, and can be expected to have great potential to contribute to biodiversity conservation.

We encourage more explicit studies of wide road verges and other constructed areas in the road environment, which have the largest potential to support viable populations of species.

Figure 40. Motorway verges are often wide and may sum up to large grassland areas. Arboga, province of Västmanland, Sweden. Photo Jan Olof Helldin.

5.5.2 Disturbance and other ecological processes

Vegetation cutting

Frequent cutting as well as early cutting, probably favour plant species richness in nutrient-rich road verges in which species richness is inhibited by a few competitive plant species. Under such conditions, early and frequent cutting in combination with removal of the cut material can be expected to deplete the nutrient contents and reduce competition, thereby favouring species richness. From a conservation perspective, however, these types of road verges may be less prioritised since they are species-poor, dominated by grasses, and, even when being improved, may be species-poor compared to many other roadside habitats. In species-rich verges, usually having poorer nutrient status and less grass dominance, a single cutting per year, performed after most plants have finished their reproduction, is highly likely to favour plant species richness through enhanced flowering and seed production.

Reviews of studies of cutting regime effects on flora and vegetation have failed to identify clear consistent patterns that could support general recommendations for vegetation management. Single studies may provide clear evidence for advantages of one cutting regime compared to another, but different studies show disparate results. This is not surprising considering the great ecological variation across roadside habitats. We conclude that lack of consistent patterns across studies are not due to lack of consistent vegetation responses to cutting, but that overall patterns are hidden by ecological variation. A key to extracting guidelines for vegetation management from existing studies and knowledge should be to better understand why certain types of vegetation respond in certain ways to certain management regimes. It should be possible to establish a solid ecological foundation for cutting regimes with rather limited efforts by combining knowledge from road verges (including practical guidelines) and from meadows and pastures. Such an analysis should aim at guiding both the choice of road verges to cut for biodiversity, and suitable cutting regimes (timing, frequency, biomass removal etc) for those prioritised roadside habitats.

Removal of the cut material seems to generally favour plant species richness in road verges and other grasslands. In order to translate this general conclusion into management recommendations, it is, however, necessary to consider the cost efficiency of this rather expensive and complicated procedure. This calls for more specific studies of the magnitude of the effect of removal in different types of road verges. From a conservation perspective, it may not be cost-efficient spending resources on removal of nutrient-rich species-poor vegetation, because even improved vegetation may be rather species-poor. Similarly, removal may not be cost-efficient for low-productive species-rich vegetation, where the removal of the small amount of litter would only marginally increase species richness.

Burning

The number of studies of burning in roadside habitats are too few and scattered to allow any secure assessment of burning and roadside biodiversity. It seems that burning may be favourable if performed in a way that imitates fire regimes – natural or anthropogenic – that the local species are adapted to. The evidence is more ambiguous regarding burning as an alternative to cutting, i.e. as management method for grasslands; this is not specific for roadside grasslands but applies for grasslands in general.

Drought

Road constructions are generally well drained, and frequently include sun-exposed slopes, with both factors potentially contributing to episodes of drought-induced vegetation die-off. We have, however, not found any literature reporting studies of such drought-induced disturbance. It is likely that specific reviews of literature on the ecology of drought may suggest drought to be an important ecological process in some specific types of roadside habitats.

Disturbance of the ground and soil

This review has found several studies that implicitly, but rarely explicitly, indicate that mechanical disturbance of the ground is an important ecological process in roadside environments, and that many species-rich roadside habitats are formed and maintained by such disturbance. A systematic approach to research on ground disturbance in roadside habitats is however lacking, which we believe constitutes a critical deficit in our knowledge about roadside ecology.

Figure 41. Regular road maintenance include many activities that cause physical disturbance to the ground and field layer. Grönbo, province of Västmanland, Sweden. Photo Jan Olof Helldin.

We recommend specific reviews of and research on the importance of ground and soil disturbance in roadside habitats. The reviews should preferably also include studies from other disturbance-induced habitats. The role of ground disturbance also needs to be considered in the classification of roadside habitats (see e.g. Sjölund et al. 1999). Classification is treated in a separate sub-project of *EPIC-roads* and is not discussed any further here.

5.5.3 Plant competition and vegetation succession

One of the most conspicuous effects of ground disturbance is that it initiates a vegetation succession. This implies that disturbance-induced roadside habitats may be regarded as successional habitats. As discussed above, the importance of ground disturbance, and thus of succession, in roadside habitats, may have been overlooked in roadside research.

Succession can be slowed down by vegetation management, and eventually reach a more or less stable stage that is maintained by the cutting. Under many conditions, such as nutrient-rich soils, or conditions favourable for establishment of a dense cover of mosses or creeping woody vegetation, however, the vegetation becomes rather species poor compared to earlier successional stages. This, together with the potential importance of disturbance and succession raises the question of whether species richness in some roadside habitats cannot actually be preserved by cutting or other frequent management, because it is linked to a certain successional stage that will inevitably pass. In such habitats, it is important to identify a suitable frequency of ground disturbance, and suitable disturbance regimes, in order to restart the succession. Probably, in many cases the normal frequency of grading and ditching is sufficient, but this remains to be studied.

5.5.4 Importance of the landscape

Land use in arable fields often has a negative impact on the biodiversity in roadside habitats, mainly through fertilisation and use of pesticides. Thus, from a management perspective, roadsides in agricultural land have lower priority if the aim is to promote high species richness or species of conservation concern in road verges. There might, however, be differences between types of roads regarding effects of agrochemicals, which should be investigated further. Even if roadsides in arable land may be species-poor, they can still constitute an important source, e.g. of flower resources in an otherwise ecologically deteriorated landscape.

Further, adjacent forest can be expected to contribute to forming the roadside habitat, but very few studies have investigated effects of tree shade and litter on roadside habitats. Proximity to forest (or presence of trees in general), as well as the type of forest and trees, are probably important criteria for roadside habitat classification, and thus need further investigation. This mainly requires new research, since there seems to be very little published information.

Landscape species pool and ecological similarity

The reviewed literature provides many examples of the significance of the surrounding landscape for colonisation of roadside habitats and for subsequent exchange via dispersal. Effects have been found of both the current and the historical landscape, and on species composition estimates of both single species and species groups. The results vary between studies, depending on the landscape context and the system studied, and it is not possible or relevant to try to give an overall estimate of landscape effects.

Landscape effects on local roadside biodiversity, however, have large implications for roadside construction and management, in two ways in particular. First, the roadsides' potential to form habitats harbouring species of conservation concern is not entirely a question of how the roadsides are constructed and managed. In landscapes with large potential for colonisation of species of conservation concern, measures for improving the roadside habitat are more likely to give the desired results. Therefore, it might be more cost-efficient to assess the landscape regarding colonisation potential before costly measures are taken. Such assessment will also give guidance for how the roadside should be constructed and managed. On the other hand, if roadside habitats have a great potential to favour the landscape's biodiversity, but this potential is unlikely to be realised due to dispersal (colonisation) limitations, facilitated dispersal, i.e. sowing, planting and other introduction, may be a cost-efficient measure.

Second, if the current roadside biodiversity is largely a legacy of landscapes from the past, biodiversity cannot be expected to return if lost through, e.g., major reconstruction of the road. It is possible that even grading or ditching that removes the topsoil may irreversibly destroy roadside biodiversity. This calls for development of methods that enable maintenance and reconstruction without removing the roadsides' biodiversity.

Species of conservation concern often represent vanishing habitats. The fact that roadside habitats may harbour species from past landscapes implies that roadsides may be considerably different from the surrounding landscape and still be important for conservation of the landscape's biodiversity.

6. Implications of the review for road construction and management

This review has identified a number of particularly important environmental factors influencing conservation value of roadside habitats, e.g., species richness and abundance of red-listed or other more demanding plant species and their associated invertebrates. The importance of the factors is well supported by the reviewed literature, but for each factor, the literature usually shows too disparate and vague results to allow any unambiguous conclusions about specific relationships between environmental conditions and biodiversity. We believe, however, that for most factors, such relationships, as well as practical recommendations, can be established through specific knowledge compilations and analyses.

Our review nevertheless enables discussing some environmental factors in a way that can serve as base for practical recommendations. Two types of information in particular has proven useful:

- Environmental factors that, at a general level, show rather consistent positive effects on conservation value across studies. Examples are nutrient-poor conditions, native and local plant species, and vegetation management that is adapted to target species (here mainly species of conservation concern).
- Environmental factors that show highly different effects on biodiversity in different studies, but for which we are able to discuss the mechanisms behind these differences. Examples are vegetation cutting regime in relation to nutrient richness and species composition, and ecological similarity between roadsides and adjacent landscapes.

We discuss these factors throughout this review, but here we summarise the main findings in an applied perspective. The conclusions can be presented in three packages, serving as base for three practical guidelines:

1. Construction of roadside habitats for biodiversity of conservation concern
2. Management of ground and vegetation for biodiversity of conservation concern in roadside habitats
3. Construction and management of roadside habitats in a landscape perspective

We have not been able to extract enough information for a guideline for where and how to prioritise dispersal corridors for biodiversity through landscapes. One recommendation for how to optimise corridor functions of roadsides can be given, however: to create roadside habitats of conservation concern whenever possible, and especially in landscapes where core habitats (that may be connected by roadside habitats) are abundant.

Below we present each package of conclusions by summarising the key results of the literature review together with an interpretation of the results in an applied perspective. This information was used to develop guidelines for roadside habitats in Hanslin et al. (2019).

6.1 Construction of roadside habitats for biodiversity of conservation concern

6.1.1 Key results of the review

- ✓ Roadside habitats can be rich in vascular plants and invertebrates, also regarding specialists and threatened species.
- ✓ As in most other habitats, plant species richness in roadside habitats is higher on calcareous soils than on acidic soils. Greater plant species richness, in turn, supports a more species-rich fauna of invertebrates.
- ✓ Roadside habitats can be colonised by plants from surrounding habitats. There are however considerable knowledge gaps regarding the efficiency of spontaneous colonisation, for example, which species groups colonise and, in particular, from what distances colonisation normally occur.
- ✓ Many roadside habitats are characterized by frequent disturbance to the ground. Disturbances creates bare soil and initiates vegetation succession and the establishment of pioneer species, many of which are of conservation concern, but also including invasive species.
- ✓ Low productivity is beneficial for plant species richness and for species of conservation concern, for two reasons:
    - o Low productivity slows down vegetation succession after soil disturbance, leading to longer periods of early and intermediate succession phases. Those phases are often more species-rich compared to later phases, in which the vegetation is dominated by fewer, competitive species. Early phases have more of bare soil, which is beneficial for many ground-dwelling and digging insects, and for the establishment of plant species from adjacent habitats. Longer periods with sparse vegetation thus increase the chances of spontaneous colonization.
    - o Low productivity is essential for high species richness also in mowing-generated grass swards, because it prevents the domination of tall competitive species. Mowing is further discussed in 6.2.2.

- ✓ Low productivity is often associated with well-drained, for example sandy, soils, and the choice of material for building the road is therefore crucial. Low-productive and dry conditions may be created also by high evapotranspiration in sun-exposed slopes.
- ✓ In some landscapes, nutrient-rich habitats may be hotspots for biodiversity. However, such habitats are usually difficult to construct and maintain in roadside environments, because the vegetation on nutrient-rich soils needs certain regular management not to become dominated by a few competitive species.
- ✓ Roadside ditches and other drainage constructions may provide wet or moist habitats and vegetation types of great value for biodiversity.
- ✓ Measures for vegetation establishment, e.g. reuse of topsoiling and seeding, are rarely performed for biodiversity conservation reasons, but practices are usually applied in order to establish a vegetation cover rapidly. In some practical guidelines reuse of topsoil from the road corridor is suggested as a measure for establishing the local flora, but there are hardly any studies of the outcomes of topsoil reuse.
- ✓ Newly constructed roadside habitats are extremely vulnerable to the establishment of invasive plant species that largely transform the habitats.

6.1.2 Interpretation of the results

- ➢ Roadside habitats can make a considerable contribution to biodiversity conservation, through being suitable for many specialist species, being large in cumulative area (and often also in area of local habitat), and offering cost-efficient conservation options, not least in centres of urbanisation.
- ➢ Road construction and management include considerable manipulation of the soil and ground. Since soil type and ground conditions are crucial for roadside habitats, road construction and maintenance thus offers great potential for creating biodiversity-rich habitats that contribute to biodiversity conservation.
- ➢ There are many knowledge gaps regarding relationships between soil type and roadside biodiversity. Knowledge gaps also include common practices such as the reuse of stripped topsoil in order to establish new vegetation.
- ➢ The conservation benefits of roadsides differ among countries depending on which groups of species are nationally protected, threatened and red-listed. Roadsides can provide a certain group, or range, of habitats, and the number of species of conservation concern that belongs to that group is larger in some countries than others. Through the design of roadsides it is possible to

influence, within certain limits, which habitats are created, and the design therefore should be adapted to conservation policies.

- In contrast to most other types of nature, roadsides have rarely been subject to systematic classification based on structure, species communities, ecological conditions, processes etc. In order to create a foundation for assessment of biodiversity potentials and management needs, roadside habitats should be described using policy-relevant ecological frameworks, e.g. similar to the European Nature 2000 framework.
- In spite of several important knowledge gaps, interpretation of research, biodiversity assessments and practical experience suggests a number of key factors for biodiversity, related to soil and substrate, which can be used as a base for practical recommendations.
- In general, low-productivity soils have the best potential for forming biodiversity-rich habitats. Knowledge is lacking on whether there are also landscapes in which biodiversity is favoured by the creation of nutrient-rich roadsides. The importance and properties of wet ditch habitats have also been poorly investigated, although some examples indicate potential for creating moist habitats when building infrastructure.
- Successional, sparse and initially ruderal vegetation on mineral-rich topsoil is easier to create in roadside habitats than grass sward vegetation, which takes a long time to develop.
- For the establishment of plant species of conservation concern in roadsides, it is not possible to rely entirely on spontaneous colonisation from surrounding habitats. Dispersal of some species or from some sites may need to be facilitated by active transfer of seeds or plants.
- Biodiversity connected to trees and forests is not addressed in this study, but roads probably have the potential to favour biodiversity of light-demanding shrubs and old trees, especially in the edge between an open road corridor and an adjacent forest, and in hedgerows and tree avenues.

6.2 Management of ground and vegetation for biodiversity of conservation concern in roadside habitats

6.2.1 Key results of the review

- ✓ The ecological significance of vegetation management in roadside habitats has been acknowledged and studied, often referring to a resemblance between cut roadsides and managed semi-natural grassland. The significance of ground disturbance and the successional characteristics of roadside vegetation has attracted considerably less attention.

- ✓ The role of an interplay between disturbance and cutting for the vegetation composition and succession in roadsides has hardly been addressed at all.
- ✓ In spite of a relative wealth of studies on roadside cutting and vegetation, rather few studies relate their results to conservation goals or species of conservation concern. Commonly used response variables, such as species, richness can not directly be translated into conservation value.
- ✓ The most commonly studied components of vegetation management are timing and frequency of cutting (once, twice or more per year), and removal of the cut material.
- ✓ Empirical studies show disparate results regarding all three components. Biodiversity effects of a certain modification of management, for example later cutting or more frequent cutting, vary between studies from positive to neutral and negative. The discrepancies between studies are probably caused by differences in the vegetation types studied, in particular differences in vegetation productivity.
- ✓ Although there are obvious interaction effects between timing of cutting and frequency of cutting, relationships between those two components have not been systematically evaluated. This is the case also for relationships between frequency of cutting and soil productivity.
- ✓ Mowing for conservation purposes has been studied in meadow habitats, but results and experiences from such studies have rarely been considered in roadside contexts.
- ✓ Although the significance for biodiversity of sparse vegetation and occurrence of bare soil in roadside habitats have been demonstrated in several studies, it has rarely been studied which factors, including ground and vegetation management, that influence the vegetation cover.

6.2.2 Interpretation of the results

- ➢ An ecological design of roadside management should consider both soil (ground) and vegetation, and the interactions between those factors. Knowledge about such factors could probably be compiled through interpreting ecological literature from roadside habitats and from other habitats in an applied roadside management perspective. So far this has not been done, and the possibilities of designing management of roadside habitats for biodiversity are therefore somewhat limited by lack of knowledge. However, the literature on roadsides provide a number of indications of management effects on biodiversity that can be used for developing guidelines.

- It can be assumed that, following ground disturbance, the vegetation in nutrient-poor or dry conditions reaches a stage of very slow succession, with low and sparse vegetation and good colonisation potential for demanding species from sand habitats, dry meadows, steppe-like habitats etc. There is little need for ground disturbance (to restart succession) and cutting other than to prevent establishment of woody vegetation.
- On more nutrient-rich soils, the succession following ground disturbance go towards tall and species-poor vegetation in which herbs and small plant species are outcompeted mainly by grasses. Here regular cutting is required in order to slow down succession and reduce competition. Mulching accelerates succession towards tall species-poor swards by accumulating nutrient-rich matter in the soil.
    - In high nutrient levels, two or more cuttings per year, combined with removal of the cut material may be needed to keep vegetation and competition low. Such intense cutting, however, restricts the flora and fauna to species that can cope with repeated cutting. Many species of conservation concern can not, as indicated by information about red-listed species as well as by studies of meadow ecosystems. High nutrient levels therefore reduce the potentials of maintaining high species richness including demanding grassland species of plants and invertebrates, i.e. habitats and vegetation of high conservation concern.
    - In moderately high nutrient levels, one cutting event combined with removal of the cut material is enough to keep the vegetation low and to slow down succession. Since more species can cope with a single cutting than repeated cutting, moderately rich soils have better potentials to form species-rich vegetation and to harbour demanding grassland species compared to richer soils. The timing of cutting is then an important factor.
- It has not been empirically or theoretically evaluated under which nutrient conditions and in which successional stages repeated cutting has desired effects on plant diversity, especially regarding biodiversity (including invertebrates) of conservation concern. This knowledge gap also applies to biomass removal. Much of the needed knowledge could probably be synthesized by using information from other mowing- or grazing-generated habitats. Such a synthesis should be done for different conservation targets, such as demanding plant species of conservation concern, invertebrates, and pollen/nectar resources, including cutting-tolerant nectar plants.

- Effects of repeated cutting imposes positive effects on plant species richness of biomass removal and nutrient depletion, but negative effects on several less disturbance-tolerant organisms. This trade-off can probably to some extent be reduced through performing cutting when plants and invertebrates are less sensitive, e.g. in the autumn. Suitable cutting schemes can be developed by combining information about soil properties, vegetation structure and composition, and ecology of different species groups, especially tolerance and phenology.
- Cutting and biomass removal on soils with low enough nutrient levels may in the long run create a stable sward similar to semi-natural meadow or pasture habitats. If this is not the case, and the vegetation becomes tall and less species-rich, the succession should probably be restarted, e.g. by scraping off the accumulated organic top layer.
- If scraping is performed for drainage or other reasons where a diverse flora still remains, measures should be taken to preserve the flora, e.g. by leaving unscraped islands of vegetation, or by re-sowing target species or the entire vegetation. Re-sowing could be done using seeds or hay collected before scraping, or by using smaller portions (not a cover of) of re-used topsoil with seed bank.
- In nutrient-poor and dry conditions, some competitive species may still establish, for example tall drought-tolerant grasses. Species richness can be maintained by a cutting regime that hampers these competitors, for example one early cutting (preferably when or slightly before the competitor flowers) with or without removal of hay (depending on productivity).
- If invasive plant species establish, vegetation management needs to change focus from favouring habitats and species of conservation concern to mitigation of the invasives. Such mitigation management usually includes intensified and earlier cutting, which disfavours many species of conservation concern. Thus, even if the invasives can be controlled by adapted management, species richness and conservation value of the habitat can be assumed to be strongly reduced by the presence of invasive species.
- Timing of cutting should be adapted to the phenology and cutting tolerance of the vegetation, in particular to target species of conservation concern. Examples of how different species groups are favoured by different cutting time are given in Hanslin et al. (2019).

Figure 42. Experimental scraping and unscraped islands of vegetation. Uppsala, province of Uppland, Sweden. Photo Tommy Lennartsson.

6.3 Construction and management of roadside habitats in a landscape perspective

6.3.1 Key results of the review

- ✓ Roads and their habitats cut through almost every type of landscape in Europe, although they are most common in centres of urbanisation in the lowlands.
- ✓ The influence of roadside habitats on the diversity and abundance of the local species, including species of conservation concern, varies from positive to neutral and negative depending on the interaction between landscape type (mainly the landscape's habitat configuration) and roadside type.
- ✓ One of the major explanations for roads contributing to biodiversity conservation is that some roads provide habitats for essential resources and reproduction for species of conservation concern in the surrounding landscape. This often implies that roadsides harbour species from historically richer landscapes and land-use forms.

- ✓ Although there are several indications of roads serving as dispersal corridors or stepping-stones, empirical studies are ecologically and geographically diverse and show diverging results. There is thus little information about the factors in the roadside and landscape that contribute to dispersal functions of roadsides, the species groups favoured and possible dispersal rates and distances.
- ✓ Direct evidence of roadsides contributing to green infrastructure is provided by the actual occurrence of reproducing populations or foraging individuals in roadside habitats. This contributes to a denser pattern of species distributions and creates a potential for dispersal along the road.
- ✓ Adjacent habitats sometimes strongly influence the local conditions in the roadside habitat in a negative way, e.g. through shading and leaf litter (adjacent forest) or fertilisation and biocides (adjacent arable fields).

6.3.2 Interpretation of the results

- ➢ The ecological similarity between the roadside habitats and the habitats in the surrounding landscape is of paramount importance for a road’s impact on local and regional biodiversity, including its contribution to conservation (cf. Hanslin et al. 2019).
- ➢ In open or previously open landscapes where many species depend on the type of habitats that occur along roads, roadsides may increase the availability of important habitats and resources, thereby favouring landscape biodiversity.
- ➢ In other landscapes, for example forested landscapes, open roadside habitats are less likely to offer habitats for the local (forest) flora and fauna. In such cases, total biodiversity may increase, but without favouring the landscape’s species. Roadside habitats may even pose threats by introducing invasive species.
- ➢ In many landscapes, roadside habitats mimic or preserve historical habitats that have disappeared in the surroundings due to changed and intensified land use. Roadside habitats thereby constitute a biological cultural heritage, which may be important for conservation. This implies that roadside habitats may be important for conservation despite being ecologically different from the current surrounding habitats. In such cases, roadside habitats may constitute biodiversity hotspots similar to various remnant semi-natural or natural habitats.
- ➢ The roadside habitats may have important functions as corridors or stepping stones for species, for example for open-landscape species through abandoned and overgrown landscapes. The most important factors supporting this dispersal function are that roads provide either habitats for reproduction and

multi-generation dispersal, or important resources such as flower resources that are used by pollinators along the road. Another factor is increased dispersal by vehicles or roadside management equipment. Other than thus making roadside habitats as suitable as possible for biodiversity, there is not sufficient knowledge for recommending measures for how and where to make roadsides conduits for dispersal.

- Because of negative effects of some types of adjacent habitats and land-use forms, many stretches of roadsides cannot be expected to be important for biodiversity. This is especially the case for habitats exposed to fertiliser and pesticides from adjacent arable fields. Forest may restrict roadside biodiversity through shading, where the long-term effect depends on the longevity of the forest stand. Open-land species in the roadside may expand following cutting of the forest.
- Conversely, roadsides through biodiversity-rich landscapes, e.g. nature reserves, may show higher biodiversity.
- Importantly, far from all species groups in a landscape can be favoured by roadside habitats. This implies that a new road may eradicate habitats, ecological resources and species of conservation concern without offering any alternative roadside habitats.
- Roadside habitats and their species are frequently discussed in a biodiversity conservation context, but analysis is required on the extent to which roadsides can also contribute to the conservation of cultural heritage, by harbouring biological cultural heritage from past landscapes, ecosystems and land-use forms.
- Historical land-use in the original habitats of species may inform roadside management, e.g. in terms of timing of vegetation cutting and type and frequency of ground disturbance.

Acknowledgements

The research presented in this report was carried out as part of the CEDR Transnational Road Research Programme Call 2016. The funding for the research was provided by the national road administrations of Austria, Germany, Ireland, Netherlands, Norway, Slovenia and Sweden. We are grateful for comments on this review by the members of the CEDR PEB group, especially Pia Bartels, Toine Morel, and Anders Sjölund. We also thank Jan Olof Helldin for thorough reading of and valuable comments on the manuscript, for providing photos and for doing the final editing of the publication.

References

Aavik, T., Augenstein, I., Bailey, D., Herzog, F., Zobel, M. and Liira, J. 2008. What is the role of local landscape structure in the vegetation composition of field boundaries? Applied Vegetation Science 11:375-386.

Aavik, T. and Liira, J. 2010. Quantifying the effect of organic farming, field boundary type and landscape structure on the vegetation of field boundaries. Agriculture, Ecosystems and Environment 135:178–186.

Akbar, K.F., Hale, W.H.G. and Headly, A.D.D. 2009. Floristic composition and environmental determinants of roadside vegetation in North England. Polish Journal of Ecology 57:73-88.

Akbar, K.F., Hale, W.H.G., Headly, A.D.D. and Ashraf, I. 2010. Evaluation of conservation status of roadside verges and their vegetation in North England. Polish Journal of Ecology 58:459–467.

Allem, A.C. 1997. Roadside habitats: a missing link in the conservation agenda. The Environmentalist 17:7-10.

Anderson, E-L., Lenning, J. and Lindell, A. 2011. Växtlighet i vägmiljö. Trafikverket Report 2011:140, Borlänge, Sweden.

Andersson, H. and Askling J. 2005. Seminarium om biologisk mångfald i artrika torrmarker i järnvägsmiljöer 2004-02-05. Calluna AB. Miljösektionen, Banverket. Rapport 2005:6.

Andersson, P., Koffman, A., Sjödin, N.E. and Johansson, V. 2017. Roads may act as barriers to flying insects: Species composition of bees and wasps differs on two sides of a large highway. Nature Conservation 18:47–59.

Ansong, M. and Pickering, C. 2013 Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. PLoS ONE. doi:10.1371/journal.pone.0080275.

Archbold, O.W. 1995. Ecology of World vegetation. Chapman and Hall, London.

Arenas, J.M., Escudero, A., Mola, I. and Casado, M.A. 2017a. Roadsides: an opportunity for biodiversity conservation. Applied Vegetation Science 20(4):527–537.

Arenas, J.M., Lázaro-Lobo, A., Mola, I., Escudero, A. and Casado, M.A. 2017b. The influence of site factors and proximity of adjacent vegetation on tree regeneration into roadslopes. Ecological Engineering 101:120–129.

Åström, M., Pettersson, L.B., Öckinger, E. and Hedin, J. 2013. Habitat preferences and conservation of the marbled jewel beetle Poecilonota variolosa (Buprestidae). Journal of Insect Conservation 17:1145–1154.

Auestad, I., Rydgren, K., Jongejans, E. and de Kroon, H. 2010. *Pimpinella saxifraga* is maintained in road verges by mosaic management. Biological Conservation 143:899–907.

Auestad, I., Rydgren, K. and Austad, I. 2011. Road verges: Potential refuges for declining grassland species despite remnant vegetation dynamics. Annales Botanici Fennici 48:289-303.

Auestad, I., Rydgren, K. and Spindelböck, J.P. 2013. Management history affects grassland seed bank build-up. Plant ecology 214:1467–1477.

Auestad, I., Rydgren, K. and Austad, I. 2016. Near-natural methods promote restoration of species-rich grassland vegetation—revisiting a road verge trial after 9 years. Restoration ecology 24:381-389.

Auffret, A.G. 2011. Can seed dispersal by human activity play a useful role for the conservation of European grasslands? Applied Vegetation Science 14:291–303.

Auffret, A.G. and Cousins, S.A.O. 2013. Grassland connectivity by motor vehicles and grazing livestock. Ecography 36:1150–1157.

Avon, C., Bergés, L., Dumas, Y. and Dupouey, J-L. 2011. Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. Forest Ecology and Management 259:1546–1555.

Baltzinger, M., Archaux, F., Gosselin, M. and Chevalier, R. 2011. Contribution of forest management artefacts to plant diversity at a forest scale. Annals of Forest Science 68:395–406.

Barker, A.V. and Prostak, R.G. 2009. Alternative management of roadside vegetation. Horticultural Technology 19:346-352.

Batáry, P., Körösi, A., Örvössy, N., Kövér, S. and Peregovits, L. 2009. Species-specific distribution of two sympatric *Maculinea* butterflies across different meadow edges. Journal of Insect Conservation 13:223–230.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482–91.

Baum, K.A. and Sharber, W.V. 2012. Fire creates host plant patches for monarch butterflies. Biology Letters. 8: 968-971.

Baxter-Gilbert, J.H., Riley, J.L., Neufeld, J.H., Litzgus, J.D. and Lesbarrères, D. 2015. Road mortality potentially responsible for billions of pollinating insect deaths annually. Journal of Insect Conservation 19:1029–35.

Beier, P. and Noss, R.F.1998. Do habitat corridors provide connectivity? Conservation Biology 12:1241–52.

Bellamy, P.E., Shore, R.F., Ardeshar, D., Treweek, J.R. and Sparks, T.H. 2000. Road verges as habitat for small mammals in Britain. Mammalian Review 30:131–139.

Bennie, J., Hill, M.O., Baxter, R. and Huntley, B. 2006. Influence of slope and aspect on long-term vegetation change in British chalk grasslands. Journal of Ecology 94:355-368.

Berg, Å., Ahrné, K., Öckinger, E., Svensson, R. and Söderström, B. 2011. Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. Biological Conservation 144:2819–2831.

Bernes, C., Bullock, J.M., Jakobsson, S., Rundlöf, M., Verheyen, K. and Lindborg, R. 2017. How are biodiversity and dispersal of species affected by the management of roadsides? Environmental Evidence 6:24. DOI 10.1186/s13750-017-0103-1.

Berry, K.H., Weigand, J.F., Gowan, T.A. and Mack, J.S. 2016. Bidirectional recovery patterns of Mojave Desert vegetation in an aqueduct pipeline corridor after 36 years: I. Perennial shrubs and grasses. Journal of Arid Environments 124:413-425.

Bjørndalen, J.-E. 1972. Jernbanefloristiske notater fra Bergen og Haugastøl. Blyttia 30:125-133.

Bochet, E., Tormo, J. and García-Fayos, P. 2010. Native Species for Roadslope Revegetation: Selection, Validation, and Cost Effectiveness. Restoration Ecology 18(5):656–666.

Bochet, E. and García-Fayos, P. 2004. Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia, Spain. Restoration Ecology 12:166–174.

Bochet, E. and García-Fayos, P. 2015. Identifying plant traits: A key aspect for species selection in restoration of eroded roadsides in semiarid environments. Ecological Engineering 83:444–451.

Boháč, J., Hanousková, I. and Matějka, K. 2004. Effect of habitat fragmentation due to traffic impact of different intensity on epigeic beetle communities in cultural landscape of the Czech Republic. Ekologia Bratislava 23:35-46.

Bouchet, D.C., Cheptou, P.O. and Munoz, F. 2017. Mowing influences community-level variation in resource-use strategies and flowering phenology along an ecological succession on Mediterranean road slopes. Applied Vegetation Science, 20:376–387.

Brandt, J., Henderson, K., Uthe, J. and Urice, M. 2015. Integrated Roadside Vegetation Management, Technical manual. Faculty Book Gallery. 116, Univ. Of Northern Iowa, Cedar Falls, USA.

Bratli, H., Økland, T., Halvorsen Økland, R., Dramstad, W.E., Elven, R., Engan, G., Fjellstad, W., Heegaard, E., Pedersen, O. and Solstad, H. 2006. Patterns of variation in vascular plant species richness and composition in SE Norwegian agricultural landscapes. Agriculture, Ecosystems and Environment 114:270–286.

Bromley, J., McCarthy, B. and Shellswell, C. 2019. Managing grassland road verges, a best practice guide. Plantlife, Salisbury, UK.

Brown, R.N. and Sawyer, C.D. 2012. Plant Species Diversity of Highway Roadsides in Southern New England. Northeastern Naturalist, 19:25-42.

Bubova, T., Vrabec, V., Kulma, M. and Nowicki, P. 2015. Land management impacts on European butterflies of conservation concern: a review. Journal of Insect Conservation 19:805–821.

Buonopane, M., Snider, G., Kerns, B.K. and Doescherb, P.S. 2013. Complex restoration challenges: Weeds, seeds, and roads in a forested Wildland Urban Interface. Forest Ecology and Management 295:87-96.

Čepelová, B. and Münzbergová, Z. 2012. Factors determining the plant species diversity and species composition in a suburban landscape. Landscape and Urban Planning 106: 336-346.

Cerdá, A. 1998. The influence of aspect and vegetation on seasonal changes in erosion under rainfall simulation on a clay soil in Spain. Canadian Journal of Soil Science 78:321-330.

Chaudron, C., Chauvel, B. and Isselin-Nondedeu, F. 2016a. Effects of late mowing on plant species richness and seed rain in road verges and adjacent arable fields. Agriculture, Ecosystems and Environment 232:218–226.

Chaudron, C., Perronne, R., Bonthoux, S. and Di Pietro, F. 2016b. Influence of management practices on plant assemblages of road–field boundaries in an agricultural landscape. Applied Vegetation Science 19:644–654.

Chaudron, C. and Isselin-Nondedeu, F. 2017. Assessing the effects of mowing machinery on seed dispersal pattern: a test of two methods of seed tracking. Botany Letters 164:413–423.

Chaudron, C., Perronne, R. and Di Pietro, F. 2018a. Functional response of plant assemblages to management practices in road–field boundaries. Applied Vegetation Science 21:33–44.

Chaudron, C., Perronne, R., Bonthoux, S. and Di Pietro, F. 2018b. A stronger influence of past rather than present landscape structure on present plant species richness of road-field boundaries. Acta Oecologica 92:85–94.

Chiuffo, M.C., Cock, M.C., Prina, A.O. and Hierro, J.L. 2018. Response of native and non-native ruderals to natural and human disturbance. Biological Invasions 20:2915–2925.

Clark, C.M. and Tilman, D. 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. Nature 451:712–715.

Cochard, A., Pithon, J., Jagaille, M., Beaujouan, V., Pain, G. and Daniel, H. 2017. Grassland plant species occurring in extensively managed road verges are filtered by urban environments. Plant Ecology and Diversity 10:217–229.

Coffin, A.W. 2007. From roadkill to road ecology: A review of the ecological effects of roads. Journal of Transport Geography 15:396-406.

Cole, L.J., Brocklehurst, S., Robertson, D., Harrison, W. and McCracken, D.I. 2017. Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. Agriculture, Ecosystems and Environment 246:157–167.

Cotswolds Conservation Board 2015. The management of roadside verges. Position statement. Gloucester, U.K.

Council of Europe 1987. Map of the natural vegetation of the member countries of the European Community and the Council of Europe, CoE, Strasbourg.

Cousins, S.O.A. and Eriksson, O. 2001. Plant species occurrences in a rural hemiboreal landscape: effects of remnant habitats, site history, topography and soil. Ecography 24:461-469.

Cousins, S.O.A. 2006. Plant species richness in midfield islets and road verges – The effect of landscape fragmentation. Biological conservation 127:500–509.

Crawley, M.J. 1997a. The structure of plant communities. In: Crawley M.J. (ed.), Plant Ecology. Blackwell, 2nd edition, ch. 14.

Crawley, M.J. 1997b. Life history and environment. In: Crawley M.J. (ed.), Plant Ecology. Blackwell, 2nd edition.

Dai, X.H., Xu, J.S. and Ding, X.L. 2013. Circular distribution pattern of plant modulars and endophagous herbivory within tree crowns: The impact of roadside light conditions. Journal of Insect Science Vol. 13 Article 141.

Daniels, J.C. 2017. Survey of Key Monarch Habitat Areas along Roadways in Central and North Florida. Retrieved from http://www.fdot.gov/research/Completed_Proj/Summary_RD/FDOT-BDV31-977-49-rpt.pdf

De Blois, S., Domon, G. and Bouchard, A. 2002. Factors affecting plant species distribution in hedgerows of southern Quebec. Biological Conservation 105:355–367.

de la Riva, E.G., Casado, M.A., Jiménez, M.D., Mola, I., Costa-Tenorio, M. and Balaguer, L. 2011. Rates of local colonization and extinction reveal diverse plant community assembly mechanisms on road verges in central Spain. Journal of Vegetation Science 22: 292 - 302. Doi: 10.1111/j.1654-1103.2010.01248.x

Delgado, J.D., Arroyo, N.L., Arevalo, J.R. and Fernandez-Palacios, J.M. 2013a. Road edge effects on litter invertebrate communities of subtropical forests. Journal of Natural History 47: 203–236. http://dx.doi.org/10.1080/00222933.2012.743610.

Delgado, J.D., Morales, G.M., Arroyo, N.L. and Fernandez-Palacios, J.M. 2013b. The responses of leaf litter invertebrates to environmental gradients along road edges in subtropical island forests. Pedobiologia 56:137-146.

Dennis, A. 1992. Conservation of rare and threatened species in linear reserves. The Victorian Naturalist 109:121–125.

Dennis, P. and Fry, G.L.A. 1992. Field margins - can they enhance natural enemy population densities and general arthropod diversity on farmland. Agriculture Ecosystems and Environment 40:95-115.

Dymitryszyn, I. 2014. The effect of the construction and renovation of a highway bypass in Central Poland on the carabid beetle fauna (Coleoptera: Carabidae). European Journal of Entomology 111:655–662.

Edwards, F.A., Finan, J., Graham, L.K., Larsen, T.H., Wilcove, D.S., Hsu, W.W. and Hamer, K.C. 2017. The impact of logging roads on dung beetle assemblages in a tropical rainforest reserve. Biological conservation 205:85-92.

Egizi, A., Kiser, J., Abadam, C. and Fonseca, D.M. 2016. The hitchhiker's guide to becoming invasive: exotic mosquitoes spread across a U.S. state by human transport not autonomous flight. Mol. Ecol. 25:3033–3047.

Entsminger, E.D., Jones, J.C., Guyton, J.W., Strickland, B.K. and Leopold, B.D. 2017. Evaluation of mowing frequency on right-of-way plant communities in Mississippi. Journal of Fish and Wildlife Management 8:125-139.

Erb, L.A., Willey, L.L., Johnson, L., Hines, J.E. and Cook, R.P. 2015. Detecting Long-Term Population Trends for an Elusive Reptile Species. Journal of Wildlife Management 79:1062-1071.

Eritja, R., Palmer, J.R.B, Roiz, D., Sanpera-Calbet, I. and Bartumeus, F. 2017. Direct Evidence of Adult Aedes albopictus Dispersal by Car. Nature Article number 14399.

Eversham, B.C. and Telfer, M.G. 1994. Conservation value of roadside verges for stenotopic heathland Carabidae: corridors or refugia? Biodiversity and Conservation 3:538-545.

Fahrig, L. and Rytwinski, T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14(1):21 (online).

Fallahchai, M.M., Haghverdi, K. and Mojaddam, M.S. 2018. Ecological effects of forest roads on plant species diversity in Caspian forests of Iran. Acta Ecologica Sinica 38:255–261.

Fekete, R., Nagy, T., Bódis, J., Biró, É., Löki, V., Süveges, K., Takács, A., Tökölyi, J. and Molnár, V.A. 2017. Roadside verges as habitats for endangered lizard-orchids (*Himantoglossum* spp.): Ecological traps or refuges? Science of the Total Environment, 607–608:1001–1008.

Fekete, R., Mesterházy, A., Valkó, O. and Molnár, V.A. 2018. A hitchhiker from the beach: the spread of the maritime halophyte *Cochlearia danica* along salted continental roads. Preslia 90: 23–37.

Fischer, S.J., Williams, E.H., Brower, L.P., and Palmiotto, P.A. 2015. Enhancing Monarch Butterfly Reproduction by Mowing Fields of Common Milkweed. The American Midland Naturalist 173:229-240.

Flick, T., Feagan, S. and Fahrig, L. 2012. Effects of landscape structure on butterfly species richness and abundance in agricultural landscapes in eastern Ontario, Canada. Agriculture, Ecosystems and Environment 156:123-133.

Forcella, F. and Harvey, S.J. 1983. Eurasian weed infestation in western Montana in relation to vegetation and disturbance. Mandroño 30:102-109.

Forman, R.T.T. 2000. Estimate of the Area Affected Ecologically by the Road System in the United States. Conservation Biology 14:31-35.

Forman, R.T.T. and Baudry, J. 1984. Hedgerows and hedgerow networks in landscape ecology. Environmental Management 8:495–510.

Forman, R.T.T. and Alexander, L.E., 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–232.

Fox, E., Brown, J. and FitzPatrick, Ú. 2019. Pollinator-friendly management of transport corridors. All-Ireland Pollinator Plan, Guidelines 9. National Biodiversity Data Centre Series No. 20, Waterford, Ireland.

Freemark, K.E., Boutin, C. and Keddy, C. J. 2002. Importance of farmland habitats for conservation of plant species. Conservation Biology 16:399-412.

Galea, M, Wojcik, V., Davies Adams, L. and Cole, E. 2016. Technical Manual for Maintaining Roadsides for Pollinators Establishment, Restoration, Management and Maintenance A Guide for State DOT Managers and Staff. Pollinator Partnership, San Fransisco, USA.

Garcia-Palacios, P., Bowker, M.A., Maestre, F.T., Soliveres, S., Valladares, F., Papadopoulos, J., and Escudero, A. 2011. Ecosystem development in roadside grasslands: biotic control, plant–soil interactions, and dispersal limitations. Ecological Applications 21:2806–2821.

Gardiner, M.M., Riley, C.B., Bommarco, R. and Öckinger, E. 2018. Rights-of-way: a potential conservation resource. Frontiers in Ecology and the Environment 16(3):149–158. https://doi.org/10.1002/fee.1778

Geerts, S. and Pauw, A. 2011. Easy technique for assessing pollination rates in the genus *Erica* reveals road impact on bird pollination in the Cape fynbos, South Africa. Australian Ecology 36:656–662.

Gerhardt, K. Lennartsson, T. and Westin, A. 2018. Kunskapssammanställning om bryn. Appandix L in: L. Karlsson et al. Övergångszoner mellan skogs- och jordbruksmark. Ett samverkansprojekt inom miljömålsrådet 2017. Swedish Board of Agriculture Report 2018:14. Pp. 53-85.

Gilbert-Norton, L., Wilson, R., Stevens, J.R. and Beard, K.H. 2010. A meta-analytic review of corridor effectiveness. Conservation Biology 24:660–668.

Grashof-Bokdam, C.J. and Langevelde, F. 2005. Green veining: landscape determinants of biodiversity in European agricultural landscapes. Landscape Ecology 20:417-439.

Gustavsson, E., Lennartsson, T. and Emanuelsson, M. 2006. Land-use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. Biological Conservation 138:47-59.

Haaland, C. 2017. How to preserve a butterfly species within an urbanising settlement and its surroundings: a study of the scarce copper (*Lycaena virgaureae* L.) in southern Sweden. Journal of Insect Conservation 21:917–927.

Halbritter, D.A., Daniels, J.C., Whitaker, D.C. and Huang, L. 2015. Reducing Mowing Frequency Increases Floral Resource and Butterfly (Lepidoptera: Hesperioidea and Papilionoidea) Abundance in Managed Roadside Margins. Florida Entomologist 98:1081-1092.

Hale, R. and Swearer, S.E. 2016. Ecological traps: current evidence and future directions. Proceedings of the Royal Society B: Biological Sciences, 283 (1824), 20152647.

Hambrey Consulting 2013. The management of roadside verges for biodiversity. Scottish Natural Heritage Commissioned Report No. 551.

Hanley, M.E. and Wilkins, J.P. 2015. On the verge? Preferential use of road-facing hedgerow margins by bumblebees in agro-ecosystems. J Insect Conserv. 19:67–74.

Hanslin, H.M., Kroeger, S.B., Hovstad, K.A., Lennartsson, T., Wissman, J., D'Amico, M., Habel, J.C., Kollmann, J., Uhe, L. and Behrendt, S. 2019. Ecological effects of roads – a review of the literature. Report from CEDR Call 2016: Biodiversity;

EPICroads Ecology in practice: Improving infrastructure habitats along roads. https://www.cedr.eu/docs/view/61b9f4c62492c-en

Hanslin, H.M., Kroeger, S.B., Bastianelli, G., Lennartsson, T., Axelsson Linkowski, W., Wissman, J., Westin, A., D'Amico, M., Fischer, C., and Kollmann, J. 2021. Practical Guidelines Ecology in practice: Improving infrastructure habitats along roads. Report from CEDR Call 2016: Biodiversity; EPICroads Ecology in practice: Improving infrastructure habitats along roads. https://www.cedr.eu/docs/view/61b9f6068dd82-en

He, H. and Monaco, T. 2017. Litter accumulation and nutrient content of roadside plant communities in Sichuan Basin, China. Plants 6(3).

Heemsbergen, H., van der Sluijs J. and Verhoek G. 1989. Handleiding voor het maaien van bermen langs rijkswegen in de directie Noord-Brabant van de Rijkswaterstaat. Stichting Studie Centrum Wegenbouw (SCW), Ede, the Netherlands.

Helldin, J.O., Wissman, J. and Lennartsson, T. 2015. Abundance of red-listed species in infrastructure habitats - ‘responsibility species’ as a priority-setting tool for transportation agencies' conservation action. Nature Conservation 11:143-158.

Helldin, J.O., Lennartsson, T., Stenmark, M., Weibull, H., Westin, A. and Wissman, J. 2019. Biodiversitet i jernbanehabitater – biologisk kulturarv og grøn infrastruktur. Jernbanehistoria 2019:7-35, Odense.

Heneberg, P., Bogusch, P. and Řezáč, M. 2017. Roadside verges can support spontaneous establishment of steppe-like habitats hosting diverse assemblages of bees and wasps (Hymenoptera: Aculeata) in an intensively cultivated central European landscape. Biodiversity and Conservation 26:843–864.

Henriksen, C.I. and Langer, V. 2013. Road verges and winter wheat fields as resources for wild bees in agricultural landscapes. Agriculture, Ecosystems and Environment 173:66-71.

Hillhouse, H.L., Schacht, W.H., Soper, J.M. and Wienhold, C.E. 2018. Effects of Nitrogen and Phosphorus Fertilizer and Topsoil Amendment on Native Plant Cover in Roadside Revegetation Projects. Environmental Management 61:147–154.

Holderegger, R. and Di Giulio, M. 2010. The genetic effects of roads: A review of empirical evidence. Basic and Applied Ecology 11. 6:522-531.

Holdridge, L.R, Grenke, W.C., Hatheway, W.H., Liang, T. and Tosi, J.A. 1971. Forest environments in tropical life zones. Pergamon, Oxford.

Homyack, J.A., O'Bryan, C.J., Thornton, J.E. and Baldwin, R.F. 2016. Community occupancy of herpetofauna in roadside ditches in a managed pine landscape. Forest Ecology and Management 361:346-357.

Hopwood, J.L. 2008. The contribution of roadside grassland restorations to native bee conservation. Biological Conservation 141:2632-2640.

Hopwood, J.L. 2010. Pollinators and roadsides, managing roadsides for bees and butterflies. Xerxes Society for invertebrate conservation, Portland, USA.

Humbert, J-Y., Pellet, J., Buri, P. and Arlettaz, R. 2012. Does delaying the first mowing date benefit biodiversity in meadowland? Environmental Evidence 1:9 online.

Huxtable, C.H.A., Koen, T.B. and Waterhouse, D. 2005. Establishment of native and exotic grasses on mine overburden and topsoil in the Hunter Valley, New South Wales. Range Journal 27:73–88.

Irl, S.D.H., Steinbauer, M.J., Epperlein, L., Harter, D.E.V., Jentsch, A., Pätz, S. Wohlfart, C. and Beierkuhnlein, C. 2014. The Hitchhiker's guide to island endemism: biodiversity and endemic perennial plant species in roadside and surrounding vegetation. Biodiversity and Conservation 23:2273–2287.

Itzak, M.J.J. 2013. Seed harvester and scavenger ants along roadsides in Northern Israel. Zoology in the Middle East 44, 2008:75–82.

Jaconis, S.Y., Culley, T.M. and Meier, A.M. 2017. Does particulate matter along roadsides interfere with plant reproduction? A comparison of effects of different road types on *Cichorium intybus* pollen deposition and germination. Environmental Pollution 222:261-266.

Jacot, K., Eggenschwiler, L., Beerli, C., Bosshard, A. and Suter, M. 2012. Significance of different types of meadow edges for plant diversity in the Swiss Alps. Agriculture, Ecosystems and Environment 153:75-81

Jakobsson, A. and Ågren, J. 2014. Distance to semi-natural grassland influences seed production of insect-pollinated herbs. Oecologia 175:199-208.

Jakobsson, S., Fukamachi, K. and Cousins, S.A.O. 2016. Connectivity and management enables fast recovery of plant diversity in new linear grassland elements. Journal of Vegetation Science 27:19-28.

Jakobsson, S., Bernes, C., Bullock, J.M., Verheyen, K. and Lindborg, R. 2018. How does roadside vegetation management affect the diversity of vascular plants and invertebrates? A systematic review. Environmental Evidence 7:17, doi.org/10.1186/s13750-018-0129-z.

Jansen, S.H.D.R., Holmgren, M., van Langevelde, F. and Wynhoff, I. 2012. Resource use of specialist butterflies in agricultural landscapes: conservation lessons from the butterfly *Phengari*s (Maculinea) nausithous. Journal of Insect Conservation 16:921–930.

Jantunen, J., Saarinen, K., Valtonen, A. and Saarnio, S. 2006. Grassland vegetation along roads differing in size and traffic density. Annales Botanici Fennici 43:107–17.

Jarvis, S., Fielder, H., Hopkins, J., Maxted, N. and Smart, S. 2015. Distribution of crop wild relatives of conservation priority in the UK landscape. Biological Conservation 191:444-451.

Jaźwa, M., Heise, W. and Klimek, B. 2016. Substrate Factors Determine Roadside Vegetation Structure and Species richness: A Case Study Along a Meridional Gradient in Fennoscandia. Bullentine of Environmental Contamination and Toxicology 97:554–560.

Johnson, A. 2008. Best practices handbook for roadside vegetation management, final report. Minnesota Dept. of Transportation, St. Paul, USA.

Kadej, M., Zając, K., Smolis, A., Tarnawski, D. and Malkiewicz, A. 2016. Isolation from forest habitats reduces chances of the presence of *Osmoderma eremita* sensu lato (Coleoptera, Scarabaeidae) in rural avenues. Journal of Insect Conservation 20:395–406.

Kallioniemi, E., Åström, J., Rusch, G.M., Dahle, S., Åström, S. and Gjershaug, J.O. 2017. Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. Agriculture, Ecosystems and Environment 239:90–100.

Karim, M.N. and Mallik, A.U. 2008. Roadside revegetation by native plants I. Roadside microhabitats, floristic zonation and species traits. Ecological engineering 32:222–237.

Karlsson, T. 2008. Gaddsteklar i Östergötland – Inventeringar i sand- och grusmiljöer 2002-2007 samt övriga fynd i Östergötlands län. Länsstyrelsen Östergötland, rapport 2008:9.

Kasten, K., Stenoien, C., Caldwell, W. and Oberhauser, K.S. 2016. Can roadside habitat lead monarchs on a route to recovery? J Insect Conserv. 20:1047–1057.

Kimaro, H.S. and Kisingo, A.W. 2017.Influence of public road proximity on ground-dwelling insect communities. Int. J. Hum. Capital Urban Manage 2(3):181-188.

King, J.R. and Tschinkel, W.R. 2016. Experimental evidence that dispersal drives ant community assembly in human-altered ecosystems. Ecology 97:236-249.

Kleijn, D. and Snoeijing, G.I.J. 1997. Field boundary vegetation and the effects of agrochemical drift: botanical change caused by low levels of herbicide and fertilizer. Journal of Applied Ecology 34:1413-1425.

Kollmann, J., Uhe, L., D'Amico, M., Habel, J.C., Kröger, S., Lennartsson, T. and Hanslin, H.M. in press. Roadsides as novel ecosystems and potential ecological traps: reviewing the state of knowledge. In: D'Amico, M., Barrientos, R. and Ascensão, F. (eds.) Road Ecology: Synthesis and perspectives. Springer.

Koyanagi, T., Kusumoto, Y., Yamamoto, S., Okubo, S. and Takeuchi, K. 2009. Historical impacts on linear habitats: The present distribution of grassland species in forest-edge vegetation. Biological Conservation 142:1674–1684.

Knapp, M., Saska, P., Knappova, J., Vonička, P., Moravec, P., Kůrka, A. and Anděl. P. 2013. The habitat-specific effects of highway proximity on ground-dwelling arthropods: Implications for biodiversity conservation. Biological Conservation 164:22–29.

Kraushar, M. 2011. Serious green. Roads and Bridges 49:44-46.

Krodkiewska, M., Strzelec, M., Spyra, A. and Lewin, I. 2019. The impact of environmental factors on benthos communities and freshwater gastropod diversity in urban sinkhole ponds in roadside and forest contexts. Landscape Research 44(4):477–492.

Kuitel, P. and Lavee, H. 1999. Effect of slope aspect on soil and vegetation properties along an aridity transect. Israel Journal of Plant Sciences 47:169-178.

Kütt, L., Lõhmus, K., Rammi, I.J., Paal, T., Paal, J. and Liira, J. 2016. The quality of flower-based ecosystem services in field margins and road verges from human and insect pollinator perspectives. Ecological Indicators 70:409-419.

Lanciaux, M. 2013. La gestion differenciee des bords de routes departementaux en region picardie. Mémoire de 2 ème année de Master Sciences De l'Univers, Environnement, Écologie (SDUEE) Spécialité Écologie, Biodiversité, Évolution (EBE) Parcours Ingénierie Ecologique et Gestion des écosystèmes (IEG).

Landschap Overijssel undated. Bloemenweide: aanleg, ontwikkeling en beheer. Dalfsen, the Netherlands.

Larsson, M. and Knöppel, A. 2009. Biologisk mångfald på spåren. Zoologisk och botanisk inventering av järnvägsmiljöer med fokus på hotade arter, skötsel och framtidsperspektiv. Banverket, Expert och utveckling, Borlänge.

Le Coeur, D., Baudry, J. and Burel, B. 1997. Field margins plant assemblages: variation partitioning between local and landscape factors. Landscape and Urban Planning 37:57-71.

Le Viol, I., Mocq, J., Julliard R. and Kerbiriou, C. 2009. The contribution of motorway stormwater retention ponds to the biodiversity of aquatic macroinvertebrates. Biological Conservation 142:3163–3171.

Lennartsson, T. 2010. En analys av åtgärdsprogram för hotade arter i jordbrukslandskapet - Arter som vägvisare för skötsel. Swedish Environmental Agency Report 6356.

Lennartsson, T. and Simonsson, L. 2007. Biologisk Mångfald och klimatförändringar: vad vet vi, vad behöver vi veta, vad kan vi göra? I: SOU 2007:60, Sverige inför klimatförändringarna – hot och möjligheter; Slutbetänkande av Klimat- och sårbarhetsutredningen. Bilaga B 30, Swedish Ministry of Environment, Stockholm.

Lennartsson, T. and Westin, A. 2019. Ängar och slåtter – Historia, ekologi, natur- och kulturmiljövård. Swedish Heritage Board, Stockholm.

Lenoir, L. and Lennartsson, T. 2010. Effects of timing of grazing on the above- and below-ground arthropod communities in semi-natural grasslands. Journal of Insect Science 10:60.

Lunt, I.D. and Bennett, A.F. 2000. Temperate woodlands in Victoria: distribution, composition, and conservation. In: Hobbs R.J. and Yates C.J. (eds.) Temperate eucalypt woodlands in Australia: biology, conservation, management, and restoration, ch 3:17-31. Surrey Beatty and Sons, Chipping Norton, Australia.

Mainroads Western Australia 2016. Environmental guideline, Revegetation, topsoil management, Waterloo Crescent, Australia.

Marshall, E.J.R. and Moonen, A.C. 2002. Field margins in Northern Europe: Their functions and interactions with agriculture. Agriculture Ecosystems and Environment 89:5–21.

Martin-Sanz, R.C., Fernandez-Santos, B. and Martinez-Ruiz, C. 2015. Early dynamics of natural revegetation on roadcuts of the Salamanca province (CW Spain). Ecological Engineering 75:223–231.

Matson, P.A. 1997. Agricultural intensification and ecosystem properties. Science 277:504–09.

McCann, T. 2012. The woody species diversity of hedges in relation to environment, landscape, history, management and structure in Northern Ireland. PhD thesis. University of Ulster, Ireland.

McKenna, D.D., McKenna, K.M., Malcom, S.B. and Berenbaum, M.R. 2001. Mortality of Lepidoptera along roadways in central Illinois. Journal of the Lepidopterists' Society 55:63-6.

Medlock, J.M. Hansford, K.M., Schaffner, F., Versteirt, V., Hendrickx, G., Zeller, H. and Van Bortel, W. 2012. A review of the invasive mosquitoes in Europe: ecology, public health risks, and control options. Vector-Borne Zoonotic Diseases 12:435–447.

Meek, R. 2014. Temporal distributions, habitat associations and behaviour of the green lizard (*Lacerta bilineata*) and wall lizard (*Podarcis muralis*) on roads in a fragmented landscape in Western France. Acta Herpetologica 9:179-186.

Milberg, P. and Lamont, B.B. 1995. Fire enhances weed invasion of roadside vegetation in southwestern Australia. Biological Conservation 73:45-49.

Milton, S.J., Dean, W.R., Sielecki, L.E. and van der Ree, R. 2015. The function and management of roadside vegetation. In: Van der Ree R., Smith D.J. and Grilo C. (eds.), Handbook of Road Ecology. John Wiley and Sons, pp. 373-381.

Munguira, M.L. and Thomas, J.A. 1992. Use of road verges by butterfly and burnet populations, and the effects of roads on adult dispersal and mortality. Journal of Applied Ecology 29:316-329.

Muñoz, P.T., Torres, F.P. and Megias, A.G. 2015. Effects of roads on insects: a review. Biodiversity and Conservation 24:659–682.

Müllerová, J., Vítková, M. and Vítek, O. 2011. The impacts of road and walking trails upon adjacent vegetation: Effects of road building materials on species composition in a nutrient-poor environment. Science of the total environment 409:3839-3849.

Murariu, C., Hahn, E., Georgiadis, L. et al. 2019. Ghid Privind integrarea măsurilor de conservare a biodiversității în planificarea, pregătirea, evaluarea, implementarea și monitorizarea proiectelor de transport rutier și feroviar. Interreg Danube transnational programme, Bucharest, Romania.

Myrdal, J. 2012. Boskapsskötseln under medeltiden. En källpluralistisk studie. Nordiska museets handlingar 139. Nordiska museets förlag, Stockholm.

Natural England 2015. Summary of evidence: Wood-pasture and parkland EIN011. Worcester, UK.

Neher, D.A., Asmussen, D. and Lovell, S.T. 2013. Roads in northern hardwood forests affect adjacent plant communities and soil chemistry in proportion to the maintained roadside area. Science of the Total Environment 449:320-327.

Nilsson, A. 1902. Svenska växtsamhällen. Tidskrift för skogshushållning 30.

Nilsson, O. 2012. Inventering av kärlväxter och dagfjärilar vid vägkanter längs väg S 847 och S 851, Långban – Gåsborn, Filipstads kommun, Värmlands län. Trafikverket, Rapport nr 2012:217.

Noordijk, J., Schaffers, A. and Sýkora, K.V. 2008. Diversity of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) in roadside verges with grey hair-grass vegetation. European Journal of Entomology 105:257-265.

Noordijk, J., Raemakers, I., Schaffers, A. and Sýkora, K. 2009a. Arthropod richness in roadside verges in the Netherlands. Terrestrial Arthropod Reviews 2(1):63-76.

Noordijk, J., Delille, K., Schaffers, A.P. and Sýkora, K.V. 2009b. Optimizing grassland management for flower-visiting insects in roadside verges. Biological Conservation 142:2097-2103.

Noordijk, J., Schaffers, A.P., Heijerman, T., Boer, P., Gleichman, M. and Sýkora, K.V. 2010. Effects of vegetation management by mowing on ground-dwelling arthropods. Ecological Engineering 36:740-750.

Noordijk, J., Schaffers, A.P., Heijerman, T. and Sýkora, K.V. 2011. Using movement and habitat corridors to improve the connectivity for heathland carabid beetles. Journal for Nature Conservation 19:276-284.

Norderhaug, A., Ihse, M. and Pedersen, O. 2000. Biotope patterns and abundance of meadow plant species in a Norwegian rural landscape. Landscape Ecology 15:201–218.

Oleksa, A., Gawroński, R. and Ulrich, W. 2009. Association of *Ovalisia rutilans* (Fabricius, 1777) (Coleoptera: Buprestidae) with thermophilous habitats toward its range edge in northern Poland. Baltic Journal of Coleopterology 9:39-44.

Oleksa, A., Gawroński, R. and Tofilski, A. 2013. Rural avenues as a refuge for feral honey bee population. Journal of Insect Conservation 17:465–472.

Oppermann, R., Beaufoy, G. and Jones, G. (eds.) 2012. High nature value farming in Europe. Verlag regionalkultur, Ubstaht-Weiher, Germany.

Osgathorpe, L.M., Park, K. and Goulson, D. 2012. The use of off-farm habitats by foraging bumblebees in agricultural landscapes: implications for conservation management. Apidologie 43:113–127. DOI: 10.1007/s13592-011-0083-z.

O'Sullivan, O.S. Holt, A.R., Warren, P.H. and Evans, K.L. 2017. Optimising UK urban road verge contributions to biodiversity and ecosystem services with cost-effective management. Journal of Environmental Management 191:162-171.

Ottosson, M., Lennartsson, T. and Svensson, R. 2012. Nya vägar till artrikedom. TRIEKOL Research programme, Swedish Biodiversity Centre, Publication no. 66, Uppsala.

Ottosson, M. 2014. Samarbete - vägen till lyckade naturvårdsprojekt i infrastrukturmiljön. Swedish Biodiversity Centre, Publication no. 80, Uppsala.

Ouédraogo, D.Y, Villemey, A., Vanpeene, S., Coulon, A., Azambourg, V., Hulard, M., Guinard, E., Bertheau, Y., Flamerie De Lachapelle, F., Rauel, V., Le Mitouard, E., Jeusset A., Vargac, M., Witté, I., Jactel, H., Touroult, J., Reyjol, Y. and Sordello, R. 2020. Can linear transportation infrastructure verges constitute a habitat and/or a corridor for vertebrates in temperate ecosystems? A systematic review. Environmental Evidence 9: e13.

Påhlsson, L. 1994. Vegetationstyper i Norden, Nordic Council of Ministers, Tema Nord 1994:665, Copenhagen.

Palfi, Z., Spooner, P.G. and Robinson, W. 2017. Soil disturbance effects on the composition of seed-dispersing ants in roadside environments. Oecologia 183:493-503.

Parkinson, I., Newmarch, J. and Datchler, K. 2019. Managing roadside verges for biodiversity - a new approach. Informing a High Weald Nature Recovery Area proposal. Kew Royal Botanic Gardens, Kew, UK.

Persson, T.S. 1998. Management of roadside verges: Vegetation changes and species diversity. PhD thesis, Swedish Univ. of Agricultural Sciences, Uppsala.

Phillips, B.B., Bullock, J.M., Gaston, K.J., Hudson-Edwards, K.A., Bamford, M., Cruse, D.D., Dicks, L.V., Falagan, C., Wallace, C. and Osborne, J.L. 2021. Impacts of multiple pollutants on pollinator activity in road verges. Journal of Applied Ecology 58:1017-1029.

Piekarska-Boniecka, H., Mazur, R., Wagner, A. and Trzcinski, P. 2015. Selected elements of cultural landscape structure in Wielkopolska region of Poland as habitats for the parasitoid hymenoptera Pimplinae (Hymenoptera, Ichneumonidae). Insect conservation and diversity 8:54-70.

Pitman, C.M., Flockhart, D.T.T. and Norris, D.R. 2018. Patterns and causes of oviposition in monarch butterflies: Implications for milkweed restoration. Biological Conservation 217:54–65.

Polic, D., Fiedler, K., Nell, C. and Grill, A. 2014. Mobility of ringlet butterflies in high-elevation alpine grassland: effects of habitat barriers, resources and age. Journal of insect conservation 18:1153–1161.

Pro Natura 2015. Waldstrassenränder, mehr Biodiversität mit weniger Aufwand. Bern, Switzerland.

Pro Natura 2017. Strassenböschungen – eine Chance für die Biodiversität. Bern, Switzerland.

Provincie Zuid-Holland 2019. Leidraad ecologisch bermbeheer, Handleiding om ecologisch bermbeheer toe te passen. Provincie Zuid-Holland, den Haag, the Netherlands.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Raemakers, I.P., Schaffers, A.P. and Sýkora, K.V. 2003. De betekenis van bermen en plantengemeenschappen voor ongewervelden, Report, Wageningen.

Raemakers, I. and Faasen, T. 2004. Bescherming flora A73-zuid in WP 2 & 3, plan van aanpak. Ecologia, Maarheze.

Raunkiær, C. 1907. Planterigets Livsformer og deres Betydning for Geografien. Gyldendalske Boghandel - Nordisk Forlag, Copenhagen and Kristiania.

Rauschert, E.S.J., Mortensen, D.A. and Bloser, S.M. 2017. Human-mediated dispersal via rural road maintenance can move invasive propagules. Biological Invasions 19:2047–2058.

Rentch, J. S., Fortney, R.H., Grafton, W.N., Stephenson, S.L. and Coxe, R. 2013. The Vascular Flora of Roadside Habitats in West Virginia, USA. Castanes 78:56–78.

Rewicz, A., Jaskuła, R., Rewicz, T. and Tończyk, G. 2017. Pollinator diversity and reproductive success of *Epipactis helleborine* (L.) Crantz (Orchidaceae) in anthropogenic and natural habitats. PeerJ 2017; 5: e3159; DOI 10.7717/peerj.3159

Richter, E.G. and McKnight, K.B. 2014. Ecology of northeastern roadside mosses. Journal of the Torrey Botanical Society 141:250-264.

Ries, L., Debinski, D.M. and Wieland, M.L. 2001. Conservation value of roadside prairie restoration to butterfly communities. Conservation Biology 15:401-411.

Rijkswaterstaat 2008. Overzicht van de vegetatie langs Rijkswegen. Dienst Verkeer en Scheepvaart.

Riva, F., Acorn, J.H. and Nielsen, S.E. 2018. Localized disturbances from oil sands developments increase butterfly diversity and abundance in Alberta's boreal forests. Biological Conservation 217:173–180.

Roche, B., Léger, L., L'Ambert, G., Roche, B., Lacour, G., Foussadier, R., Besnard, G., Barré-Cardi, H., Simard, F. and Fontenille, F. 2015. The spread of *Aedes albopictus* in metropolitan France: contribution of environmental drivers and human activities and predictions for a near future. PLoS One 10:1–13.

Ross, S.M. 1986. Vegetation change on highway verges in south-east Scotland. J. Biogeogr. 13:109-117.

Rotholz, E. and Mandelik, Y. 2013. Roadside habitats: effects on diversity and composition of plant, arthropod, and small mammal communities. Biodiversity and Conservation 2:1017–1031.

Runesson K. 2012. Vegetation och flora i vägkanter – effekter av olika metoder för skötsel och underhåll. Kunskapssammanställning. CBM Report 63. TRIEKOL and Swedish Biodiversity Centre, Uppsala.

Rydgren, K., Nordbakken, J.F., Austad, I., Auestad, I. and Heegaard, E. 2010. Recreating semi-natural grasslands: A comparison of four methods. Ecological Engineering 36:1672–1679.

Saure, C. 1996. Urban habitats for bees: the example of the city of Berlin. In: Matheson A., Buchmann S.L., O'Toole C., Westrich P. and Williams I.H. (eds.) The conservation of bees. Academic Press, New York, New York, USA, pp 47-54.

Saville, N.M., Dramstad, W.E., Fry, G.L.A. and Corbet, S.A. 1997. Bumblebee movement in a fragmented agricultural landscape. Agriculture Ecosystems and Environment 61:145-154.

Schaffers, A.P., Raemakers, I.R. and Sýkora, K.V. 2012. Successful overwintering of arthropods in roadside verges. Journal of Insect Conservation 16:511–522.

Schultz, N.L., Reid, N., Lodge, G. and Hunter, J.T. 2014. Broad-scale patterns in plant diversity vary between land uses in a variegated temperate Australian agricultural landscape. Australian Ecology 39:855–863.

Simões, M.P., Belo, A.F. and Suoza, C. 2013. Effects of mowing regime on diversity of Mediterranean roadside vegetation - implications for management. Polish Journal of Ecology 61:241–255.

Sjölund, A., Eriksson, O., Persson, T. and Hammarqvist, J. 1999. Vägkantsfloran. Vägverket publikation 1999:40, Borlänge, Sweden.

Skórka, P., Lenda, M., Moron, D., Kalarus, K. and Tryjanowski, P. 2013. Factors affecting road mortality and the suitability of road verges for butterflies. Biological Conservation 159:148–157.

Skórka, P., Lenda, M. and Moron, D. 2018. Roads affect the spatial structure of butterfly communities in grassland patches. PeerJ 2018; 6: e5413; DOI 10.7717/peerj.5413.

Skousen, J.G. and Venable, C.L. 2008. Establishing native plants on newly-constructed and older-reclaimed sites along West Virginia highways. Land Degradation and Development. 19:388–396. DOI: 10.1002/ldr.84

Skrindo, A.B. and Pedersen, P.A. 2004. Natural revegetation of indigenous roadside vegetation by propagules from topsoil. Urban forestry and urban greening 13:29-37.

Snoo, G.R. and van der Poll, R.J. 1999. Effect of herbicide drift on adjacent boundary vegetation. Agriculture, Ecosystems and Environment 73:1-6.

Spaans, F., Caruso, T. and Montgomery, I. 2018. The abundance and condition of hedgerow tree standards in Northern Ireland. Biology and Environment: Proceedings of the Royal Irish Academy Vol. 118B, 3:129-145.

Spellerberg, I.F. 1998. Ecological Effects of Roads and Traffic: A Literature Review. Global Ecology and Biogeography Letters 7:317-333.

Spooner, P.G 2005. On squatters, settlers and early surveyors: historical development of country road reserves in southern New South Wales. Australian Geographer 36:55–73.

Spooner, P.G. 2015. Minor rural road networks: values, challenges, and opportunities for biodiversity conservation. Nature Conservation 11:129–142. doi:10.3897/natureconservation.11.4434

Spooner, P.G. and Lunt, I.D. 2004. The influence of land-use history on roadside conservation values in an Australian agricultural landscape. Australian journal of Botany 52:445-458.

Spooner, P.G., Lunt, I.D., Briggs, S.V. and Freudenberger, D. 2004. Effects of soil disturbance from roadworks on roadside shrubs in a fragmented agricultural landscape. Biological Conservation 117:393–406.

Spooner, P.G. and Smallbone, L. 2009. Effects of road age on the structure of roadside vegetation in south-eastern Australia. Agriculture, Ecosystems and Environment 129:57–64.

Stenmark, M. 2012. Infrastrukturens gräs- och buskmarker. Hur stora arealer gräs och buskmarker finns i anslutning till transportinfrastruktur och bidrar dessa till miljömålsarbetet? Swedish Board of Agriculture Report 2012:36, Jönköping.

Suárez-Esteban, A., Delibes, M. and Fedriani, J.M. 2013a. Barriers or corridors? The overlooked role of unpaved roads in endozoochorous seed dispersal. Journal of Applied Ecology 50:767–774.

Suárez-Esteban, A., Delibes, M. and Fedriani, J.M. 2013b. Unpaved road verges as hotspots of fleshy-fruited shrub recruitment and establishment. Biological Conservation 167:50–56.

Suárez-Esteban, A., Delibes, M. and Fedriani, J.M. 2014. Unpaved roads disrupt the effect of herbivores and pollinators on the reproduction of a dominant shrub. Basic and Applied Ecology 15:524-533.

Suárez-Esteban, A., Fahrig, L., Delibes, M. and Fedriani, J.M. 2016. Can anthropogenic linear gaps increase plant abundance and diversity? Landscape Ecology 31:721–729.

Sullivan, J.J., Williams, P.A., Timmins, S.M. and Smale, M.C. 2009. Distribution and spread of environmental weeds along New Zealand roadsides. New Zealand Journal of Ecology 33:190-204.

Swengel, A. and Swengel, S. 2011. High and dry or sunk and dunked: lessons for tallgrass prairies from quaking bogs. Journal of Insect Conservation 15:165–178.

Svensson, B.M. 2013. Från vägkant till ängsvägkant – är det möjligt? En litteraturgenomgång. CBM Report 76, TRIEKOL and Swedish Biodiversity Centre, Uppsala.

Svensson, B., Lagerlöf, J. and Svensson, B.G. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera : Apidae) in an agricultural landscape. Agriculture Ecosystems and Environment 77:247-255.

Sydenham, M.A.K., Eldegard, K. and Totland, Ø. 2014. Spatio-temporal variation in species assemblages in field edges: seasonally distinct responses of solitary bees to local habitat characteristics and landscape conditions. Biodiversity and Conservation 23:2393–2414.

Szentesi, A., György, Z., Jermy, T. and Kiss, B. 2017. Seasonal changes in bruchid (Coleoptera: Chrysomelidae: Bruchinae) assemblages along managed highway ecotones. European Journal of Entomology 114:488–499.

Szmatona-Túri, T., Magos, G., Vona-Túri, D., Gál, B. and Weiperth, A. 2018. Review of habitats occupied by *Urocoras longispinus*: a little-known spider species, and responses to grassland management. Biologia 73:523–529.

Takahashi, K. and Miyajima, Y. 2010. Effects of roads on alpine and subalpine plant species distribution along an altitudinal gradient on Mount Norikura, central Japan. Journal of Plant Research 123:741–749.

Tanghe, M. and Godefroid, S. 2000. Road verge grasslands in southern Belgium and their conservation value. Fragmenta Floristica et Geobotanica 45:147–163.

Taylor, K., Brummer, T., Taper, M.L., Wing, A. and Rew. L.J. 2012. Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. Diversity and Distributions 18:942–951.

Tehrani, F.B., Majnounian, B., Abdi, E. and Amiri, G.Z. 2015. Impacts of Forest Road on Plant Species Diversity in a Hyrcanian Forest, Iran. Croatian Journal of Forest Engineering. 36:1.

Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., Danielson, B.J., Brinkerhoff, J., Damschen, E.I. and Townsend, P. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. PNAS 99:12923–12926.

Thiele, J., Schirmel, J. and Buchholz, S. 2018. Effectiveness of corridors varies among phytosociological plant groups and dispersal syndromes. PLoS ONE 13(7): e0199980.

Thomas, J.A. 1991. Rare species conservation: case studies of European butterflies. In: Spellerberg, I.F., Goldsmith, F.B. and Morris, M.G. (eds.) The Scientific Management of Temperate Communities for Conservation, pp. 149-197. Symposium 29 of the British Ecological Society, Blackwell Scientific Publications, Oxford.

Thompson, J.R. 1983. Roadside: a resource and a challenge In: Bradshaw A.D, Goode D.A. and Thorpe E.H.P. (eds.) Ecology and Design in Landscape, Blackwell, Oxford.

Thylen, A. 2007. Biologisk mangfold og jernbane - en kunskapsoversikt. Jernbaneverket Infrastruktur Teknikk, Norway.

Tikka, P.M., Koski, P.S., Kivela, R.A. and Kuitunen, M.T. 2000. Can grassland plant communities be preserved on road and railway verges? Applied Vegetation Studies 3:25–32.

Tiwari, A. and Rachlin, J. W. 2018. A Review of Road Salt Ecological Impacts. Northeastern Naturalist, 25:123-142. https://doi.org/10.1656/045.025.0110.

Trafikverket 2021. Återetablering av vegetation med tillvaratagna avbaningsmassor. Fact sheet, Borlänge, Sweden.

Trombulak. S. and Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

Truscott, A.M., Palmer, S.C.F., McGowan, G.M., Cape, J.N. and Smart, S. 2005. Vegetation composition of roadside verges in Scotland: the effects of nitrogen deposition, disturbance and management. Environmental Pollution 136:109-118.

Tsuyuzaki, S. and Titus, J.H. 2010. Roadside grassland vegetation in an oak forest, Oak Creek Wildlife Area, the Cascade Range, USA. iForest - Biogeosciences and Forestry 3, doi: 10.3832/0527-003.

Walker, J. and Reddell, P. 2007. Retrogressive succession and restoration on old landscapes. In: Walker, L.R., Walker, J. and Hobbs R.J. (eds.) Linking Restoration and Ecological Succession, Springer, New York, pp. 69–89.

Walker, L.R., Wardle, D.A., Bardgett, R.D. and Clarkson, B.D. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725-736.

Walvatne, P. et al. (ed.) 1997. How to develop and implement an integrated roadside vegetation management program. The National Roadside vegetation Management Association, Newark, USA.

van de Poel, D. and Zehm, A. 2014. Die Wirkung des Mähens auf die Fauna der Wiesen – Eine Literaturauswertung für den Naturschutz. The impact of mowing on meadow fauna – a literature review for the purposes of nature conservation. Anliegen Natur 36:36-51

van der Ree, R., Smith, D.J. and Grilo, C. (eds.) 2015. Handbook of road ecology. John Wiley & Sons, Chichester, UK.

van Eupen, M. and Knaapen, J.P. 2000. HACOBERM II; Eindrapport van een haalbaarheidsstudie naar de habitat- en corridorfunctie van wegbermen. Alterra, Wageningen.

Van Grinsveen, A.A. 2016. Monitoring Flora en Fauna Voor de rijkswegen A73 Zuid-A74, 2015 & aanvulling leemten in kennis 2016. Econsultancy, Boxmeer.

van Halder, I., Thierry, M., Villemey, A., Ouin, A., Archaux, F., Barbaro, L., Balent, G. and Benot, M.L. 2017. Trait-driven responses of grassland butterflies to habitat quality and matrix composition in mosaic agricultural landscapes. Insect Conservation and Diversity 10:64–77.

van Langevelde, F. and Wynhoff, I. 2009. What limits the spread of two congeneric butterfly species after their reintroduction: quality or spatial arrangement of habitat? Animal Conservation 12:540–548.

van Rooij, S., Geertsema, W., Opdam, P., Reemer, M., Snep, R., Spijker, J and Steingröver, E. 2014. Een Bij-zonder kleurrijk landschap in Land van Wijk en Wouden. Handreiking voor inrichting en beheer. Alterra, Wageningen.

van Rossum, F. 2009. Succession stage variation in population size in an early-successional herb in a peri-urban forest. Acta Oecologica 35:261-268.

Warren, M.S. and Stephens, D.E.A. 1989. Habitat design and management for butterflies. The Entomologist 108:123-134.

Vasconcelos, P.B., Araújo, G.M. and Bruna, E.M. 2014. The role of roadsides in conserving Cerrado plant diversity. Biodiversity and Conservation 23:3035–3050.

Way, J.M. 1977. Roadside verges and conservation in Britain: a review. Biological Conservation 12:65-74.

Weaver, J.E. 1968. Prairie plants and their environment: A fifty-year study in the Midwest. Univ. of Nebraska Press, Lincoln.

Vermeulen, H.J.W. 1993. The composition of the carabid fauna on poor sandy roadside verges in relation to comparable open areas. Biodiversity and Conservation 2:331–50.

Westin, A. and Lennartsson, T. 2017. Tvärvetenskaplig källpluralistisk metod för att förstå landskap. En historisk-ekologisk undersökning av betet på Filehajdar - en Gotländsk utmark. Swedish Biodiversity Centre Publications no 104, Uppsala.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. The Botanical Review 44:229-299.

Villemey, A., Peterman, W.E., Richard, M., Ouin, A., van Halder, I., Stevens, V.M., Baguette, M., Roche, P. and Archaux, F. 2016. Butterfly dispersal in farmland: a replicated landscape genetics study on the meadow brown butterfly (*Maniola jurtina*). Landscape Ecology 31:1629–1641.

Villemey, A., Jeusset, A., Vargac, M., Bertheau, Y., Coulon, A., Touroult, J., Vanpeene, S., Castagneyrol, B., Jactel, H., Witte, I., Deniaud, N., De Lachapelle, F.F, Jaslier, E., Roy, V., Guinard, E., Le Mitouard, E., Rauel, V. and Sordello, R. 2018. Can linear transportation infrastructure verges constitute a habitat and/or a corridor for insects in temperate landscapes? A systematic review. Environmental Evidence 7:5.

Willmert, H.M., Osso, J.D., Twiss, M.R. and Langen, T.A. 2018. Winter road management effects on roadside soil and vegetation along a mountain pass in the Adirondack Park, New York, USA. Journal of Environmental Management 225:215-223.

Woch, M. and Hawryluk, M. 2014. Flora of xerothermic sites of the Zachodniowolynska dolina Bugu special area of conservation (Eastern Poland): the influence of habitat on rare grassland species. Archives of Biological Sciences, Belgrade, 66:209-226.

von der Lippe, M. and Kowarik, I. 2008. Do cities export biodiversity? Traffic as dispersal vector across urban–rural gradients .Diversity and Distributions 14:18–25.

von der Lippe, M. and Kowarik, I. 2012. Interactions between propagule pressure and seed traits shape human-mediated seed dispersal along roads. Perspectives in Plant Ecology 14:123-130.

von der Lippe, M., Bullock, J.M., Kowarik, I., Knopp. I. and Wichmann, M. 2013. Human-mediated dispersal of seeds by the airflow of vehicles. PLoS ONE. doi:10.1371/journal.pone.0052733

Vona-Túri, D., Szmatona-Túri, T. and Kiss, B. 2017. Effects of roads and adjacent areas on diversity of terrestrial isopods of Hungarian highway verges. Biologia 72:1486-1493.

Wrzesień, M. and Denisow, B. 2016. Distribution and abundance of bee forage flora across an agricultural landscape – railway embankments vs. road verges. Acta Societatis Botanicorum Poloniae 85(3): DOI: 10.5586/asbp.3509.

Völker, I., Stangler, E., Sagemann, S. and Schäling, B. (eds.) undated. Handlungsleitfaden zur Anlage and Pflege naturnaher Grünflächen. Landkreis Ostgalläu, Markoberdorf, Germany.

Young, R. 1991. Britain's largest nature reserve. The Soil Association, London.

Yoshiki, Y., Sasaki, H. and Harauchi, Y. 2010. Effects of narrow roads on the movement of carabid beetles (Coleoptera, Carabidae) in Nopporo Forest Park, Hokkaido. Journal of Insect Conservation 14:151–157.

Zeng, S.L., Zhang, T.T., Gao, Y., Ouyang, Z.T., Chen, J.K., Li, B. and Zhao, B. 2010. Effects of Road Disturbance on Plant Biodiversity. World Academy of Science, Engineering and Technology International Journal of Environmental and Ecological Engineering 4 No:6, 2010.

Zeng, S.L., Zhang, T.T., Gao, Y., Ouyang, Z.T., Chen, J.K., Li, B. and Zhao, B. 2011. Effects of road age and distance on plant biodiversity: a case study in the Yellow River Delta of China. Plant Ecology 212:1213–1229.

Zeng, S.L., Zhang, T.T., Gao, Y., Li, B., Fang, C.M., Flory, L. and Zhao, B. 2012. Road effects on vegetation composition in a saline environment. Journal of Plant Ecology 5:206–218.

Zhu,Y. and Wang, D. 2018. Response of ants to human-altered habitats with reference to seed dispersal of the myrmecochore *Corydalis giraldii* Fedde (Papaveraceae). Nordic Journal of Botany 2018:1-7.

Zielinska, K.M., Misztal, M., Zielnska, A. and Zywiec, M. 2013. Influence of Ditches on Plant Species Diversity in the Managed Forests of Central Poland. Baltic Forestry 19:270-279.

Zielinska, K.M., Kiedrzynski, M., Grzyl, A. and Rewicz, A. 2016. Forest roadsides harbour less competitive habitats for a relict mountain plant (*Pulsatilla vernalis*) in lowlands. Scientific reports 6:31913.