CEDR Transnational Road Research Programme
Call 2016: Biodiversity

funded by Austria, Germany, Ireland,
Netherlands, Norway, Slovenia and Sweden

EPICroads – Ecology in practice: Improving infrastructure habitats along roads

Ecological effects of roads – a review of the literature

Deliverable No 1.2
12, 2019

CEDR Call 2016: Biodiversity
EPICroads
Ecology in practice: Improving infrastructure habitats along roads

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Planned delivery date:
Actual delivery date: 30/12/2019

Start date of project: 01/05/2018

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Version 30.12.2019

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Summary

The transport sector has a key role in halting loss of biodiversity, but knowledge is needed of how road construction and management can be improved to mitigate the negative impact of roads on biodiversity and ecosystem services. Through a comprehensive review of the literature on ecological effects of roads, we contribute to this knowledge platform. We show that, despite strong negative effects of transport-related processes and factors such as noise, barrier effects, roadkill and landscape fragmentation, habitats related to transport infrastructure can contain considerable biological diversity and species richness. They can also create structural and resource heterogeneity in the landscape and function as corridors for a diverse set of organisms. However, evidence of these contributions is fragmented, with high species-specificity in responses and a strong impact of landscape configuration and resources. We point out knowledge gaps that have to be addressed in R&D to improve knowledge about the ecological effects of roads and measures to improve the contribution of road infrastructure to halt the loss of biodiversity and securing ecosystem services

1 Purpose and scope

Halting the loss of biodiversity and securing ecosystem services is an important political target in the European Union and other European countries. To reach this target, it is essential to integrate the concepts of conservation and biodiversity into different sectors across society. In particular, it is important to include consideration of biodiversity in sectors with large impacts on land use and landscape planning. The transport infrastructure sector is probably one of best examples of this compelling need.

Roads, and habitats related to transportation infrastructure (HTI), can have both positive and negative effects on biodiversity, ecological processes and ecosystem services. The direction and magnitude of the impact depend, among other things, on how roads and HTI are constructed and managed. This implies that the negative impact of roads on biodiversity and ecosystem services can be mitigated through careful planning based on ecological knowledge. This in turn requires knowledge developed through applied research targeting policy makers, landscape planners and practitioners responsible for construction and maintenance of roads and other transport infrastructure.

HTI poses a dilemma in environmental planning. On the one hand, HTI can provide important novel and surrogate habitats, which can be of high ecological value for large numbers of (endangered) animal and plant species (Deckers et al. 2005; de Redon et al. 2010; Morelli et al. 2014). On the other hand, these habitats could act as ecological traps, through increased rates of road-related malformations and mortality (Orlowski 2008; Brady 2013) or reduced breeding success (Kuitunen et al. 2003; Fekete et al.

2017). Various studies and meta-analyses have indicated that roadsides provide suitable habitats, but also represent important corridors and stepping-stones across landscapes, and may link fragmented conservation areas (Deckers et al. 2005; Coffin 2007). Road management has to balance these negative and positive aspects. Our objective was to provide a knowledge platform to guide this management, through a broad literature review where we collated current knowledge and sought to identify knowledge gaps across spatial scales and organism groups.

2 Methodology - review approach

To obtain a database of relevant literature, we employed a systematic review approach to extract and structure the information. It was based on the approach used in the Swedish MISTRA EviEM project (Bernes et al., 2017), complemented with updated searches for 2017 and 2018 using the same search string. The search string from the MISTRA project is very broad (Table 1), and thus covers the questions addressed by our study. The exclusion criteria did however differ considerably.

Papers were initially screened on title and abstract by four people, using a conservative approach where papers were included when their relevance was unclear at that stage. Grey literature and papers written in languages other than English were excluded during this process. To extract detailed information from the papers, we limited the search period to 2008-2018. Other criteria for exclusion are given in Table 2. In total, 1927 papers remained for full-text screening. Excluded papers were grouped in sets of categories, as summarised in Table 2.

We focused on species potentially living in or using roadsides as a resource and where the roadsides comprise a major part of their homerange (i.e. plants, insects and small vertebrates) and did not consider cases where the roads act primarily as a barrier to dispersal (i.e. large vertebrates). In the final database, we included papers that estimate, model or review effects of roads on population processes, demography, distribution, occurrence, abundance, biodiversity, behaviour, and landscape connectivity.

Table 1. Search strings used to identify potential literature for the review. To build the search strings, the terms within the categories 'population' and 'outcomes' were combined using the Boolean operator 'OR'; The two categories were then combined using the operator 'AND'. An asterisk (*) served as a truncation (or wildcard) operator that represents any group of characters, including no character

Population	roadside*, "road side*", (road* AND (verge* OR edge*)), roundabout*, "traffic island*", "median strip*", "central reservation*", boulevard*, parkway*, (avenue* AND tree*)
Outcomes	*diversity, dispers*, species, abundance, vegetation

Table 2. Categories of papers included or excluded during full-text screening, with number of items per category. A total of 1927 papers were screened and 473 were included in the final dataset

1	Included: Papers that estimate, model or review effects of roads on population processes, demography, distribution, occurrence, abundance, biodiversity, behaviour, and landscape connectivity.	473
2	Excluded: Grey literature	299
3	Excluded: Papers earlier than 2008	122
4	Excluded: Papers on biomonitoring, pollution, dust accumulation and ecotoxicology not addressing ecological processes	115
5	Excluded: Papers on roadkill and wildlife collisions that do not provide information on the ecological effects of vehicle-wildlife collisions and roadkill, such as methods to prevent wildlife-vehicle collisions, studies that focus on road safety more generally, and studies on technical design and construction of crossing structures	54
6	Excluded: Papers with no road focus, or papers on planning, design, construction or maintenance of roads, road verges and passages where effects of roads on ecological processes are not addressed or where roads are used as a method for sampling only. This also includes technical aspects of weed control and use of pesticides. Laboratory, greenhouse or garden experiments are included here	502
7	Excluded: Descriptive papers on invasive alien species (and weeds or pests) distribution and management where the impact of these on ecological processes is not addressed	220
8	Excluded: Papers on large vertebrates, as these were outside the scope of this study. We defined large animals as vertebrates of the approximate size of red foxes and above.	106
9	Excluded: Papers on urbanisation and landscaping when effects on ecological processes are not addressed or where the role of roads is not explicit	36

For the 473 papers that were included in the final dataset, we extracted detailed information on the type of publication, bibliographical data and geographical and ecological information, along the lines of the MISTRA project. In addition, two people categorised the research themes addressed in the papers into a set of broad thematic categories. However, the numbers of papers and paper combinations in the final dataset were so large that we could not perform a formal quality appraisal of each paper and topic within papers based on their design, sample size and effect sizes. Hence, we shifted the approach to categorising the major findings of each study. Papers were worked through, one theme at a time, and relevant information was reviewed by one person (Appendix 1). This information was assimilated and is presented in two separate chapters of this report, dealing with road effect zones (Chapter 4) and landscape perspective (Chapter 5). A single paper sometimes contained information on several topics and was included for both.

There were differences in signal strength between papers, based on their design, approach and study system, but these differences were not formally weighted in the synthesis. In addition, the large variation in organisms, road types, landscapes and climates made it difficult to extract strong evidence, for each topic (because of few studies per topic) and for general conclusions about HTI (because of great heterogeneity between studies). Similar issues with strength of evidence have been found in other, more focused reviews and meta-analyses that have examined effects of roads and HTI on biodiversity (Jakobsson 2018; Villemey et al. 2018).

3 Overview results

As expected, there was great variation in the organism groups, types of roads, climates, landscape components and responses studied in the 473 papers analysed. A summary of papers in the different categories (see Tables 3 to 5) revealed a bias towards European and North American studies and a high proportion of data for smaller roads. In terms of the organism groups studied there was a more even split among groups, reflecting the fact that we excluded studies on larger mammals from the dataset. Microorganisms were not well-studied, despite their importance in plant-soil feedback and nutrient and carbon cycles. Among the 473 papers, 144 studied more than one organism group, mainly two or three vegetation types combined, but also combinations of vegetation types with invertebrates (as pollinators). Studies on mammals and birds were less frequently combined with studies on other organisms.

In full-text screening, the papers were grouped according to their study theme or topic (Table 6). Each paper could belong to more than one category and the categories were in part overlapping, but we identified a few major groups:

- Edge effects (including abiotic and biotic effects) were quantified for a range of organisms and landscapes.

- The quality of HTI as habitats was addressed in many studies, including studies on roadsides as refuges and species of conservation concern. Studies on invertebrates and different types of vegetation dominated this category.
- The landscape perspective, including fragmentation and studies of population genetics, was covered in many papers, with mammals, birds and invertebrates as the main focus.
- Studies on dispersal, movement and connectivity were conducted at a range of scales. Studies on the impact of road networks and connectivity were few.
- Roadside construction, restoration and management was covered in 74 papers, most on restoration and management
- At least 162 papers addressed some aspects of effects of roads on biodiversity. This number is probably an underestimate, as a large number of indicators used were more or less related to biodiversity. Species richness was one of the most commonly used estimators of biodiversity.

Despite growing acknowledgement of the importance of soil biota in vegetation dynamics (Bardgett & van der Putten 2014, Kandlikar et. al. 2019), soil organisms were covered in only a few studies, on springtails, other litter invertebrates and mycorrhiza. Even fewer papers investigated soil microbial biomass and functional diversity.

Only a very few papers addressed the impact of pollution on biodiversity and ecological processes, and most of these papers studied aquatic systems. This is in strong contrast to the large number of papers on biomonitoring and documentation of contaminant levels along roadsides (Table 2). Similarly, a small number of papers investigated ecological effects of invasive species in HTI, whereas a large number documented occurrence and dispersal along roads (Table 2).

For the different themes, the number of papers was small compared with the number of important factors included (Table 6). This made it difficult to draw general conclusions. In Chapters 4 and 5, we summarise the information from the different themes, identify knowledge gaps and draw some conclusions. Numbers in superscripts refer to a unique paper ID (for a full list, see attachment).

Table 3. Proportion of papers from different broad geographical regions, excluding reviews

Region	%
Africa	1
Asia	14
Australia	9
Europe	41
North America	29
South America	6
More than one region	1

Table 4. Proportion of papers investigating ecological effects of roads of different sizes. Many studies investigated more than one type of road. Large roads are roads heavily used, small roads are less heavily used and unpaved roads are small, unpaved roads, as used by Jakobsson et al 2018.

Road type	**%**
Large	26
Large and small	12
Large, small and unpaved	6
Small	22
Small and unpaved	12
Unpaved	20

Table 5. Proportion of papers examining a set of broad organism groups

Organism group	**%**
Invertebrates	16
Amphibians	5
Reptiles	4
Birds	14
Small mammals, incl. bats	11
Lichens and mosses	3
Grasses	13
Herbaceous plants	20
Woody plants	13
Microorganisms	1
Systems	1
More than one group	22

4 Road effect zones

Edge effects of roads, through changes in biotic and abiotic conditions, can have considerable impacts on different organisms. Habitat loss through road building may be much larger than the land take for construction alone, and the increase in edge density is potentially one of the strongest negative effects of fragmentation (Porensky & Young 2013). Edge habitats caused by road construction can have other negative effects on the species inhabiting roadside areas (e.g. increased exposure to traffic noise, artificial light and pollution). They can also have some potentially positive effects, including access to resources for foraging, but also modified biotic interactions such as exclusion of large herbivores. Although factors causing edge effects are spatially correlated, we split them into different sets of topics, as described in more detail in sections 4.1-4.4. The number of papers on the impact of artificial light were too few to include in the summary.

4.1 Effects of traffic noise

Traffic noise can dominate the soundscape near roads in the form of low-frequency background noise, which may interfere with vocal communication in birds, amphibians and insects and with echolocation in bats. We found with 20 papers on this topic, including one general review, 12 studies on birds, four on frogs and two on bats. Although the studies covered a wide range of road sizes, most papers investigated larger roads in forest landscapes. Several papers reported a negative relationship between traffic noise and the occupancy or behaviour of birds[1397,1633,1845,1878], frogs[1914] and bats[1459], which also influenced community composition. Such impacts were observed both during breeding seasons and post-breeding migration in birds. There were also studies showing lack of response to noise[2069].

However, identifying the relationships between noise and observed occurrence is not simple, because other negative effects of roads (through both direct and indirect mechanisms) often interact with those of traffic noise. Examples are changes in vegetation composition, light levels and predator occurrence. A recurring problem with studies on traffic noise is that many studies did not correct for such collinear factors and there seemed to be a high degree of context dependence, both concerning species composition and landscape features. The studies that corrected for edge effects and differences in noise propagation in the landscape found contrasting results, from strong effects of traffic noise on abundance and species composition[1845] to traffic noise not being a significant factor structuring breeding bird communities and abundance along roads[2069]. A strong impact of low-frequency noise on the composition of bird species assemblages, discriminating against species nesting close to the ground and species communicating at low frequencies, was reported in a few studies[1633,1672]. The effect zone was in many cases directly related to how far noise travelled in the landscape, a variable determined by topography and tree cover. Consequently, effect zones were larger in open landscapes.

Responses to traffic noise can involve avoidance or behavioural plasticity, but only a few of the papers investigated mechanisms of noise effects. Noise effects may involve processes as direct noise avoidance or indirect effects such as reduced feeding or predator avoidance. Some species studied, but not all, were reported to be able to learn and to adjust their vocal output, and some only called in low-noise periods. Species-specific effects were also found to depend on how call activity correlates with the diurnal patterns of traffic noise. Birds that call at low frequency were rarely found close to roads, suggesting that traffic noise acts as a filter on species composition. There are also indications that traffic noise imposes selection pressure on call characteristics of frogs and grasshoppers near roads[1914,1789], i.e. species that have limited ability to adjust their sound output through plasticity.

4.2 Road impact on biotic interactions

The accumulation and dispersal of exotic species along roads is well documented (Lázaro-Lobo & Ervin 2019, Lemke et al. 2019). This has implications for biodiversity and ecological processes along roads, ultimately through spread of these species into the surrounding landscape. In many of the papers reviewed, the consequences of dispersal along roads, such as introgression with native populations[1383], negative effects on native species through competition etc., were implied but not supported by data, or there was a lack of proper controls[1389]. We excluded papers that did not address effects of roads beyond acting as dispersal corridors. This resulted in eight papers, of which four were reviews, one was experimental and three were descriptive papers studying wetland, forest or alpine systems. All eight papers addressed effects on vegetation and one also addressed consequences for invertebrates (ticks)[33]. While the small number of studies makes it difficult to generalise, one conclusion that can be drawn is that the use of roadsides as corridors by invasive plant species increases floristic homogenisation along roads[8,66,1533]. Such spatial homogenisation will counteract positive contributions from roads to spatial habitats and resource heterogeneity in the landscape.

Table 6. Summary of themes addressed in the 473 papers reviewed, and number of papers in total for the category and for different organism groups. The total number of papers on organisms does not equal 473, as many papers addressed more than one organism group.

	No. of papers	Review/ synthesis	Mammals	Birds	Amphibians	Reptiles	Invertebrates	Woody plants	Other vegetation
Invasive species	7	3	0	0	0	0	1	4	4
Edge effects and ecotones	108	3	20	25	6	4	19	27	28
Noise effects	20	1	2	11	4	0	0	0	0
Pollution/ecotoxicology	7	1	0	0	1	0	3	1	2
Ecological traps	8	2	1	6	2	2	0	0	0
Landscape perspective	127	8	23	34	10	8	24	19	20
Population genetics	20	2	7	1	1	2	1	0	5
Fragmentation	23	2	9	3	1	1	1	4	2
Dispersal, movement and connectivity	105	11	32	15	6	4	15	15	20
Road verge as habitat	121	6	14	17	6	5	37	21	36
Demographic and population processes	80	3	14	25	8	4	16	8	15
Biodiversity	162	2	4	18	7	3	43	69	90
Road verge establishment and restoration	74	4	7	5	2	1	21	7	37
Roadkill/collisions	29	3	10	12	7	8	2	0	0
Roadside as refuge	11	0	1	2	0	0	4	2	
Conservation	41	2	1	6	0	0	17	8	16
Urbanisation	33	2	4	9	1	0	6	6	8
Soil (biota)	12								

Roads were also reported to have indirect effects on species occurrence by affecting predator behaviour. Several papers showed that generalist predators like corvids were able to establish populations along roads[35,122]. Such populations benefit from roadkill, but also predate on bird nests along roads. Corvid establishment was reported to be further aided by the presence of infrastructure, such as power lines, telephone poles and shelterbelts, which served as perches or breeding sites. Hence, measures to reduce road impacts, such as the use of shelterbelts and similar structures along roads in open landscapes, can have positive and negative impacts on residential species. The outcome depends on how abiotic conditions and interactions with predators are affected. Other predators can also benefit from road construction[1774]. Predators like foxes and other carnivores use roads and roadsides to travel through landscapes or forage[2055], and thus prey populations inhabiting roadside verges are more exposed to these predators. Community composition in road verges can be influenced by different factors. Roads and road edges may provide habitats for dominant species, with relevant implications for community composition. One of the best examples is the large social honeyeater nesting along roads, which uses aggressive behaviour to exclude successfully all smaller bird species potentially nesting along roadsides. Furthermore, (fenced) road verges exclude larger herbivores, supporting the establishment of woody plant species. This may affect source-sink population dynamics and, in the long term, the genetic composition of affected populations, through effects on the growth rate of the different populations and how they contribute to the next generations.

The presence of roads also interferes with seed dispersal in the landscape, through effects on the movement of organisms that transport seeds[1673]. This transport occurs via seed attachment to animal fur, via defecation of seeds by frugivorous mammals and birds[2063,2065], and through smaller organisms such as ants, which transport seeds on a smaller scale. Since disturbance regimes along roads tend to affect species composition and promote less efficient generalist species[2190], linear elements used for movement by larger animals may obtain more seeds, while local dispersal by organisms like ants may be weakened[126].

More subtle interactions were also documented in the dataset. For example, it was found that a small-scale road avoidance and road mortality of a prey species combined with a large-scale road avoidance by their predators can direct population densities of the prey in relation to distance to road, in this case giving higher prey densities at intermediate distances to the road [1940]. This illustrates that both direct abiotic effects and indirect biotic effects should be considered in the delineation of road impact zones.

4.3 Abiotic components of edge effects

At road edges, light, wind, temperature, humidity, contaminants, soil nutrients and moisture, litter and dust deposition, noise and other variables were reported to be affected, usually in a correlated manner and with different extinction profiles with distance from the road. Of the 108 papers addressing different aspects of edge effects, most addressed effects from roads into forests or grasslands, but a few studies also quantified changes in abiotic conditions[15,46]. The extent of edge effects, mainly observed as changes in species density or community composition, varied from a few metres to several hundred metres, depending on species and landscape context.

Contaminants from roads, such as gaseous emissions, particulate matter or road runoff, have the potential to affect ecological processes in roadsides and in edge habitats along roads through ecotoxicological effects, interactions with soil chemistry or other abiotic conditions. In our initial screening of the literature, we found a large number of papers addressing road impacts on individual performance, specifically studies that screened plant leaves and soil for contaminants, while few papers investigated the ecological implications of these patterns. In the final dataset, there were only seven papers on the latter theme, including one review. Most of these papers addressed the impact of road salt runoff on aquatic organisms or effects of particulate matter, soil contaminants and nitrate on vegetation. The small number of papers prevents any conclusions being drawn about effects of contaminants on ecological processes.

Edge type appeared to be an important factor determining the intensity of edge effect, and road edges were reported to have stronger negative effects on vegetation composition than other managed or natural edges[90]. Such negative effects are amplified in the case of wider or highly trafficked roads.

4.4 Ecological traps

An ecological trap occurs when an organism chooses to settle in a low-quality habitat, causing a reduction in fitness. Roads may potentially provide habitats preferred by organisms, but the biotic and abiotic conditions may have negative effects on population dynamics. Only eight papers in our dataset addressed ecological traps, including two reviews. Even within this small set of papers, there were few studies actually quantifying trap effects, and instead they just assumed a trap function[43,136]. The organisms studied in the experimental papers were birds (four papers), reptiles and amphibians (one paper each). The few studies that actually quantified fitness components related to trap effects found that interactions of vehicles, road infrastructure and adjacent land use moderated the actual effects of roads.

A small number of studies investigated stress levels of organisms using roadsides and edges as habitats[1467,1872,1884,2015], and found that they can apparently tolerate the high disturbance levels. These studies reported contrasting patterns, where some species had high physiological stress levels and reduced body condition, while others were less affected judged by the levels of stress hormones or body conditions. Transitions to chronic stress have a high risk of affecting the fitness of individuals living in roadside habitats, and thus associated population dynamics. Solid documentation of fitness components in addition to stress hormone levels, seems however required. Indirect effects were also reported, where e.g. increased male bird densities in edge habitats caused higher stress levels in territorial males living in neighbouring habitats[1479].

The two review papers on ecological traps[1434,1620] identified large knowledge gaps. Most papers addressed species occupancy, and not performance and consequences at the population level[1434]. Hence, there is actually a lack of data relating to trap effects. Better data are needed to understand how roads affect fitness, including survivorship, reproduction, dispersal and species interactions. The potential of HTIs, as part of a larger network of habitat patches, can then be evaluated for long-term solutions[1620].

5 Landscape perspective

In a landscape perspective, the effects of roads on biodiversity and ecological processes are determined by both direct and indirect mechanisms, ranging from individuals to populations and communities. Such effects are strongly dependent on the landscape context. How roadsides function as habitats, refuges and corridors, and how roads affect fragmentation and consequences of fragmentation, are central to this landscape effect. These processes can be understood using a metapopulation framework (Gilpin & Hanski 1991) describing how species dynamics at larger spatial scales depends on the dynamics of smaller local populations and how individuals disperse between local populations. Here local populations colonise and occupy isolated habitat patches, and individuals disperse between patches depending on the connectivity and spatial arrangement of patches. Local populations may go extinct and habitat patches recolonised from other local populations. Roads contribute to this fragmentation and isolation of local habitat patches and measures to increase connectivity along and across roads will contribute to population dynamics at the larger scale. This framework may also be applied to communities (metacommunities, Leibold et al. 2004).

We found 127 papers addressing impacts of roads in a larger landscape context. Birds were the most studied organisms (36 papers), followed by small mammals (27 papers), invertebrates (22 papers), reptiles (nine papers) and amphibians (10 papers). Different aspects of vegetation responses were addressed in 31 papers, including three on cryptogams. Only 12 papers addressed more than one of these organism groups, mostly vegetation-pollinator interactions. Nine papers addressed population genetic effects or used genetic patterns to infer processes, 31 papers addressed different biodiversity aspects such as changes in species pools and community composition, and 34 papers addressed effects on dispersal, movement and connectivity, including barrier effects. Ten papers addressed conservation or refuge issues. Below we combine the information from these papers with that found in the categories of roadsides as habitats, fragmentation and connectivity.

5.1 Importance of HTI as habitat and refuge in landscape

Roadsides appear to have the potential to function as a habitat for many organisms, especially generalists, but also rare and threatened species, with some cases suggesting that roadsides may offer opportunities for conservation. We found 121 papers addressing roadsides as habitats, an additional seven papers on the function of such habitats as refuges and 25 on their role in conservation. These were primarily papers on species occurrence, with only a very few addressing how the roadsides support different aspects of population growth.

These papers illustrated the potential of roadsides as habitats in a range of systems, from deserts to rainforests. However, the function of roadsides as habitats and their contribution to conservation will depend on the relative importance of roadside resources in the landscape, and both positive and negative contributions have been reported. Although not all of the papers discussed causes of the direction or magnitude of their results, two partly independent mechanisms seem to account for the diverging results. Regarding direction of impact, HTI are characterised by disturbances. Roads can therefore be expected to have negative impacts on biodiversity in pristine landscapes, but positive effects in agricultural landscapes, in which a large proportion of the species present are favoured by disturbances. Regarding the magnitude of the effect, it can be expected to depend on the relative importance of roadside resources in the landscape. Stronger positive effects of road verges as habitats are likely to be found in intensified agricultural, urbanised or forestry landscapes lacking remnants of (semi-)natural systems, than in diverse semi-natural landscapes. In both types of landscape, negative effects may occur if the roadside habitat functions as a trap.

A large proportion of the papers reviewed mentioned that the function of HTI as high-quality habitats and refuges depends on species-specific requirements regarding roadside characteristics. Requirements listed included bare ground for certain invertebrates[118], specific flower resources for pollinators[36], shelter for small mammals[1539], basking sites for reptiles[128] and seed sources for birds[179]. Various criteria such as width of the roadside, structural heterogeneity and continuity of structures (as hedgerows) were also reported to influence the function of the roadside in the landscape and its contributions to biodiversity.

Many of the studies pointed out the importance of distance or connections to larger off-road habitat patches for the occurrence of a species in roadsides[36,2159]. This could be an indication of limited dispersal distance and slow species accumulation in roadsides. However, it is more likely that road verges are not able to provide sufficient resources for positive population growth, because they do not facilitate reproduction or cause high population turnover that requires recolonisation from other patches. The latter two processes would result in roadside assemblages acting as sink populations over time. The importance of road construction and design for population dynamics needs however further studies.

A recurring observation was that the taxonomic, functional and structural diversity of the vegetation present defined available resources and niches for different species[10,36]. In some cases, these factors were of higher importance than landscape variables[2113]. Microhabitat and management differentiation across and along road verges contributed to this heterogeneity by supporting different plant communities, and hence diversity[83]. Different vegetation characteristics are important for different organisms, e.g. some require floral resources, some require dense and tall vegetation for shelter or hideout and some require specific species as host plants for larvae, or an environment with less dense turf and exposed soils. Targeted management of roadsides should involve management of vegetation to provide the required resources. As an example, verge heterogeneity can be explored to provide specialist resources, notably sun-exposed sandy parts of the verge providing for stenotopic species[67]. Restoration through optimising management is highly site-specific and may take a long time, depending on the resistance to change and local species pools[1410]. Additional measures such as adding species may be required.

Most of the studies reviewed just addressed species occurrence, and not components of population dynamics. Hence, it is often difficult to evaluate whether species occurrence in roadsides is just a spillover from connected natural habitats, constituting sink populations, or to what extent roadside can contribute to population maintenance. Some of the papers included information on reproduction, typically reported as observations of individuals of different ages and sizes[145], but these papers rarely included estimates of population growth. This is a serious limitation to our understanding of HTIs. However, populations that only occur in roadsides and maintain populations there over time were found to have a population growth rate of 1 or larger, making it possible to draw conclusions on population dynamics without knowing the details.

For some plant species, there is increased reproductive output along roadsides due to exclusion of vertebrate herbivory[1759] and larger plant sizes in road verges[37,1980]. Such responses are likely not universal, but dependent on species attributes, context and management regime. Roadsides may also maintain populations of insects, thereby contributing to pest control in nearby agricultural areas. This has been documented for some parasitic wasp species[133,1934]. A few studies have also found that roadsides can provide resources and facilities during winter in seasonal climates, such as overwintering possibilities for insects[145] and food resources such as seeds for granivorous birds[123]. However, this aspect has not been investigated in detail to date.

High-quality roadside habitats can sometimes support population dynamics, similarly to undisturbed habitats[1614]. However, the studies reviewed here usually reported far from ideal conditions. In particular, road mortality was cited as a critical factor affecting population growth, especially in combination with suboptimal abiotic and biotic conditions (including management regimes). Many species also have a need for continuity in structures that is not provided by current management regimes, calling for more targeted management using mosaics and gradients of management intensity[125],[1474]. Such spatial and temporal continuity in habitat characteristics is tightly linked to management strategies, given that cutting vegetation causes discontinuity in floral resources and tall vegetation structure[1654,1894], and coppicing of trees and hedgerows creates large gaps in canopy cover[1576].

In papers examining demographic and population processes, there was much focus on mortality. Studies investigating how roads affect a more complete set of population variables were not common. However, there were examples in the dataset of how herbivore and parasite pressure, reproductive allocation and output, recruitment, age-distribution and individual turnover affect different components of population dynamics in roadside populations. From the few studies available, the importance of habitat quality and landscape context is evident[1614,1998,2126], with species able to maintain positive growth rates despite high road mortality in high-quality habitats that are also connected to off-road habitats. However, for some species groups like birds and dragonflies, road mortality was important[1769].

The heterogeneity along roadsides and the contribution of roadsides to habitat and resource heterogeneity at landscape level are both important for biodiversity and ecological functions. In this context, past landscape use was reported to have a large impact on the available species pool and community composition in remnant patches[31,88]. Hence, species occurrence in roadsides is influenced by distance and connectivity to patches of semi-natural or natural vegetation. For some taxa like butterflies, species richness and abundance in roadside ditches were also correlated with configurational heterogeneity in the landscape[55]. Despite having low plant species richness at small spatial scales, considerable spatial heterogeneity in road verges may contribute to a larger species pool at the landscape level[94,146].

The use of roadsides as habitats was also shown to depend on the surrounding landscape, e.g. grassland road verges attract fewer grassland birds when surrounding areas are urban or forested[97], and urbanisation acts as a filter on grassland plant species in roadsides[1507]. In addition, roadsides play a limited role for conservation in landscapes with a degraded regional species pool[1717]. In such cases, measures to restore species pools of species with limited dispersal abilities would be required.

Biodiversity of vegetation was often reported to be higher close to roads[104,1545,1550,1587,1591], caused by changes in species composition as a response to altered resource availability and the role of roads as dispersal corridors. Roadsides accumulate species over time[184], sometimes taking up to a few decades before species richness levels off. Tree diversity and richness often decrease close to roads, while diversity and richness of herbs and shrubs increase[41], including a shift towards more disturbance-tolerant species and exotic species[1627,1906]. This shift in strategies depends on abiotic conditions and management regimes, favouring ruderal and annual species in some cases and perennial competitors in others. Predicted climate changes and nitrogen deposition may reinforce these processes. In other organisms, the diversity patterns will depend on their responses to the vegetation and their dependence on the landscape context or the characteristics of the roadside. The presence of edge specialists also influences these patterns. Hence, roadsides contribute to the local species pool in both managed and more natural landscapes[100,146]. For some organisms, such as collembola[1772] and mycorrhiza[42], roadsides may contain resources of conservation concern and resources for recolonisation of other patches.

There is also a methodological consideration, as most studies in the dataset used simple indicators of biological diversity, providing information that is perhaps not sufficient for management or conservation. Suggested methods use core habitat specificity and contributions to the landscape species pool to separate patches with high number of specialists from patches with similar numbers of generalists[1571]. This is a step towards a tool for prioritising areas of greater biological diversity.

The importance of roadsides for conservation is not well explored. Roadside vegetation in many cases resembles historical semi-natural grasslands[89], containing plant resources of conservation concern[81], but also providing resources for other organisms of concern[65,116]. Roadside avenues and solitary trees are also important as nesting sites and resources for several organisms of conservation concern. However, a preference for weakened or damaged trees in some of these species[119,120] is in conflict with road safety measures. In addition to the vegetation, other aspects of the roadside are important for habitat quality, such as exposure, availability of bare soil and soil characteristics[118]. However, such qualities are species- (or guild)-specific and have to be targeted for the actual context. The role of roadsides in approaches to

conservation of species may differ even among closely related species. For instance, one paper in the dataset showed that two reintroduced butterflies with similar life histories differed in that one needed improved habitat quality, while the other depended on higher connectivity among patches[171]. In general, HTI have a limited role in conservation in regions with depleted species pools[1717].

The number of HTI with moderate conservation potential often far exceeds the number with high conservation potential, but many of those with moderate potential can be improved with proper management[4]. Restoration of roadside vegetation through management and other interventions is central to this work[77,176,1685]. To provide for the function as a replacement habitat and improve patch quality, much of the foundation of habitat functions is determined during restoration after road construction and later strengthened by management. Methods for more targeted restoration have been developed, such as spontaneous succession and interplay with soil biota for low-input restoration[60], restoration using topsoil[239] or hay transfer[140,1409], or conventional approaches involving sowing native species. These approaches contribute to restoration and habitat quality[1409]. Cutting is the major management option in roadside vegetation. Cutting slows down succession and increases vegetation species richness and diversity compared with uncut roadsides[1462], but is affected by an interaction between cutting frequency and hay removal[1712]. Evidence on the impacts of the same treatments on invertebrates is not conclusive[176,1712].

Restoration potential was found to differ between road types, especially between large (wide and heavily trafficked) and smaller roads (narrower with less traffic), with roadsides along smaller roads being easier to restore. These differences are likely due to differences in how abiotic conditions are altered during construction, management regimes and traffic volumes. Abiotic conditions are altered during construction, often with introduction of new material and nutrients and altered hydrology, usually towards drier conditions[1438]. These changes often favour invasive and/or ruderal species over local native plant species.

5.2 Consequences of fragmentation by roads

Roads have effects on the movement and dispersal of both sessile and mobile organisms across and along roads. Roadsides have the potential to act as corridors, connecting larger habitat patches to support gene flow, re-establishment, seasonal migration, social interactions etc., but the evidence reported for each of these mechanisms varied widely. We found 23 papers addressing effects of roads on fragmentation and an additional 18 papers addressing effects of roads on population genetics. Small mammals were the most studied group, in about 40% of the studies reviewed. The focus ranged from edge effects to dynamics at the landscape level.

Roads can be relevant barriers to animals due to both road avoidance and mortality by collisions, but also through fencing and other installations such as noise barriers. Road width and traffic volume are usually the most important factors determining the intensity of the barrier effect. Road avoidance has been documented in many species, as a combination of road structure avoidance (including both gap avoidance and road-substrate avoidance), emission avoidance and vehicle avoidance. How organisms relate to roads is linked to behavioural plasticity (e.g. flying height across roads[1592,1695] or ability to differentiate traffic volumes[1497]), foraging strategies[1758] and body size, where barrier effects are usually larger for smaller organisms[1394,1728,1929]. Road avoidance is also related to brain size in birds[1696], probably owing to learning ability or ability to analyse situations. Road avoidance can also be weather-dependent, as in amphibians[64], and can show seasonal patterns related to breeding in a wide range of species, often affecting the sexes differently, especially males searching for mates, but also females searching for good nesting sites, as is the case in turtles. Barrier effects are also site-specific, where movement choices are affected by landscape patterns[1641] but also smaller-scale factors, all the way down to surface micro-topography. The screened papers indicated that barrier effects are higher for forest species, which may be linked to gap avoidance[2121,1496,57], partly to avoid predators[180]. A consequence is reduced home range areas and reduced access to resources in some species[1466]. Species-specific responses are strong and fragmentation can affect species preferring edges and disturbed sites, as well as forest specialists[2121]. Reduced mobility of small mammals also interferes with processes such as seed dispersal of key tree species[1521,1893], leading to increasing isolation and spatial aggregation of genotypes.

For less mobile organisms, effects of fragmentation are further related to how they cope with changes in abiotic conditions and edge effects[38,1527,1747]. These responses are highly species-specific. Another consequence of fragmentation is a higher proportion of species from the surrounding landscape establish in smaller habitat patches. Effects of fragmentation on less mobile organisms are not well studied, although consequences of isolation can be inferred from their dispersal ability[1747].

Fragmentation by roads contributes to reduced functional connectivity and genetic isolation of populations in many species, depending on the strength of barrier effects, (sub)-population sizes, breeding systems and seasonal migration patterns[1679]. The number of relevant studies was low (20 papers), but they illustrated the complexity and context dependence in evaluating the impact of roads and fragmentation on population genetics[54,1679]. A few studies also quantified mechanisms and long-term consequences of how fragmentation affects the relative importance of reduced population size and genetic drift. Proper management to increase connectivity can promote gene flow[2127] and restore genetic structures[187].

At the same time, increased connectivity along roads may increase hybridisation between previously isolated populations and species[170], and such interspecific hybrids may be more frequent in highly disturbed locations along roads[121]. This includes expansion of novel genotypes along roads as a cryptic invasion, changing population genetic structures of native species[1570]. Roads may also affect selection pressure on specific traits that govern establishment, survival and reproduction in roadside habitats[187], but this has not been sufficiently studied[1472].

5.3 HTI as corridors in the landscape

The function of roadsides as linear corridors for increased connectivity is expected to be one of the main positive contributions of road networks to biodiversity and ecological processes. Although the potential of roadsides and HTI as corridors was mentioned and discussed in many of the papers reviewed, only seven papers studied the function of roadsides as corridors contributing to connectivity in more detail.

The suitability of roadsides as potential corridors was studied in a limited number of small mammals[114,1576] and in some insect and bird species, and in most cases roadsides were found to function as both corridor and habitat. Grassland-like roadsides function as corridors for small mammals in open habitats, while spatial continuity of structures like hedgerows, tree rows and individual trees[1670] is important for forest-dwelling species and small birds, especially in harsh matrices like urban areas and in open landscapes. The importance of corridor intersections was little studied, but a few studies pointed out the importance of intersections for gene flow and recolonisation of patches[172]. Combined with knowledge about how distance and connections to habitat patches in the landscape affect biodiversity in roadsides, this implies that connections towards roadsides, and not only along roadsides, perhaps are more important for the contribution of roadsides to the population dynamics of affected species.

For vegetation, road verges may function as corridors for seed dispersal. In the relevant studies in the dataset, there was no apparent effect on species with wind-dispersed seeds, but roadsides were found to function as corridors for plant species with low to moderate dispersal distances[161]. Seeds can be spread by mammals that use linear elements for foraging and movement, and they are usually transported either through ingestion of fleshy fruit or through attachment to animal fur. Dispersal of seeds by birds may also be facilitated by planting trees, from where they deposit ingested seeds[1540]. Traffic in itself is a vector for seed dispersal, as it can transport seeds over larger distances[1414,2129,2131]. Further, roadside management increases seed dispersal and increases connectivity for plant species, because seeds and other diaspores are transported via e.g. cutting machinery.

It is important not to overestimate the spatial range of corridor functions when roadsides themselves do not function as habitats. As an example, there is reported to be an upper limit to how far apart habitat patches exploited by reptiles can be[178].

5.4 Scale and context dependence of road effects

A few of the studies reviewed pointed out contrasting patterns emerging at different spatial scales. Roadsides can have positive effects at a local scale, by providing habitats and generating heterogeneity, while effects of road networks at a larger scale tend to be negative[163,1539]. Based on these studies, roadsides are potentially not able to compensate for negative barrier and fragmentation effects by offering additional habitats and local connectivity. While there has been little work done on this topic, we expect such patterns to be highly species-specific, depending on how species use resources in the landscape, their road avoidance, effective population sizes, seasonal migrations and exchange of genes between populations. An interesting consideration is that, although major roads have a larger impact zone, the effects of smaller roads on landscape fragmentation are considerable[103]. The impact of fragmentation is well documented, and available habitat without crossing roads may explain more of the species richness than total habitat in an area or distance to major roads[1574].

Effects of roads on biodiversity and ecological processes also interact with other land uses in the landscape[1464], and road density is often reported correlated with negative impacts from urbanisation and agricultural intensification on biodiversity and ecological processes. These drivers are not always simple to distinguish for mobile species using resources in a larger landscape.

6 Knowledge gaps

This screening of the literature revealed a set of major knowledge gaps, which we summarise below.

- To understand how roads affect biodiversity and ecological processes, it is critical to move the focus from species occurrence patterns to population and community processes. This is perhaps the most serious knowledge gap. Hard data covering longer time-spans are required to predict consequences of roads on populations and communities, and to identify ecological trap situations and measures that contribute to population maintenance.

- At the landscape scale, the effects of road networks need to be investigated for a broader set of organisms and communities, including less mobile species, documenting the impact on population dynamics, genetic structures and community dynamics.

- The potential role of roadsides as habitats and corridors may be constrained by the landscape configuration, but this connection is not well understood. Knowledge of how to use landscape information in planning roads and restoring connections both along and towards roads during and after construction has the potential to reduce the ecological footprint of roads. This includes approaches for addressing corridor networks and intersections.
- Corridor quality may affect speed of dispersal, e.g. suboptimal habitat corridors may increase gene flow compared with corridors that function as high-quality habitats as movement is slowed down. Such patterns are not well understood, but need to be addressed to realise the potential of roadsides as corridors. Both road construction and roadside management are key to achieve this.
- Most studies address only one species or a small set of related species, which makes it difficult to detect trade-offs in responses to roadside characteristics. Conflicts can be expected, a simple example being the conflict between measures to provide habitats for small mammals along roads and measures to prevent road-related mortality of predators such as owls. Knowledge is needed to detect these trade-offs and conflicts, but also tools that help in prioritising measures in a given landscape context, thus reducing trade-offs where possible.
- A better understanding is needed of critical components of the landscape during road construction and maintenance measures to strengthen these components to increase the ecological integrity of the landscape. One approach may be to develop tools to document landscape elements and habitat patches that are important for roadside ecology and provide sufficient connectivity to these.
- Provision of corridors along roads may cause larger problems with roadkill and barrier effects at road intersections. Intersections are important as nodes in a corridor landscape, but it is a challenge to maintain their structural and functional connectivity. It is therefore important to evaluate different solutions to avoid this.

7 Conclusions

This review of the literature showed that, despite strong negative effects of processes and factors such as noise, barrier effects, vehicle collisions and landscape fragmentation, HTI can contain considerable biological diversity and species richness,

contribute to structural and resource heterogeneity in the landscape, and function as corridors for a diverse set of organisms. However, evidence of these contributions is fragmented, with high species-specificity in responses (especially in animals), but also a strong impact of the landscape configuration and resources. Our main findings are as follows:

Roadsides function as a habitat for many species of plants and less mobile organisms, or are part of a larger system of habitat patches in the landscape for more mobile species. Vegetation composition (including taxonomic, functional and structural diversity) and management are of fundamental importance for habitat quality, especially to provide continuity in resource availability and functional connectivity. To achieve this, implementation of mosaic or rotational management and gradients of management intensity is crucial. Most of the available literature focuses on species occurrence patterns and very few studies address how roadsides support different aspects of population dynamics, which indicates that more thorough studies are needed on species of conservation concern. Road ecology would benefit from a stronger focus and direct estimates of ecological and physiological processes.

Biodiversity for many organisms increases towards roads. This is due to edge effects, but includes also accumulation of ruderal and exotic species along roads. The edge characteristics of roadsides provide resources for many organisms, including species of conservation concern, but edge effects can often arise at considerable distances from the road. This pattern reduces the core area of habitats along roads and contributes to the landscape fragmentation caused by road networks. Edge effects are determined by a set of collinear abiotic factors that are difficult to separate and decrease in intensity with distance from the road but are also influenced by biotic interactions such as predator behaviour and competition from matrix species.

Roadsides make considerable contributions to the species pool and biodiversity in landscapes dominated by monocultures in agriculture and forestry, or urbanisation. This makes the habitat and corridor functions of roadsides more important, but also more vulnerable to negative effects of roads and less buffered against the impact of stochastic disturbances.

The landscape context is of importance for biodiversity and ecological processes in roadsides, affecting factors such as available species pool, habitat patch networks and diffusion resistance of the surrounding (matrix) landscape. Urbanisation has strong negative impacts on biodiversity in roadsides, likely through a combination of these factors. Distance and connections to patches of semi-natural systems seem to be very important for many organisms occurring in roadsides, contributing to shorter dispersal distances and more successful colonisation, but roadsides may also be dependent on source populations to maintain populations.

Functional connectivity along roadsides has only been documented for a small set of species, in a small number of studies. However, these studies clearly show potential to develop systems that act as corridors in the landscape. Connectivity towards and away from the roads, integrating HTI in a larger landscape with natural and semi-natural components, may be as important as connectivity along roads.

One of the strongest indications in the literature is of high species-specificity in response to edges, landscape configuration and roads, even between closely related species. Considerable trade-offs in responses of different species to potential management measures make it difficult to provide a general framework and recommendations for road construction and management. Within a given road project, a major task will be to identify and prioritise critical components and trade-offs and to develop an environmentally friendly and biodiversity-promoting strategy for road construction and maintenance.

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Appendix. Overview of papers in the final database and their contributions to information in the different theme categories

ID	Reference	Review/Synthesis	Invasive	Edge eff/ecotone	Population genetics	Landscape perspective	Demography and population processes	Biodiversity	Dispersal/conn/movement	Roadside management/construction	Verge as habitat/resource	Fragmentation	Ecological trap	Roadkill/collisions	Pollution/ecotox	Refuge	Noise	Conservation	Urbanization	Soilbiota
1	Aavik et al. 2008 Applied Vegetation Science 11: 375-386							1												
2	Aavik et al. 2009 Ecological Indicators 9: 892-901							1												
3	Aavik et al. 2010 Agriculture Ecosystems & Environment 135: 178-186			1		1		1												
4	Akbar et al. 2010 Polish Journal of Ecology 58: 459-467							1			1							1		
5	Amelon et al. 2014 Journal of Wildlife Management 78: 483-493					1														
6	Amey et al. 2018 Memoirs of the Queensland Museum – Nature 61: 71-81										1									
7	Arevalo et al. 2008 Plant Biosystems 142: 614-622			1																
8	Arévalo et al. 2010 Plant Ecology 209: 23-35							1	1											
9	Arredondo et al. 2018 Proc. of the Royal Society B: Biological Sciences 285: 20181125				1				1											
10	Ascensao et al. 2012 Biodiversity and Conservation 21: 3681-3697							1		1	1									
11	Avon et al. 2010 Forest ecology and management. 259: 1546-1555			1				1												
12	Bain et al. 2014 Molecular Ecology 23: 5619-5627				1	1	1													
13	Bainard et al. 2017 Agriculture, Ecosystems and Environment 249: 187-195					1		1												1
15	Baltzinger et al. 2011 Annals of Forest Science 68: 395-406							1												
17	Batary et al. 2009 Journal of Insect Conservation 13: 223-230			1																
18	Baumann et al. 2018 Remote Sensing of Environment 216: 201-211			1		1						1								
19	Baxter et al. 2017 Rangeland Ecology and Management 70: 493-503					1														
20	Benítez-Malvido et al. 2014 Global Ecology and Conservation 2: 107-117					1		1												
21	Berkman et al. 2018 Canadian Journal of Zoology 96: 622-632				1	1			1			1								

22	Bissonette et al. 2009 Ecology and Society 14: 27			1							1									
23	Bochet et al. 2015 Ecological Engineering 83: 444-451									1										
25	Brady 2012 Scientific Reports 2: 235				1		1													
26	Brearley et al. 2010 Biological Conservation 143: 60-71			1					1											
27	Camacho et al. 2017 Ecosphere 8: e01611						1				1									
29	Celuch et al. 2008 Folia Zoologica 57: 358-372			1		1														
30	?epelová et al. 2012 Landscape and Urban Planning 106: 336-346					1					1									
31	Chaudron et al. 2018 Acta Oecologica 92: 85-94					1		1			1					1				
32	Chiarello et al. 2008 Biodiversity and Conservation 17: 3209-3221			1			1													
33	Civitello et al. 2008 Journal of Medical Entomology 45: 867-872		1				1													
34	Clark et al. 2010 Conservation Biology 24: 1059-1069				1				1											
35	Coates et al. 2014 Journal of Arid Environments 111: 68-78					1								1						
36	Cole et al. 2017 Agriculture, Ecosystems and Environment 246: 157-167					1		1			1									
37	Collins et al. 2009 Journal of the Torrey Botanical Society 136: 445-456					1	1													
38	Concostrina-Zubiri et al. 2018 Science of The Total Environment 628-629: 882-892			1								1								
39	Couto et al. 2017 Herpetologica 73: 10-17					1		1												
40	Crane et al. 2014 PLoS ONE 9: e107178					1												1		
41	Cui et al. 2009 Environmental Monitoring and Assessment 158: 545-559							1												
42	Dai et al. 2013 Applied and Environmental Microbiology 79: 6719-6729							1												1
43	Damon et al. 2009 Western North American Naturalist 69: 149-154										1		1							
44	Davis et al. 2011 Ecosphere 2: 108						1									1				
45	de Sales Dambros et al. 2013 Journal for Nature Conservation 21: 279-285			1																
46	DeGregorio et al. 2014 Ecology and Evolution 4: 1589-1600						1													
47	Delgado et al. 2017 Vector-Borne and Zoonotic Diseases 17: 376-383			1							1									
48	Delgado et al. 2008 Ostrich 79: 219-226			1		1		1												
49	Dibner et al. 2014 Herpetological Conservation and Biology 9: 38-47					1	1				1									
50	Dong et al. 2010 Int Conf on Ecological Informatics and Ecosystem Conservation 2: 1213-1219					1												1		
51	Drapela et al. 2008 Ecography 31: 254-262					1		1												
52	Edwards et al. 2017 Biological Conservation 205: 85-92			1				1												
54	Fenderson et al. 2014 Ecology and Evolution 4: 1853-1875				1	1			1											
55	Flick et al. 2012 Agriculture Ecosystems & Environment 156: 123-133					1		1												

57	Ford et al. 2008 Journal of Mammalogy 89: 895-903								1											
58	Freitag et al. 2008 Bulletin de la Societe Vaudoise des Sciences Naturelles 91: 47-68										1									
59	Fuentes-Montemayor et al. 2009 Journal of Animal Ecology 78: 857-865			1			1													
60	Garcia-Palacios et al. 2011 Ecological Applications 21: 2806-2821							1		1										
61	Geerts et al. 2011 Austral Ecology 36: 656-662			1			1													
62	Goodwin et al. 2017 Urban Ecosystems 20: 889-895							1			1									
64	Gravel et al. 2012 Amphibia-Reptilia 33: 113-127								1											
65	Haaland 2017 Journal of Insect Conservation 21: 917-927					1					1							1	1	
66	Hayasaka et al. 2012 Flora 207: 126-132							1											1	
67	Heneberg et al. 2017 Biodiversity and Conservation 26: 843-864							1		1	1							1		
68	Henriksen et al. 2013 Agriculture Ecosystems & Environment 173: 66-71					1		1												
69	Hillhouse et al. 2018 Environmental Management 61: 147-154									1										
70	Hindmarch et al. 2017 Landscape and Urban Planning 164: 132-143					1			1		1								1	
71	Homyack et al. 2014 Forest Ecology and Management 334: 217-231							1			1									
72	Izuddin et al. 2015 Biodiversity and Conservation 24: 2063-2077			1				1											1	
73	Jacot et al. 2012 Agriculture, Ecosystems & Environment 153: 75-81							1												
74	Jakobsson et al. 2016 Journal of Vegetation Science 27: 19-28							1	1											
75	Jansen et al. 2012 Journal of Insect Conservation 16: 921-930						1		1		1							1		
76	Jarvis et al. 2015 Biological Conservation 191: 444-451								1									1		
77	Jellinek et al. 2014 Animal Conservation 17: 544-554					1			1											
79	Johansen et al. 2017 Applied Vegetation Science 20: 631-640							1		1										
80	Jones et al. 2014 Ecology and Evolution 4: 79-90					1		1				1								
81	Jüriado et al. 2017 Fungal Ecology 30: 76-87					1		1			1									
83	Karim et al. 2008 Ecological Engineering 32: 222-237							1		1	1									
84	Kartzinel et al. 2013 Molecular Ecology 22: 5949-5961							1												
85	Kaufman et al. 2008 Transact of the Kansas Academy of Science 111: 275-282						1			1										
86	Konvicka et al. 2011 European Journal of Entomology 108: 219-229							1										1	1	
87	Kowal et al. 2012 Journal of Insect Conservation 16: 613-627			1															1	
88	Koyanagi et al. 2009 Biological Conservation 142: 1674-1684					1		1												
89	Koyanagi et al. 2012 Urban Ecosystems 15: 893-909																	1		
90	Labadessa et al. 2017 Applied Vegetation Science 20: 572-581			1																
91	Lawson et al. 2011 Southeastern Naturalist 10: 303-320							1												

92	Le Viol et al. 2009 Biological Conservation 142: 3163-3171					1		1								1				
93	Le Viol et al. 2012 Ecological Engineering 47: 146-154							1			1									
94	Le Viol et al. 2008 Biological Conservation 141: 1581-1590					1		1			1									
95	Lee et al. 2012 Environmental Pollution 163: 273-280			1				1												
97	Leston & Koper 2017 Avian Conservation and Ecology 12: article 4					1				1	1								1	
98	Li et al. 2011 Shengtai Xuebao/ Acta Ecologica Sinica 31: 7492-7499						1													
99	Li et al. 2010 Transp. Research Part D: Transport and Environment 15: 525-528			1				1												
100	Lindborg et al. 2014 Biological Conservation 169: 206-213					1		1												
101	Lindell et al. 2011 Wilson Journal of Ornithology 123: 502-507						1													
102	Liu et al. 2010 Frontiers of Environmental Science & Engineering in China 4: 349-360			1						1										
103	Liu et al. 2011 Transp. Research Part D: Transport and Environment 16: 591-594					1														
104	Lotfalian et al. 2012 Journal of Forest Science 58: 446-455			1				1												
105	Mallen-Cooper et al. 2008 Victorian Naturalist 125: 64-75																			
108	McLaren et al. 2011 Canadian Journal of Zoology 89: 1214-1222						1		1			1								
109	Melis et al. 2010 Journal of Insect Conservation 14: 159-168			1				1												
110	Mjadwesch et al. 2008 Ecological Management and Restoration 9: 100-109									1										
111	Monadjem et al. 2010 African Journal of Ecology 48: 1083-1091			1		1														
112	Morgan et al. 2010 Auk 127: 581-589			1							1									
113	Muellerova et al. 2011 Science of the Total Environment 409: 3839-3849							1		1										
114	Mulligan et al. 2013 Restoration Ecology 21: 678-685					1			1											
115	Noordijk et al. 2010 Ecological Engineering 36: 740-750							1		1										
116	Noordijk et al. 2009 Terrestrial Arthropod Reviews 2: 63-76					1										1		1		
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