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Pilar Tamayo
University of Granada

Felipe Pascual
University of Granada

Adela González Megías
University of Granada

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REVIEW PAPER

Effects of roads on insects: a review

Pilar Tamayo Muñoz · Felipe Pascual Torres · Adela González Megías

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Abstract In the last few decades, mounting evidence points to a negative impact of roads on several groups of animals. Most studies on the effects of roads on animal populations concentrate on vertebrates, and only a few on insects. It is difficult to determine the real effects of roads on insects due to the variety of methods used. We review recent literature examining the ecological impact of roads on insects. The objectives of our synthesis are to gain insight into the effects of the construction and operation of a road on insect groups, and to determine the gaps of knowledge. We found that roads negatively affect the abundance and diversity of insects due to two main factors: (1) the high mortality of some groups when crossing the road, with more impact at higher traffic volumes. (2) The unwillingness of many species to cross a road or live close to it. Roads are major barriers for small or flightless species, although the response varied for flying species. Finally, both experimental and observational evidence support the idea that air pollutants and de-icing salt used for the road maintenance negatively affect insects.

Keywords Road mortality · Insects · Traffic volume · Habitat fragmentation

Introduction

Transport infrastructures such as roads and railways contribute to the development of many regions and thus improve the quality of the human life (Koivula et al. 2005; Arroyave et al.

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P. T. Muñoz · F. P. Torres · A. G. Megías
Departamento de Biología Animal, Facultad de Ciencias, Universidad de Granada, Granada, Spain

A. G. Megías (✉)
Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, Avda Fuentenueva s/n, Granada, Spain
e-mail: adelagm@ugr.es

2006). However, road construction involves the fragmentation and alteration of natural habitats (Findlay and Houlahan 1997; Van Bohemen 1998; Georgii et al. 2011). Indeed, although roads cover small proportions of the landscape, the ecological impact is extensive. For example, roads cover less than 1 % of the land in the USA, yet they are estimated to affect 20 % of the landscape (Forman et al. 2003).

In the last few decades, mounting evidence points to a negative impact of roads on several groups of animals (Forman and Alexander 1998; Spellerberg 1998; Trombulak and Frissell 2000; Forman et al. 2003). The impacts of roads on wildlife include a variety of causes such as the barrier effects against dispersal (Keller and Largiader 2003; Roedenbeck et al. 2007; Jones and Bond 2010; Jackson and Fahrig 2011) and direct mortality due to collision with vehicles (Lode 2000; Carpio et al. 2009; Kambourova-Ivanova et al. 2012). The negative effects depend on the speed of the vehicles, traffic volume, road width, time of day/year and habitat diversity along the road (Reijnen et al. 1997; Trombulak and Frissell 2000; Forman et al. 2003; Litvaitis and Tash 2008).

Most studies investigating the effect of roads on animals have concentrated on vertebrates (Caletrio et al. 1996; Clevenger et al. 2003), mainly mammals and birds (Benítez-López et al. 2010; McGregor et al. 2008; Gryz and Krauze 2008), and to a lesser extent on amphibians and reptiles (Carr and Fahrig 2001; Andrews et al. 2005 MacKinnon et al. 2005; Bouchard et al. 2009). However, the ecological consequences of roads on invertebrates remain relatively unknown (Riffell 1999; Valladares et al. 2011). Therefore, more studies addressing the effect of roads on insects are needed (Andrews 1990; Seibert and Conover 1991; McKenna et al. 2001; Soluk et al. 2011). To date, studies on the impact of roads on insects have focused on a few iconic insect orders such as Odonata (Riffell 1999; Soluk et al. 2011), Lepidoptera (Munguira and Thomas 1992; McKenna et al. 2001), and Coleoptera (Koivula and Vermeulen 2005; Carpio et al. 2009; Melis et al. 2010). In some cases, the effect of roads on insects has been negative, i.e. beetles and bumblebees, where the roads pose barriers to movement (Keller and Largiader 2003; Bhattacharya et al. 2003). In other cases, the mortality rate due to roads was non-significant for butterflies and moths (Munguira and Thomas 1992), or beetles (Koivula and Vermeulen 2005; Carpio et al. 2009). Finally, the effect can even be positive for some species, such as some ant species, which find new sources of food in habitats near roads (Itzhak 2008).

It is difficult to determine the overall effects of road on insects due to the variety of methods used. However, there are two main reasons to study the impact of roads on insects: (1) Insects are the most diverse group of organisms in the world, with more than 80 % of the species in earth, and (2) Insects are vital for the functioning of most terrestrial ecosystems. A loss in insect diversity can collapse the population of many vertebrate species that prey on them, and can even alter nutrient recycling in many ecosystems. Road construction is increasing in almost every country, and many old roads are being enlarged with new lanes (Forman et al. 2003). However, the effect of roads on wildlife is a relatively recent issue for road planners, builders, and managers to take into account at the planning stage (Glista et al. 2009). At the moment, and despise the accumulate evidence of the negative effects of roads on wildlife, road-planning decisions in most countries has been minimally influenced by this evidence (Roedenbeck et al. 2007).

Here, we review current literature examining the ecological impact of roads on insects. The objective of our synthesis is to gain insight into the effects of the construction and operation of a road on insect groups, and to determine the gaps of knowledge. Specifically, we identify the different approaches and response variables used to address this topic. Then, we summarise the main roads effects on insects highlighting the most relevant information. Finally, we outline some guidelines for the future to ensure a better understanding of this topic.

Literature search criteria

We conducted several complementary searches to ensure that our data set was as inclusive as possible. First, we conducted an electronic search for the following keywords: "road", "insect", "highway", "motorway", the main insect orders ("beetle", "butterfly" etc.), using all possible combinations (both English and Latin names). Most references were found using "Scopus" and "Google Scholar". We excluded articles that did not focus on the effect of roads on insects but rather on restoration or mitigation actions after road construction (i.e. plant diversity in road verges).

We also checked the literature cited to find additional references. We excluded papers that were not written in Spanish, French or English, as well as papers published in non-refereed journals. We found 50 studies published between 1969 and 2013, with 62 % of them published in 2001–2013.

Effects of roads on insects

Authors used a variety of approaches and focused on several non-exclusive factors to study the effect of roads on insects (Fig. 1). In this review, we focus on the four main topics found in the literature: First, the most imminent effects originate from the construction of the road itself (Fig. 1). Surprisingly less than 4 % of the studies on roads focused on this topic. Second, a higher number of papers focused on insect mortality due to collision with vehicles (39 % of the papers; Table 1). In this case, the mortality rate would depend on traffic volume, road size, etc. Third, nearly 26 % of the papers focused on the effect of roads as barriers to dispersal by examining success of individuals attempting to cross the road, population density in the road's vicinity, or local species diversity (Table 2). Finally, more than 32 % of the studies focused on the effect of pollutants associated with the use and maintenance of the road (Table 3). In this review, we compiled detailed descriptions of the main results found for these main topics.

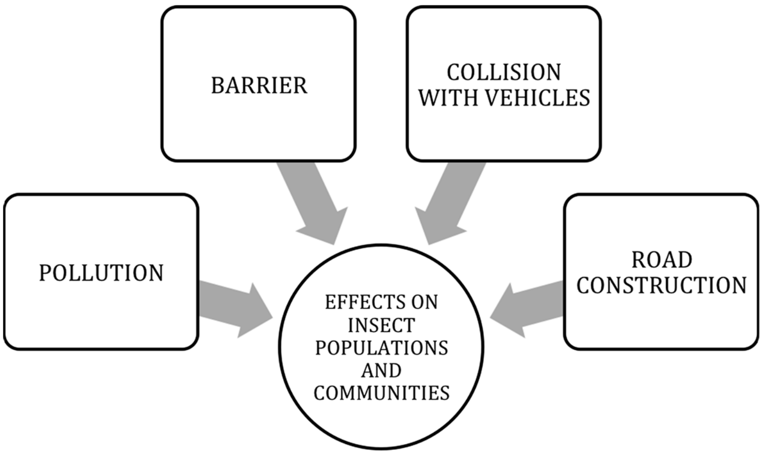

Fig. 1 Overview of the major potential road impacts on insects

Table 1 Main articles showing the effect of roads on insects based on collision with vehicles

References	Group	Methodology	Results
Collision with vehicles			
Yamada et al. (2010a, b)	Insects	Road-killed insects collected 12 times on two transects of 1.2 km on two asphalt roads of similar characteristics from June to September	Along both roads, 5,004.3 dead insects/km were collected. Mean number of dead insects/km/transect was 33.3 individuals. Coleoptera, Diptera and Lepidotera were the most common. Specifically, 444.1 dead dragonflies and 955.9 dead butterflies were collected per kilometre in both roads
Seibert and Conover (1991)	Insects	Road-killed insects collected 50 times from two transects of 1.6 km from June to August on a highway	In total, 1,064 insects belonging to 11 orders were collected. Hymenoptera, Diptera and Lepidotera were the most common
Skórka et al. (2013)	Lepidoptera	60 transects of 200 m (two parallel lines, one on each side of the paved road). 12 surveys of each transect from April to September	In total, 561 roadkilled butterflies of 34 species were collected. The number of roadkilled species per transect was 5.8 ± 0.4 and the number of roadkilled individuals per transect was 9.4 ± 0.7
De la Puente et al. (2008)	Lepidoptera	Road-killed insects collected from 4 transects of 420 m during springs of 2004 to 2006. Model calculated total mortality	During transects, 293 dead butterflies of 22 species were collected. This represents a total of 0.08 road-killed butterflies per m of road. The model estimated mortality between 6,294 and 1,433,000 individuals in the whole section of road during the surveys
Munguira and Thomas (1992)	Lepidoptera	Road-killed insects collected from four transects of 100 m on a paved road over 44 days in June to August	A total of 144 adults of butterfly and burnet were found killed beside the road. Between 0.6 and 6.8 % of the sedentary butterfly species were road killed
Rao and Girish (2007)	Lepidoptera, Odonata	Road-killed insects collected from 27 sampling days of three paved roads. The sections of the roads were surveyed during three sundays and six weekdays	The most abundant insect carcasses were Odonata (61.4 %) and Lepidoptera (34.6 %). Road kill density was 1.6–8.01 kills/day/km for insects in general, and 0.45–3.11 for Lepidoptera. A total of 491 road-killed butterfly individuals of 59 species were found
Riffell (1999)	Odonata	Road-killed insects collected 26 times from a transect of 500 m on a highway (both sides of the road) from June to August	A total of 1,140 corpses were found of 26 species of dragonflies. Mean mortality of all Odonata was 87.7/km/day

Table 1 continued

References	Group	Methodology	Results
Soluk et al. (2011)	Odonata	Road-killed dragonflies collected from 36 roadside surveys along segments of four roadways of different traffic volume between July and August. Traffic volume varied between 0.4 and 1,042 vehicles/h	A total of nine species of dragonflies were monitored. Estimated mean number killed ranged from 2 to 35 dragonflies/km/day
Gravel vs. tar road and asphalt colour			
Kriska et al. (1998)	Ephemeroptera	Mayflies attracted using rectangular test surfaces of different types of asphalt road	The darker and smoother the asphalt, the greater its attractiveness to water-seeking polarotactic mayflies
Hayward et al. (2010)	Coleoptera (Scarabaeidae)	Road-killed individuals of a dung beetles species counted in two transects sampled nine times over five days inside Addo Elephant National Park. One transect was along a tar road and another along a gravel road	A total of 634 individuals of *Circullum bachus* found dead during the study period (70 ± 19 individuals/transect). No differences between tar and gravel roads in the number of dead beetles
Traffic volume and road size			
Seshadri and Ganesh (2011)	Insects	Road-killed insects sampled and removed from between five and ten transects of four roads. Sampling was performed three times during a religious festival (ca. 70 vehicles/h) and three times prior to the festival (ca. 5 vehicles/h) inside Kalakad Mundanthurai Tiger Reserve	A total of 1,413 individuals belonging to 56 species were killed (56 % were invertebrate species). Invertebrate mortality increased linearly with traffic volume. No data offered only for insects
McKenna et al. (2001)	Lepidoptera	Road-killed insects sampled along 13 roadside transects weekly during 6 weeks. Traffic rates ranged from 0 to 1,083 vehicles/h. Transects varied in length	A total of 1,824 butterfly and moth individuals were killed. Higher mortality rates when traffic volume was between 562 and 821 vehicles/h
Rao and Girish (2007)	Lepidoptera	Road-killed insects collected from 27 sampling days in three roads that varied in traffic volume (from approx. 47 to 122 vehicles/h). The sections of the roads were surveyed during three sundays and six weekdays at each road. Traffic volume on Sundays increased between 127.0 and 166.4 %	Insects road kills on Sundays increased between 167.8–182.2 % and 177.6–223.9 % for butterflies. Insect and Lepidoptera road kill densities vary in among sites (between 1.6–8.01 kills/day/km for insects and 0.45–3.11 kills/day/km for butterflies) due to traffic volume
Skórka et al. (2013)	Lepidoptera	60 transects of 200 m (two parallel lines, one on each side of the road). 12 surveys of each transect from April to September. Transects varied in traffic volume (range 23.2–401.5 vehicles/h) and width of the road (5.6–7.2 m)	The number of road killed species was explained by traffic volume (among other factors) and the abundance of road killed butterflies was explained by road width and traffic volume (among other factors)

Table 1 continued

References	Group	Methodology	Results
Soluk et al. (2011)	Odonata	Road-killed dragonflies collected from 36 roadside surveys along segments of four roadways between July and August. Traffic volume varied between 0.4 and 1,042 vehicles/h. Segments varied in length	Mortality rate per km and day significantly varies among roads from 0.66 to 10.96 kills/km/day. Dragonfly mortality rate was positively correlated with traffic volume
Insect characteristics			
De la Puente et al. (2008)	Lepidoptera	Road-killed insects collected from 4 transects of 420 m during spring of 2004–2006. A model calculated total mortality	Mobility: sedentary species were less road killed than more mobile species, which moved more often and travelled longer distances
Skórka et al. (2013)	Lepidoptera	60 transects of 200 m (two parallel lines, one on each side of the road). 12 surveys of each transect from April to September. Transects varied in traffic volume (range 23.2–401.5 vehicles/h) and width of the road (5.6–7.2 m)	Body size: small butterflies were over-represented in the road kills Mobility: no effect of butterfly mobility on butterfly mortality
McKenna et al. (2001)	Lepidoptera	Road-killed insects sampled along 13 roadside transects weekly during 6 weeks. Traffic rates ranged from 0 to 1,083 vehicles/h. Transects varied in length	Sex: mortality rates higher for males than females of monarch butterflies Behaviour: the differences found in the mortality of two monarch butterflies species explained by one being repelled from plants near roads due to the chasing of the other species
Rao and Girish (2007)	Lepidoptera	Road-killed insects collected from 27 sampling days in three roads that varied in traffic volume (from approx. 47 to 122 vehicles/h). The sections of the roads were surveyed during 3 Sundays and 6 weekdays at each road. Traffic volume on Sundays increased between 127.0–166.4 %	Behaviour: greater mortality for species flying below 2 m height Sex: males were more abundant traffic casualties than were females
Riffell (1999)	Odonata	Road-killed insects collected 26 times from a transect of 500 m in a highway (both sides of the road) from June to August	Sex: mortality rates higher for females than males of *Somatochlora*
Soluk et al. (2011)	Odonata	Road-killed dragonflies collected from 36 roadside surveys along segments of four roadways of different traffic volume between July and August. Traffic volume varied between 0.4 and 1,042 vehicles/h. Transects varied in length	Behaviour: greater mortality for species flying below 2 m height, but not a general pattern. Species were much less likely to cross the road with higher traffic intensity than expected when compared to the other roads

Table 2 Main articles showing the effect of roads on insects based on the barrier effect

Reference(s)	Species group	Methodology	Effect of road on insect:
Diversity and abundance			
Haskell (2000)	Insects	One transect perpendicular to the roadside at 36 unpaved roads from June to July in one year Sampling: Soil cores taken along the 100 m transect	Edge effect: negative effect on abundance and diversity of macro-invertebrate soil fauna
Przybylski (1979)	Insects	Four plots at three different habitats (meadows, apple orchards and cheat crops) were selected along a road in one year. Traffic in the road around 5,000 vehicles/day Sampling: 25 vegetative sweeps four times at each plot along at two distances from the road (0–49 m and 50–100 m)	Edge effect: negative effect on species diversity
Luce and Crowe (2001)	Coleoptera, Diptera, Hymenoptera	Ten transects perpendicular to a gravel road. 20 surveys from June to August in one year Sampling: Pitfall traps and vegetative sweeps from 0 to 15 m from the roadside	Edge effect: no effect of distance on species diversity
Carpio et al. (2009)	Coleoptera (Scarabaeidae)	Nine transects perpendicular to a paved road. Continuous survey during September to February Sampling: Pitfall traps located from 0 to 100 m distances from the roadside	Edge effect: species diversity and abundance tended to decrease during the 6 months after the opening of the road. The number of rare species tended to increase towards the forest interior
Knapp et al. (2013)	Coleoptera (Carabidae, Staphylinidae)	Five transects perpendicular to road in five highway sections. Five surveys during May to September Sampling: pitfall traps located from 0 to 100 m distances from the roadside. Transects in open and forest habitats	Edge effect: negative effect on forest specialist diversity. Positive effect on habitat generalists and open habitat specialists
Koivula (2005)	Coleoptera (Carabidae)	Two transects of 350 m parallel to the roadside at 25 and another two 50 m from the road side in four unpaved roads. Continuous survey from June to September in 1 year Sampling: Pitfall traps located at 25–50 m distances from the roadside	Edge effect: only open-habitat specialists caught in traps closer to the road. Negative effect on forest specialists

Table 2 continued

Reference(s)	Species group	Methodology	Effect of road on insect:
Dunn and Danoff-Burg (2007)	Coleoptera	Five transects perpendicular to the roadside of five roads. Three road types: one-lane unpaved, two-lane paved, four-lane highway. One sampling in July in 1 year	Edge effect: no effect of distance from road on beetle diversity and composition across road types
		Sampling: pitfall traps located from 0 to 120 m distances from the roadside	Road type: lower diversity and abundance of beetles near highways and two-lane roads
Melis et al. (2010)	Coleoptera (Carabidae)	25 transects perpendicular to the roadside of three paved roads. Three road types: 1,540 vehicles/day, 400 vehicles/day and <200 vehicles/day. Six surveys from June to July in a year	Traffic volume + edge effect: Negative effect of traffic on beetle abundance but no effect in low-traffic areas. Higher diversity near the roads
		Sampling: Pitfall traps located from 0 to 120 m distances from the roadside	
Bohac et al. (2004)	Coleoptera (Carabidae, Staphylinidae)	Ten transects near roadside of four roads. Two road types: two highways and two two-lane paved roads. One survey from May to November for 2 years	Traffic volume: higher diversity of beetles close to a small road than to a highway
		Sampling: Pitfall traps located near the roadside	
Koivula and Vermeulen (2005)	Coleoptera (Carabidae)	14 intersections of highways from May to September during 1 year. Surveys at two forest fragments: small (0.2–1.8 ha) and big fragments (0.5–37.4 ha)	Fragments: Large patches hosted higher catches of carabids than small ones. Species richness was slightly higher in the large, compared to the small fragments. The most abundant species were relatively evenly distributed among the patches
		Sampling: Pitfall traps located near the roadside	
Genetic analysis			
Keller and Largiader (2003)	Coleoptera (*Carabus violaceus*)	Individuals collected from fragments. Fragments (from 1 to 400 ha) caused by a highway and two two-lane roads	Less allelic richness in small forest fragment isolated by a highway than in other areas
		Genetic population structure with six microsatellite loci	
Keller et al. (2004)	Coleoptera (*Abax parallelepipedus*)	Individuals collected from fragments. Fragments (from 1 to 400 ha) originated by a highway and two two-lane roads	Less allelic richness in small forest fragment isolated by a highway than in other areas
		Genetic population structure with five microsatellite loci	

Table 2 continued

Reference(s)	Species group	Methodology	Effect of road on insect:
Keller et al. (2005)	Coleoptera (*Carabus violaceus*)	Individuals collected from two fragments (80 and 25 ha) located at both sides of a highway Genetic population structure with five microsatellite loci	Population decline stronger in small fragment. Roads divided a continuous population into several isolated subpopulations
Holzhauer et al. (2006)	Ortoptera (*Metrioptera roeseli*)	Individuals collected from 14 grasslands surrounded by roads of different sizes Genetic population structure with RAPD	Crossing roads and land use other than grassland along the transect between sampling locations tended to decrease genetic similarity, whereas grassland and parallel roads tended to increase genetic similarity between bush-crickets
Insect movement			
Koivula and Vermeulen (2005)	Coleoptera (Carabidae)	Mark-recapture (to estimate individual movements). From May to February during 2 years. Road: two-lane highway	Ten carabid species marked. Only one species crossed the road
Mader (1984)	Coleoptera (Carabidae)	Mark-recapture (to estimate individual movements). From April to October during five years at two highways and two paved roads	Both stenotopic woodland carabids and eurytopic forest-dwelling species never or only rarely crossed any of the roads
Mader et al. (1990)	Coleoptera (Carabidae)	Mark-recapture (to estimate individual movements). From April to May during a year at one paved, one gravel and one unpaved road	The carabids preferred to move parallel to the road instead of crossing the paved and gravel roads
Noordijk et al. (2006)	Coleoptera (Carabidae)	Mark-recapture (to estimate individual movements). From March to June during a year by a two-lane paved road	1,301 individuals belonging to two species of carabid were marked. None of the individuals of one species crossed the road, and only 6 % of the other crossed. Of this second species, the proportion crossing was fewer that expected for random movements
Yamada et al. (2010a, b)	Coleoptera (Carabidae)	Mark-recapture (to estimate individual movements). From June to October during a year at four roads inside Nopporo National Park: one paved, two gravel and one unpaved roads	None of the species showed a tendency to cross the roads except a few individuals of *Carabus granulatus yezoensis*, but they only crossed the abandoned grassy unpaved road
Bohac et al. (2004)	Coleoptera (Carabidae, Staphylinidae)	Mark-recapture (to estimate individual movements). From March to June during a year at a two-lane paved road	Only a few individuals of carabid and staphylinid beetles crossed the road

Table 2 continued

Reference(s)	Species group	Methodology	Effect of road on insect:
Bhattacharya et al. (2003)	Hymenoptera	Mark-recapture (to estimate individual movements). From July to August during a year at a six-lane paved road. Two displacement experiments, releasing individuals in other places, were also performed	Bumblebees were never observed crossing the road unless they were displaced, or forced to seek additional forage sites
Askling and Bergman (2003)	Lepidoptera	Mark-recapture (to estimate individual movements). Four-lane highway. From June to August during a year at a four-lane paved road, and a roundabout	8,415 individuals of 55 species marked. Some species crossed the road relatively often and other species seldom crossed the road despite their abundance
Munguira and Thomas (1992)	Lepidoptera	Mark-recapture (to estimate individual movements). From June to August during a year at a paved road, and a roundabout	Most butterfly and moth species crossed roads without difficulty

Table 3 Main articles showing the effect of roads on insects based on pollutants

References	Species group	Methodology	Results
Gases and salt effects			
Williamson and Evans (1972)	Coleoptera, Opilionida, Isopoda, Araneae, Diplopoda	Pitfall traps in rows parallel to the edge of the road (from 0 to 300 m) and left in position for 7 days in June Measure lead levels in soil, plants and animals at two study sites	Levels of lead below 50 ppm of dry weight in most groups. Declining levels of lead in soil, plants, and arthropods with increasing distance from the road but only in one of the study sites
Maurer (1974)	Coleoptera (Carabidae)	Lead content estimated in three beetle species collected by hand near a busy road and a very small road	Two of the three species showed higher concentrations of lead content in individuals collected near the busy road
Goldsmith and Scanlon (1977)	Orthoptera	Grasshoppers were sampled by netting in two areas from September to October in one year. Areas differing in traffic volume of the nearby road (from 1,048 to 21,040 vehicles/day). Lead concentration in grasshoppers was calculated	Grasshoppers showed no differences in lead content in different areas
Beyer and Moore (1980)	Lepidoptera	Caterpillar and leaves collected by hand from cherry trees at two different distances from a paved road in May, 1 year. Lead concentration in caterpillars was calculated. Road traffic of 40,000 vehicles/day	Lead residues in caterpillars were negatively correlated with the distance from the road
Udevitz et al. (1980)	Insects	Insects collected by sweep net at two places, near a road (7,422 vehicles/day) and 2 km from this road. Lead concentration in insects was calculated	The concentration of lead was higher in insects near an interstate road than in remote areas
Wade et al. (1980)	Coleoptera (Carabidae) Homoptera	Insects collected by pitfall traps from July to October, 1 year. Traps located in six transects parallel to the road (from 0 to 150 m) on six major roads and ten control sites with pitfall traps	The highest levels of lead and zinc in soil, vegetation, and invertebrates were found in samples nearest the road except for zinc levels in invertebrates. Lead in insects and other invertebrates decreased 64 % from 2 to 150 m from the road
Robel et al. (1981)	Coleoptera (Scarabaeidae)	Pitfall traps to collect dung beetles in two sites from June to July, 1 year. One site near a road (7,422 vehicles/h) and a control site 5 km from any major road. Lead concentration measured in soil, dung and dung beetles	Lead concentration near the road was higher in vegetation but not in dung or dung beetles
Giles et al. (1973)	Coleoptera, Odonata, Dyctioptera	Insects were collected by sweeping at two places. One site near the road (13,000 vehicles/day), and one site 300 from a rural road. Lead concentration in insects was calculated	Lower levels of lead in arthropods at a higher distance from the road. Higher lead concentrations in predatory insects

Table 3 continued

References	Species group	Methodology	Results
Price et al. (1974)	Hymenoptera, Coleoptera, Orthoptera, Hemiptera	Insects were collected by sweeping at two places in six sites from May to September. Four places near a road (12,900 vehicles/day), and two places in a meadow. Lead concentration in insects was calculated	Lead content was higher in areas closer to roads. In high emission areas there is an increase of lead concentration through the food web (from suckers, chewers, and predators, respectively). In low-emission areas no differences were found between trophic levels.
Port and Thompson (1980)	Lepidoptera	Samples of plants and Lepidoptera larvae from hedges of roads in June, 1 year. Nitrogen, Sodium and Lead concentration in plants was calculated	More insects in the hedges where the N content on plants was higher. The increased N content of the plants probably increased the insect populations
Spencer et al. (1988)	Homoptera	Experiment with different quantities of N and salt solution as a test of plant quality as food for aphids. Counts of the number of aphids on plants	Significant correlations of aphid numbers with total N and soluble N concentrations but there was no effect of proximity to the road on aphid numbers
Braun and Flückiger (1985)	Homoptera	Experiment exposing plants to ambient and filtered air. Aphid numbers were counted	Aphid abundance more than four-fold higher when exposed to ambient air
Muskett and Jones (1980)	Insects	Insects collected by pitfall traps located at different distances from a road (40,000 vehicles/day) Quantification of metal-in air, soil and plants levels at different distance from roadside	Various metals: Lead, cadmium and nickel in air declined with distance to the road. Same pattern observed for lead and cadmium in soil. Complex seasonal changes in metal concentration in grass. No effect of pollution on insect species diversity
Martel (1995)	Diptera	Experiment exposing plants to road pollutants and de-icing salt gradient (selecting places near and far away from a road). Effects measured on the performance of a gall-forming insect	Gall-forming larvae had a greater biomass when they were grown on plants exposed to road air pollutants, although these effects were tempered by a simultaneous exposure to de-icing salt
Spencer and Port (1988)	Homoptera	Experiments to determine plant growth and aphid development in pots with soils from different distances from the roadside	Higher concentration of de-icing salt in soil near the road. Better performance of plants and aphids in pots with soil from near the roadside
Braun and Flückiger (1984)	Homoptera	Experiment exposing plants to de-icing salt treatment to determine aphid abundance on plants	Aphid abundance increased with de-icing salt concentrations
Petranka and Doyle (2010)	Diptera	Experiments in outdoor mesocosm (pools) manipulating experimental salinity (imitating de-icing salt effect) to measure the effect on invertebrates and zooplankton	Aquatic habitats are biologically compromised by de-icing agents, favouring salt-tolerant insect such as mosquitoes

Road construction

The most immediate effect of a road on insects occurs during construction. The removal of the original habitats is lethal for many insect populations. The effect would be expected to be more severe for flightless species or species associated with water and soil, with no capacity to move from their habitats. For example, the deposit of sediments in nearby aquatic areas during road construction led to the death of many aquatic insects, favouring species more resistant to disturbed habitats such as chironomid flies (Hess 1969). Moreover, during road construction, soil removal kills many soil organisms, and destroys ant nests (Heller and Rohe 2000). Despite the potential high impact of road construction on many insect species, there is a lack of studies on this specific topic.

Collision with vehicles

Invertebrates in general, but especially insects, are often struck or run over when they try to cross the road (Seibert and Conover 1991). Therefore, traffic may be destructive to insect populations by collision with vehicles (Fig. 1). Additionally, this effect can be worsened by the effects on insects from the light, noise, and vibrations produced by the cars (Melis et al. 2010). For example, vehicle lights attract many flying insects, inducing lethal impact (Seshadri and Ganesh 2011). These negative effects increase because dead insects attract predators, which also may die by colliding with vehicles (Seshadri and Ganesh 2011).

We found eight articles that specifically quantified the mortality of some insect groups due to car collision (Table 1). Comparison of the results of different studies proved to be difficult despite the similar methods used (transects along the road) due to the variability in the extent of the study, the number and types of road assessed, and the particularities associated to the transects. For example, some authors estimated insect mortality per day by removing dead insects from transects (Soluk et al. 2011) whereas others calculated road kills per day without removing the dead insects (Riffell 1999) or partially removing them (Rao and Girish 2007). This incongruence in methods could explain the twofold difference across studies in dragonfly mortality per day and km due to collision with vehicles (Table 1). Other studies provided only the total number of insect casualties found, with no specification of the number of individuals per transect and km (Seibert and Conover 1991, Rao and Girish 2007).

Most studies focused on conspicuous and relatively large insects such as butterflies and dragonflies (Table 1), concluding that the number of insects killed by vehicles probably affects population dynamics. However, Munguira and Thomas (1992) indicated that the mortality of some groups such as Lepidoptera due to traffic collision is insignificant compared with that due to natural causes. In general, most authors highlight the need of assessing long-term impact of road kills on insect populations.

Traffic volume and road size

Insect mortality due to collision with vehicles could vary with traffic volume, which is usually correlated with road size (Fig. 1; Table 1). Only five articles dealt specifically with this topic (Table 1). There are two different approaches: studies comparing roads with contrasting traffic volume (three studies), and those comparing the same road at different time periods with different traffic volumes (two studies; Table 1). In general, there is a strong positive correlation between traffic volume and insect mortality (Rao and Girish 2007; McKenna et al. 2001; Seshadri and Ganesh 2011; Soluk et al. 2011; Skórka et al.

2013). Surprisingly, McKenna et al. (2001) found higher mortality rates at intermediate traffic volume compared to high and low traffic rates. The authors proposed that on roads with high speed limits, the mortality of Lepidoptera might be reduced by the "catapult" effect (McKenna et al. 2001). Apparently at speeds over 55 mph or more, cars generate gusts of wind that prevent the butterfly from colliding with the vehicle (McKenna et al. 2001).

The traffic rate is not constant on roads, usually increasing during weekends and holidays inside National Parks, and thus insect mortality has been found to peak during these periods (Rao and Girish 2007; Seshadri and Ganesh 2011). Some authors also suggest a weaker effect of the road on nocturnal insects compared with diurnal ones because night-traffic volume is generally lower than during the day (Lövei and Sunderland 1996; Seshadri and Ganesh 2011).

The actual effect of the traffic volume on insects is sometimes difficult to quantify because of the problems of identifying individuals to species (Seibert and Conover 1991). These authors argue that, although they sampled 1,000 individuals hit by cars (belonging to 11 different orders), only 249 individuals could be identified to the species level. An additional problem occurs when trying to detect carcasses of small insects, which in many cases are drawn into the wake of passing cars.

Paved versus unpaved roads

For insects, there is evidence for the influence of the road size and road-surface conditions (paved vs. unpaved) on many groups (Mader et al. 1990; Seibert and Conover 1991; Raemakers et al. 2001; Keller and Largiader 2003; Dunn and Danoff-Burg 2007). Even small paved roads existing in the countryside could be barriers for some species of ground beetles (Mader et al. 1990). However, few papers directly address this question (Kriska et al. 1998; Hayward et al. 2010; Table 1). Some evidence suggests that more than the presence or absence of asphalt, the effect depends on the speed limit (Hayward et al. 2010). Indeed, no effect of the paved versus unpaved roads was found for dung beetle mortality inside a national park, probably due to the reduced speed limit on the roads inside this area (Hayward et al. 2010).

Pavement can be considered a trap that attracts many insect species. For example, certain fresh-water species are attracted by mirages caused by the polarization of the light on different artificial surfaces (Horváth et al. 1998; Kriska et al. 1998, 2009), a phenomenon observed in dragonflies (Kennedy 1917; Puschnig 1926; Fraser 1936; Whitehouse 1943; Schwind 1991, 1995). The greater the degree of polarization of the reflected light, the more attractive the surface is to aquatic insects (Schwind 1995). This attraction is particularly evident when the insects are looking for oviposition sites (Fränzel 1985; Horváth et al. 1998). Kriska et al. (1998), found a negative impact of paved roads on Ephemeroptera due to similar polarization characteristics of the light-reflection on paved roads and on mountain streams where mayflies emerge. In addition, mayflies benefit from open areas with high temperatures (asphalt), which prolongs the insect's reproductive activity in May.

This effect is not unique to roads, as these species are also attracted to dark plastic surfaces used in agriculture (Kriska et al. 1998; Kriska et al. 2009), concrete floors, bright car bodies (especially dark) or windshields, solar panels, wet city streets (Kennedy 1938; Neville 1960; Wildermuth 1998; Horváth and Zeil 1996; Horváth et al. 1998; Bernáth et al. 2001; Wildermuth and Horváth 2005; Kriska et al. 2009), and even black gravestones in cemeteries (Horváth et al. 2007).

Insect characteristics

The effects of roads on insects also depend on insect characteristics, such as sex, body length, and behaviour (Fig. 1; Table 1). There are differences between sexes in their ability to cross the roads. For some dragonflies, the females are more susceptible to collision than males (Riffell 1999). This bias occurs because females tend to fly farther away from the wetland areas looking for food (Foster and Soluk 2006). For butterflies, mortality rates are higher for males than females (McKenna et al. 2001; Rao and Girish 2007). In these cases, different hypotheses have been proposed to explain the sex biases in road casualties: (1) males chase other butterflies (McKenna et al. 2001), and (2) males are attracted to the pheromones released by road-killed females (Rao and Girish 2007).

Species also differ in their mobility. Sedentary species characterized by a relatively low mobility are less likely to invade the roadway than mobile species that travel longer distances (De la Puente et al. 2008). Other studies found no effect of mobility on road mortality, but found that small butterflies were overrepresented in the road kills (Skórka et al. 2013). It is also important to consider flight behaviour of the species, mainly flying height (Rao and Girish 2007; Soluk et al. 2011). Road mortality was higher for some species of Lepidoptera (Rao and Girish 2007) and for some species of dragonflies (Soluk et al. 2011; Table 1). Road casualties could sometimes be overlooked when butterfly species have sufficient flying ability to dodge vehicles (e.g. *Tramea lacerate* and *Anthocharis cardamine*; Rao and Girish 2007; Soluk et al. 2011).

Sometimes a more aggressive behaviour explained the differences in road casualties between species (McKenna et al. 2001). The monarch butterfly (*Danaus plexippus*) chased the black swallowtail (*Papilio polyxenes*), which provoked higher road casualties for the most aggressive species (McKenna et al. 2001). In other occasions, road casualties are related to the sensitivity of the species to the noise and movement of the vehicles (Seiler 2001). Some authors propose that different groups of invertebrates differ in their responses to road surfaces and new microclimate created by roads (Seiler 2001; Dunn and Danoff-Burg 2007; Carpio et al. 2009). Many arthropods such as spiders, carabid beetles, and butterflies are repelled by these new conditions (Mader 1988; Mader et al. 1990; Niemelä 2001; Askling and Bergman 2003; De la Puente et al. 2008; Severns 2008). However, it is difficult to draw general conclusions concerning the intensity of the effect of the road on any particular group because even species of the same group respond in different ways.

Barrier effect of roads

One of the main effects of roads involves habitat fragmentation, potentially obstructing the movement of animals. In general, roads divide populations because animals tend to avoid roads or die trying to cross them. In addition, roads may also split populations by habitat degradation related to the edge effects (Mader 1979; Dunn and Danoff-Burg 2007; Carpio et al. 2009). Not all animal groups are affected in the same way or at the same intensity, as some animals are more sensitive to habitat fragmentation (De la Puente et al. 2008; Seiler 2001). Authors exploring the barrier impacts of road have examined (Fig. 1): differences in the diversity/abundance, population size and genetic isolation, and quantification of individual movements among fragments.

Effect of fragmentation on diversity and abundance of insects

Some studies found insects affected by roads due to habitat fragmentation (Mader et al. 1990; Keller et al. 2005; Koivula 2005). We found eight studies addressing specifically this question by comparing insect abundance and diversity at increasing distances from the road (Table 2). In 50 % of the studies, the diversity and/or abundance of insects increased from the roadsides to the non-altered habitats, implying a negative effect of the roads (Przybylski 1979; Haskell 2000; Carpio et al. 2009; Knapp et al. 2013). In contrast, other authors found no correlation between the distance from the roadside with the abundance or diversity of insects (Muskett and Jones 1980; Luce and Crowe 2001; Dunn and Danoff-Burg 2007). Notably, Koivula (2005) pointed out that although the diversity of carabid beetles was higher closer to the road, the species composition was very different near the road compared to the nearby forest (only one shared species of 22 and 15 species, respectively). The new species present near the roads were all open-habitat species not present in the undisturbed forest habitat. Therefore, although the road construction favoured beetle diversity, the composition of insect species was almost completely different (Koivula 2005). It seems that the altered new open habitat near roads favours open habitat specialists and negatively affects forest ground-dwelling beetles (Knapp et al. 2013).

As many animals die directly from the impact of vehicles, the intensity and sign of the fragmentation effect also depends on the intensity of the traffic and/or the width of the road (Bohac et al. 2004; Melis et al. 2010; Table 2). Indeed, insect diversity was lower for beetles near a highway than by a low-traffic road (Bohac et al. 2004). Major highways are expected to increase the edge effects for most animal species because they are wide and have a high traffic volume (Samways et al. 1997; Forman et al. 2003). Major roads could pose barriers to insect movement, leading to further isolation of populations within the adjacent habitats (Dunn and Danoff-Burg 2007). Wider roads also alter the depth of the layer of detritus from plant litter, significantly diminishing insect abundance and richness (Haskell 2000). The numbers of beetles in high-traffic areas increase with distance from the road, whereas in low-traffic areas no significant differences in abundance are usually found at different distances from the road (Melis et al. 2010). On the contrary, beetle richness was higher near the road than further away (Melis et al. 2010), suggesting that a high number of insect species use roads as refuge or as corridors to move to other areas.

Other authors have focused on the effect of different fragments of habitat due to road construction on insect abundance and diversity (Table 2). They found that small patches of habitat associated with roads support less diversity of insects than bigger patches (Koivula and Vermeulen 2005).

Population fragmentation: genetic analysis

Many studies found that roads constitute barriers by limiting the dispersal of insects (Mader 1984; Keller and Largiader 2003; Koivula 2005; Koivula and Vermeulen 2005). This barrier effect can have serious consequences for the population dynamics of these organisms through a loss of genetic variability in the fragments (Mader 1984; Rietze and Reck 1991; Munguira and Thomas 1992; Balkenhol and Waits 2009). We found only four studies directly addressing this topic, most of them on carabid beetles (Table 2). These beetle species are reluctant to cross paved roads (Mader 1984; Keller and Largiader 2003). Moreover, many of these species are large and apterous (Wachmann et al. 1995), although they can crawl long distances (Thiele 1977). Keller and Largiader (2003) concluded that major roads are barriers to gene flow for *Carabus violaceus*, which leads to a loss of genetic variation in fragmented populations (Keller et al. 2005). A similar result was found for another carabid species (*Abax parallelepipedus*) although in this case the results were not so obvious probably due to the high population density of this species in the fragments (Keller et al. 2004). Similarly, the genetic similarity between the individuals of the bush cricket *Metrioptera roeseli* across the road was lower than among the individuals found along the road on the same side (Holzhauer et al. 2006). Some authors suggested that roads should not be a barrier to genetic exchange between populations for groups with higher movement capability such as butterflies and moths (Munguira and Thomas 1992), but no specific analysis has been made. Although Balkenhol and Waits (2009) showed in their review that molecular approaches can substantially contribute to road ecology research, a great deal of work remains to be done with insects.

Population fragmentation: insect movement

Apart from direct mortality, the most plausible mechanism behind the barrier effect of roads is that many insects avoid crossing roads. In our review, we found only nine papers addressing this topic by marking individuals of different species (Table 2). In general, a road is considered a major barrier mainly for small or flightless species (Noordijk et al. 2006). Many of these small species tend to move along the edges of the road, forcing them to travel longer distances to find suitable areas or even driving them far away from their habitats (Mader 1984; Mader et al. 1990; Koivula and Vermeulen 2005; Noordijk et al. 2006). All studies confirmed that carabid and staphylinid beetles avoid crossing the roads and only a very small proportion of some of the species were found on the other side of the road (Mader 1984; Bohac et al. 2004; Yamada et al. 2010a, b; Table 2).

Flying species also varied in their responses to roads. Butterflies varied in their vulnerability to road traffic, although in general most species tried to cross (Table 2; Munguira and Thomas 1992; Askling and Bergman 2003). For butterfly species, vulnerability to roads was more related to the ability of species to colonise new areas, which is also partially related to the ability to fly (Askling and Bergman 2003). In these cases, some species of Pieridae (*Pieris napi* and *Gonepteryx rhamni*) cross the road quite often, while Nymphalidae (*Coenonympha arcania*, *Aphantopus hyperantus*) and Lycaenidae (*Polyommatus semiargus*) rarely cross the road (Askling and Bergman 2003). By contrast, most butterfly and moth species studied by Munguira and Thomas (1992) crossed the roads. Some road characteristics such as the width and traffic volume could limit the movement of butterflies trying to cross roads, but the air currents of the road edges are proposed as one of the main mechanisms repelling the individuals and reducing the connection between populations divided by a road (De la Puente et al. 2008). A curious response was found for bumblebees due to their site-fidelity behaviour (Table 2; Bhattacharya et al. 2003): when moving to a different habitat, these species return to their maternal patches and only when the patches are depleted of resources do individuals move to new habitats. Notably, individuals avoid crossing roads, and rather move to patches located on the same side of the road (Bhattacharya et al. 2003).

Few papers focused on the role of roads as barriers to insects by limiting their movement. This gap is worsened by the taxonomic bias; 67 % of the studies focus on a few species of carabid beetles (Table 2), and therefore it is not possible to draw more general conclusions. The evidence suggests that for flightless insects roads are clear barriers, and the possibility of flying does not guarantee that the species are not affected by the barrier effect of roads.

Pollution

Insect vulnerability to roads may also be related to the species' tolerance for pollution associated with roads. Traffic volume could indirectly affect insects through the combustion gases expelled (Przybylski 1979). High concentrations of lead have been detected in vegetation and soil along roadsides (Muskett and Jones 1980; Spencer et al. 1988; Petranka and Doyle 2010), with potential effects on animal species associated to these habitats. The accumulation of toxins could pose a health hazard for many insect species such as beetles (Robel et al. 1981) and butterflies (Beyer and Moore 1980). Currently, strong evidence supports the assumption of a higher concentration of lead in insects due to road proximity (Table 3). More than 66 % of the studies on the topic found at least three-fold higher concentrations of lead in insects near roads than in control areas (see i.e. Giles et al. 1973; Maurer 1974; Table 3). Moreover, lead concentration increased in insects through the food web (from herbivores to predators) in highly contaminated areas (Giles et al. 1973; Price et al. 1974). Some authors proposed lead concentration in soil and vegetation as the factor explaining the differences in insect abundance and diversity found at different distances from roads (Przybylski 1979; Muskett and Jones 1980).

Lead is not the only compound derived from air pollution near roads that has drawn the attention of researchers (Table 3). Air pollutants can increase the concentration of total N in plants, which could explain the increase in the number of herbivorous insects on plants near roads (Muskett and Jones 1980; Port and Thompson 1980; Braun and Flückiger 1985; Table 3). However, 50 % of the papers reported either no effect of air pollutants on insect abundance despite the positive correlation between N content in plants and insect performance (Spencer et al. 1988) or that this effect was tempered by other potential pollutants used on roads maintenance, such as de-icing salt (Martel 1995; Table 3).

Of the five papers that focus on the effect of de-icing salt on insects, only one discussed the consequences of this potential pollutant on aquatic insects (Petranka and Doyle 2010; Table 3). In this case, insects such as mosquitoes with a higher tolerance of salty waters were favoured by the use of salt on roads. Accordingly, some of the studies on insect herbivores, such as aphids, also found a positive effect of de-icing salt on insect abundance (Braun and Flückiger 1984; Spencer and Port 1988; Spencer et al. 1988), although this effect was not observed in other studies (Martel 1995).

Basically, both experimental and observational evidence supports the idea that air pollutants and de-icing salt used for road maintenance affect insects (Table 3). It remains to determine the real effect of these contaminants on insect populations over the long term as well as implications for food chains.

Insect groups in road ecology

We found 50 papers trying to elucidate the problems that roads cause for insects. When trying to answer this question, a logical step would be to choose an appropriate methodology and a suitable model group. In this review, we recurrently found a very few insect groups as model systems. The studies examined in this review focused on 19 different insect groups (Fig. 2). Most insect orders were present in only one study and many studies focus on just one order (Tables 1, 2, 3). Beetles were the only studied organisms in 34 % of the cases, followed by Lepidoptera (14 %), and Hemiptera (8 %; Fig. 2). In studies that focused on more than one order, beetles were studied in 50 % of the cases, followed by Lepidoptera (24 %), Hemiptera (16 %), and Odonata (12 %). Moreover, of the 17 papers

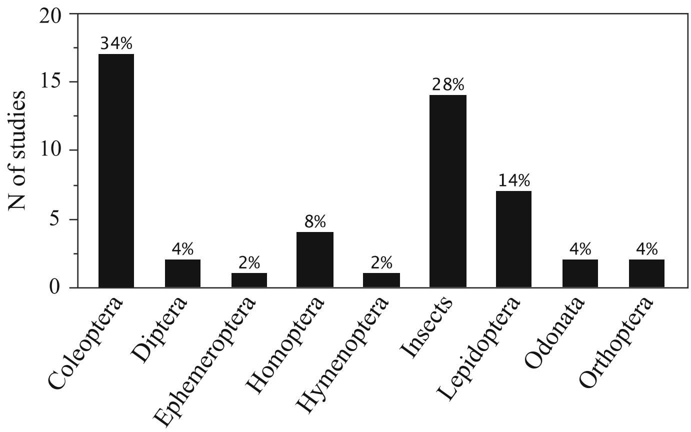

Fig. 2 Number of studies on the different insect orders

dealing exclusively with beetles, 77 % focused on Carabidae and 18 % on Scarabaeidae (Tables 1, 2, 3). Therefore, although it seems that the diversity of orders studied was fairly high, in reality most studies used only two or three different insect families and orders.

Despise this bias in the insect groups studied; most groups are selected because they represent a high proportion of the biomass in the community (i.e. beetles for their abundance and diversity) or because they are more sensitive to habitat alteration (i.e. butterflies and dragonflies). Therefore from the conservation perspective, these taxa are good indicators of the magnitude of the ecological effect of roads on insects.

Conclusions and recommendations for future research

In general, roads negatively affect the abundance and diversity of insects. The high mortality of some groups when crossing the road (with more impact at higher traffic volumes), and the unwillingness of many species to cross a road or live close to it are the two main factors. Moreover, a road is considered a major barrier mainly for small or flightless species, although the response varied for flying species. Finally, both experimental and observational evidence supports the idea that air pollutants and de-icing salt used for road maintenance negatively affect insects. However, it is not easy to draw general conclusions from the studies examined in this review. First, the methodologies followed in the studies were diverse, preventing quantitative comparative analyses. Secondly, comparison is difficult due to the variability of the orders studied, ranging from the most frequent, such as Lepidoptera, to less frequent, such as Diplura. Finally, it would be necessary to undertake long-term studies to ascertain the impact of roads on insect populations through fragmentation and edge effects. Currently, most information on the topic comes from short-term studies (usually a few months).

Therefore, we suggest the following research strategies for future efforts in road ecology:

(1) *Spatial scales* Increase the spatial scales of the studies, including replicated roads. This approach would provide a better idea of how roads affect insects.

(2) *Temporal scales* It is absolutely necessary to conduct long-term studies to accurately monitor the effects of roads on insects at both population and community levels.
(3) *Organisms under study* More studies are needed on other insect groups and it would be valuable to replicate the studies already made on some specific groups in other places to ensure consistency in the results.
(4) *Genetic effect* More studies combining genetic and non-genetic analyses are needed for a proper understanding of the intensity of the road effects on insects and the consequences at both the population and community levels.

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