UNIVERSIDAD COMPLUTENSE DE MADRID

FACULTAD DE CIENCIAS BIOLÓGICAS

TESIS DOCTORAL

Impacto de las carreteras sobre las relaciones interespecíficas

Impact of roads on interspecific relationships

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

PRESENTADA POR

Pablo Quiles Tundidor

DIRIGIDA POR

Rafael Barrientos Yuste

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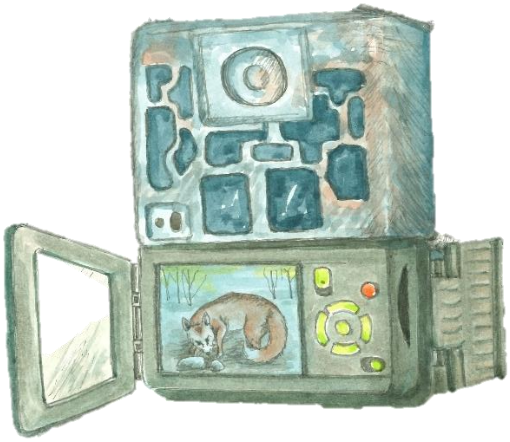
“The ‘control of nature’ is a phrase conceived in arrogance, born of the Neanderthal age of biology and philosophy, when it was supposed that nature exists for the convenience of man.”

Rachel Carson, *Silent Spring*



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Abstract

Human development goes hand in hand with urban expansion, industrialization, overexploitation of natural resources, and the expansion of the infrastructure needed to support it all. Among the latter, roads are the biggest human infrastructure on Earth, so we need to develop the knowledge necessary to understand their current impact on ecosystems and elaborate future plans to mitigate them. Road development has direct effects on ecosystems through habitat loss and wildlife-vehicle collisions. Indirectly, noise, light, and particle emissions generate avoidance behaviours, while roads allow human access to pristine habitats, break habitats into patches, and modify the habitat adjacent to them. The intensity of these effects is species-specific, which unbalance the interspecific relationships that happen within ecosystems, that are basis of ecosystem processes such as nutrient cycling and food webs. Generally speaking, species with lower reproductive rates, late maturity age, greater mobility or larger home ranges, -such as most carnivore species- suffer higher negative road impacts. In central Spain, the carnivore community has seen their larger predators extirpated, and nowadays mesocarnivores remain in an increasingly hostile environment due to continued human infrastructure development and natural resource exploitation. However, while trying to understand the impact of roads and human encroachment in general over this carnivore community, three issues arise: (i) as a diverse community, there are sharp differences in response to human impact between species, (ii) most of them are cryptic species, whose abundance data is scarce, sometimes only obtain from roadkill records and (iii) prey abundance, the main factor driving their presence, varies greatly both spatially and temporarily.

With this background in mind, this thesis aims to extend our knowledge on how human encroachment in general, and roads in particular, alter ecosystem processes through the modification of the species' interactions. In Chapter 1 we carried out a literature review on the existing knowledge about how roads may alter interspecific relationships. We found an alarming lack of studies on countries where most of the road network is predicted to grow. Regarding interspecific relationships we found a series of patterns worth highlighting: (i) prey species suffer increased predation in roads used by predators and alter their anti-predator behaviours, (ii) the prey-trap hypothesis and predator release hypothesis have little empirical support, (iii) road verges can benefit more competitive species such as generalist, invasive, and scavengers, (iv) roads degrade both pollination and seed dispersal processes, and (v) parasitism rates are usually higher closer to the road and are exacerbated by road maintenance practices. Compiling this knowledge allowed us to issue a series of management recommendations to mitigate the negative effects of roads on interspecific relationships: (i) establishment of common metrics on interspecific relationships, (ii) widen and heterogenized road margins, (iii) reduction or elimination of road salt as de-icing agent, (iv) construction of road passages in groups, (v) continuous elimination of carcases from the road surface and (vi) traffic-calming schemes on sensitive areas. In Chapter 2 we focused on the difficulties faced when trying to assess roadkill patterns, especially for elusive species such as carnivores. Using our own roadkill survey and the Spanish Atlas of Terrestrial Mammals, we tested whether opportunistic data can be used to describe carnivore roadkill patterns. To do so, we analysed the differences in the observed proportion of road-kills compared to their expected occurrence from Atlas data with species-specific 2x2 chi-squares with the Yates correction. We found out some discrepancies between both datasets, mainly less than expected roadkills for European otters and more than expected roadkills for European polecats with the use of the Atlas data. We argued the discrepancy regarding otters might result from bias in the Atlas data, as they are easily detected and probably overrepresented. For polecats, their trophic ecology might drive them to hunt rabbits on road embankments, which increase roadkill risk. Our findings then suggest that wildlife atlas data does not always mirror carnivores’ road-kill patterns. In Chapter 3, we dug deeper into the challenges present in describing roadkill patterns and specifically on polecat roadkill patterns. We used the same roadkill survey but comparing it with another dataset separated by over a decade, to test if the variables explaining roadkill hotspots were consistent throughout space and time. We identified rabbit abundance in road embankments, speed limit, distance to irrigated crops, and scrubland as the factors behind polecat roadkill probability. Rabbit abundance effect changed over time, which was probably the cause of polecat roadkill hotspots also changing spatially over time. We provided evidence that in order to mitigate roadkills, static measures could be ineffective, and they will yield better results if we consistently monitor these factors over time. Finally, in Chapter 4, we aimed to understand how human encroachment, landscape composition and prey abundance, shape the distribution and composition of the carnivore community in the intensely humanized landscape of central Spain. To test this, we conducted a three-year extensive trail camera survey and used it to fit state-of-the-art, spatial multispecies occupancy models. The use of these state-of-the-art Bayesian spatially explicit, multi-species varying coefficient occupancy models, allowed for a comprehensive understanding of species and community. In particular, we described how expansive humanized areas may reduce overall carnivore presence in the future and underlined the importance maintaining riparian forest in mostly deforested agrosystems. Critically, our study highlighted how important and complex the relationship between rabbit abundance and mesocarnivore presence on agrosystems is. Although the effect of rabbit abundance is negative for the presence of mesocarnivores, this effect can turn positive at a local scale, probably due to different wildlife management strategies. So, extensive quality data and continuous monitoring of this key prey species is paramount to improve mesocarnivore conservation.

If future human development demands further industrialization, urban and agricultural expansion, we need to find ways to mitigate the negative effect this expansion has on carnivore populations. To do so, we need to consider interspecific relationships, and carryout studies that described the factors behind human impacts on wildlife, at both the species and community level while accounting for spatial and temporal change of those factors.

Resumen

El desarrollo humano va de la mano de la urbanización, la industrialización, la explotación de los recursos naturales y la construcción de la infraestructura necesaria para soportarlo. Entre estas últimas, las carreteras son la infraestructura humana más grande de la Tierra, así que necesitamos comprender el impacto actual que tienen en los ecosistemas y elaborar futuros planes de mitigación de los mismos. El desarrollo de la red viaria tiene efectos directos sobre los ecosistemas a través de la perdida de hábitat y los atropellos de fauna. Indirectamente, el ruido y la luz de los coches alteran los comportamientos animales, a la vez que permiten el acceso humano a hábitats naturales, dividen estos en parches y modifican el hábitat a los márgenes de estas. Estos efectos tienen una intensidad diferente según la especie que los sufra, lo que desbalancea las relaciones interespecíficas que ocurren en los ecosistemas. Generalmente, especies con tasas reproductivas bajas, madurez tardía y gran movilidad o territorios (como los carnívoros), sufren con más intensidad los impactos de las carreteras. En el centro de España, la comunidad de carnívoros ha visto a sus grandes depredadore eliminados (el lobo y el lince Ibéricos) y a día de hoy los mesocarnívoros sobreviven en un ambiente cada vez más hostil debido al desarrollo humano y de sus infraestructuras. Sin embargo, para entender el impacto que el desarrollo humano y las carreteras pueden tener sobre los mesocarnívoros, surgen tres obstáculos: (i) las especies que lo componen responden de forma diferente a estos impactos, (ii) la mayoría de estas especies difíciles de detectar y a veces sus datos se abundancia provienen de registros de atropellos y (iii) la abundancia de presas, uno de los factores clave en su persistencia, varía tanto en el tiempo como en el espacio.

Con estas ideas en mente, esta tesis pretende ampliar nuestro conocimiento sobre como el desarrollo humano y las carreteras en particular, alteran procesos ecosistémicos

al modificar las interacciones entre especies. En el Capítulo 1, llevamos a cabo una revisión bibliográfica para recopilar el conocimiento actual sobre cómo las carreteras pueden alteras las relaciones interespecíficas. Encontramos una alarmante falta de estudios sobre este tema en los países en los que se espera un mayor desarrollo de la red viaria. En cuanto a las relaciones interespecíficas encontramos una serie de patrones que vale la pena destacar: (i) las presas suelen sufrir mayores tasa de depredación alrededor de la carreteras y sus estrategias antidepredatorias se ven alteradas, (ii) las hipótesis de trampa ecológica y liberación de depredadores en carreteras tienen pocos trabajos que den pruebas empíricas de que ocurran, (iii) los márgenes de las carreteras suelen beneficiar a especies más competitivas, (iv) las carreteras interfieren en procesos de polinización y dispersión de semillas y (v) las tasas de parasitismo suelen ser más altas, en parte debido a actividades relacionadas con el mantenimiento de las carreteras. En el Capítulo 2 nos centramos en las dificultades que representa intentar describir patrones de atropellos, especialmente para especies crípticas como los carnívoros. Usando nuestro propio muestreo de atropellos y los datos del Atlas de los Mamíferos Terrestres de España, testamos si datos de tipo oportunista pueden servir para describir patrones de atropellos de carnívoros. Para ello, analizamos las diferencias entre la proporción de atropellos observada para cada especie y su relativa abundancia según los datos del Atlas. Encontramos que las nutrias eran atropelladas menos de lo esperado en función de su abundancia, mientras que los turones eran atropellados más de lo esperado. Las nutrias se son fácilmente detectables y tienen su propio plan de muestreo dentro del Atlas, haciendo que estén sobre representadas en sus datos. Por su parte, la ecología trófica del turón hace que estos persigan su presa principal, el conejo, a los taludes de las carreteras, incrementado el riesgo de atropello. En resumen, nuestro estudio sugiere que no deben usarse directamente datos de tipo oportunista como los del Atlas para determinar patrones

de atropellos de carnívoros. En el Capítulo 3, profundizamos en el estudio de los patrones de atropellos del turón. Usamos el mismo muestreo de atropellos, pero esta vez lo comparamos con los datos obtenidos hace una década, para testar si los puntos negros de atropellos son estables en el tiempo y el espacio. Identificamos que los factores detrás de la aparición de puntos negros son la abundancia de conejo en los taludes de las carreteras, el límite de velocidad de la vía y la distancia a campos de regadío y a zonas de matorral. El efecto de la abundancia de conejo cambió entre ambos periodos, lo que probablemente hizo cambiar la localización de los puntos de atropello de turón en el tiempo. Nuestro trabajo demuestra que las medidas de mitigación estáticas pueden ser inefectivas a la hora reducir el riesgo de atropellos de fauna. Finalmente, en el Capítulo 4, nuestro objetivo fue entender cómo el desarrollo humano, la composición del paisaje y la abundancia de presas, determinan la composición y distribución de la comunidad de carnívoros en el paisaje humanizado del centro de España. Para testar esto llevamos a cabo tres años de muestreo de fototrampeo y usamos modelos de ocupación espacialmente explícitos de última generación. Estos modernos, permiten también modelar factores cuyo efecto varía en el espacio, lo que permite obtener resultados más precisos sobre la respuesta de las especies y de la comunidad en conjunto. Nuestros resultados describen como la expansión de las zonas humanizadas puede reducir la presencia de carnívoros, mientras que los bosques de ribera son un elemento clave para la comunidad en paisajes agrícolas deforestados. Pese a que la abundancia de conejo estuvo relacionada con una menor presencia de mesocarnívoros, su efecto se volvía positivo de forma local, probablemente debido a las diferentes estrategias de manejo de fauna. En este sentido, necesitamos datos extensos y de calidad, actualizados de forma continua sobre esta especie presa clave para la persistencia de los carnívoros.

General introduction

General introduction

Human activities have become the dominant force reshaping Earth, so much so that the Anthropocene is being considered a new epoch in the geological time scale of our planet (Waters *et al.*, 2016). As human development continues, so do urban expansion, industrialization, land-use changes, and their associated infrastructure, all of which cause long-lasting changes in ecosystems, leading to biodiversity loss (Habibullah *et al.*, 2022; Visconti *et al.*, 2016). Although these human impacts on ecosystems are synergetic in nature, and emerge from complex socio-economic scenarios (Brook *et al.*, 2008; Didham *et al.*, 2007), we need to develop the knowledge necessary to understand their current implications and evaluate future trade-offs in conservation (Mace, 2010).

One of those trade-offs would be how to mitigate the effects of infrastructures linked to human development such as roads, highways, railways or powerlines, which are necessary to facilitate the transport of people and goods, while decreasing production costs (Alamgir *et al.*, 2017; Laurance *et al.*, 2014). Among those infrastructures, road impacts on ecosystems have been the most studied, as they occupy the largest surface, with over 21 million kilometres of paved roads in the planet (Meijer *et al.*, 2018), a figure that triples if we include unpaved roads (van der Ree *et al.*, 2015). Road ecology was born in the early 2000s behind the premise of finding ways to mitigate road impacts, as expertise was accumulated after years of pre-road construction studies to assess environmental impacts before new road projects are undertaken (Forman, 2003). Road development has direct effects through habitat loss (van der Ree *et al.*, 2015), while vehicle traffic inevitable causes wildlife-vehicle collisions and avoidance behaviours in response to noise, light and particle emissions coming from the road (Auerbach *et al.*, 1997; Hintz and Relyea, 2019; McClure, 2021). But the negative effects do not end there, as they enable human access to prior remote natural habitats (Dwinnell *et al.*, 2019; Olynyk *et al.*, 2021; Santos and Tabarelli, 2002; Selås *et al.*, 2010), break unified habitats into patches (Cullen *et al.*, 2016; Sawaya *et al.*, 2019), and modify the habitat adjacent to them in a way that may attract some species – either native or alien – and deter others (Da Silva *et al.*, 2019; Darlington *et al.*, 2022; McClure, 2021).

These road impacts do not affect every species in the same way, since they have differential sensitivity. Particularly, species with lower reproductive rates, late maturity age, greater mobility or larger home ranges undergo higher negative impacts (Grilo *et al.*, 2020; Moore *et al.*, 2023; Rytwinski and Fahrig, 2012). On the contrary, species with higher reproductive rates and smaller territories can benefit from roads, when their predators suffer higher negative impacts than they do (Fahrig and Rytwinski, 2009; Rytwinski and Fahrig, 2013). This difference in species sensitivity to roads can alter the relationships among them; i.e., distort interspecific relationships (Chapter 1; see also Quiles and Barrientos, 2024) which are the motor for evolutionary changes and form the basis of ecosystem processes such as nutrient cycling and food webs (Begon and Townsend, 2021).

Carnivores usually meet the above mentioned criteria of species specially sensitive to road impacts (Grilo *et al.*, 2015, 2020; Rytwinski and Fahrig, 2012), and are a key component on most predation and competitive relationships happening in the ecosystems they inhabit. Their role in the ecosystem can be altered by roads through differential changes in habitat selection, changes in movement patterns of predators and prey (Darlington *et al.*, 2022; Johnson-Bice *et al.*, 2023; Lendrum *et al.*, 2018; Mata *et al.*, 2017) as well as by modifying both predatory and anti-predator behaviours (Camacho *et al.*, 2017; Giordano *et al.*, 2022; Monterroso *et al.*, 2020; Watabe and Saito, 2021). This is key as carnivore role in the ecosystems include important processes such as regulation of prey populations, scavenger subsidies, disease dynamics, carbon storage, stream morphology, seed dispersal and crop production (Draper *et al.*, 2022; Ripple *et al.*, 2014). Moreover, as they act as apex consumers, changes in their ecosystem functioning, can create trophic cascades that reverberate through lower trophic levels, reaching primary producers (Beschta and Ripple, 2009; Choquenot and Forsyth, 2013). Nonetheless, there are some generalist predators that suffer fewer costs of roads that can take advantage of this situation and increase their fitness over local species when their higher tolerance to roads allows them to use the resources it provides (e.g., carcasses, ease of movement, etc.; Lombardi *et al.*, 2020; Rød-Eriksen *et al.*, 2020).

Carnivores in the Mediterranean basin live in a landscape that has been transformed by human development for centuries, changing the structure of its ecosystems (Peñuelas *et al.*, 2017). In this transformed landscape, divided by an ever-growing road network, inhabits a carnivore community that has seen their large predators extirpated (Quevedo *et al.*, 2019; Rodríguez and Calzada, 2017). In central Spain, mesocarnivores have become the main actors (Monterroso *et al.*, 2020), conforming a carnivore guild consisting of four mustelids (European badger *Meles meles,* Eurasian otter *Lutra lutra*, Stone marten *Martes foina* and European polecat *Mustela putorius*), one herpestid (Egyptian mongoose *Herpestes ichneumon*), one viverrid (small-spotted genet *Genetta genetta*), two felids (European wildcat *Felis silvestris* and domestic cat *Felis catus*), and one canid (red fox *Vulpes vulpes*). In this scenario, roads impacts are reshaping the relationships between species belonging to this guild, as some species take advantage of the roadside resources but also can pay a price. In particular, badgers and European wildcats tend to avoid roads (Mata *et al.*, 2017; Ruiz-Capillas *et al.*, 2021), whereas red foxes, stone martens, genets and polecats usually use the road proximities during foraging. The latter are known to intensely exploit road verges, as they hunt European rabbits (*Oryctolagus cuniculus*) that breed on road embankments, a foraging strategy increased the frequency of polecat roadkills (Barrientos and Bolonio, 2009; Barrientos and Miranda, 2012; Carmona *et al.*, 2024).

With the use of road verges by some of these species, comes the increasing risk of wildlife-vehicle collision. The study of roadkill risk is key, as roadkills can compromise drivers' safety when big animals are involved (Seiler, 2005) and can have a big impact on population viability (Barrientos *et al.*, 2021; Beaudry *et al.*, 2008; Roger *et al.*, 2011; Row *et al.*, 2007). However, roadkill studies are especially tricky for Mediterranean carnivores as there are marked differences in roadkill sensitivity among species. Moreover, most of them cryptic species which abundance data is scarce and hard to obtain, and when available it usually comes from roadkill surveys. This makes it even more challenging to disentangle roadkill patterns and the variables behind them. Traditionally, those roadkill surveys are usually performed driving slow a given itinerary, recording carcasses of roadkilled animals and repeating them periodically. However, they are time- and budget-consuming (Canal *et al.*, 2019; Costa *et al.*, 2015). For that reason, and taking advantage of roads used by millions of people daily, researchers have turned their attention into ways to gather opportunistic data on roadkills, such as citizen science data. However, this approach has two main issues: firstly, sampling effort is often difficult to control and methodologies are commonly lax; secondly, attempt to census by means of roadkills have several biases, as roadkills are usually abundance-dependant (D'Amico *et al.*, 2018; Gehrt, 2002; Visintin *et al.*, 2016), and some species are more prone to be roadkilled than others depending on their differential use of road surroundings (see above; Chapter 2; see also Quiles *et al.*, 2021).

In order to apply mitigation measures against roadkills, road surveys must take into account spatial distribution of roadkills. The study of these concentrations of roadkills (i.e., roadkill hotspots; Crawford *et al.*, 2014) is a common topic in road ecology research, as their aim is to identify where these road sections appeared in order to implement mitigation measures. These studies usually try to identify road segments with higher-than-expected roadkill ratios and to create models to identify the variables behind them. However, these variables are not always static in time, as it is the case of the local abundance of the species involved, the resources that attract them to the road or the human land uses at the road margins. For these reasons, a continuous monitoring of the key variables that drive roadkill patterns is necessary, so the predictions of these models can be updated, and, consequently, the mitigations measures implemented can be adapted to the new situation.

As we mentioned before, relative abundance -and its variability- of the species affected by roadkills is a key factor that we should control in order to accurately describe and predict roadkill patterns. In the case of carnivore species this task could be difficult, as they are usually cryptic species difficult to detect. Nonetheless, the last decades have yield exponential trail camera development, as well as new abundance, occupancy, and capture-recapture models. Additionally, in the last few years artificial intelligence development has yielded auto identification tools (Beery *et al.*, 2019) that make large scale trail camera projects feasible. The development of those tools have allowed researchers to better estimate species abundance, population dynamics (Karanth *et al.*, 2006), species activity patterns (Monterroso *et al.*, 2014), interaction between species (Sunarto *et al.*, 2015), and community composition across various ecosystems (O’Connell *et al.*, 2011). The application of those tools to road ecology can help researchers to better understand how roads may alter carnivores’ populations dynamics and how they alter the role they play in ecosystem functioning.

In an increasingly altered environment due to human development, it is paramount that we understand the effects of roads on ecosystems, from the big picture of how they alter interspecific relationships, to the intricacies of how, where and when roadkill probability is highest for each species. In order to do so, we need to implement continuous monitoring of key species populations such as carnivores and their prey. If we achieve that, future mitigation measures would be more effective not only at preserving those species populations, but also the ecosystem processes they are a part of.

Objectives

With this background in mind, this thesis aims to extend our knowledge on how human encroachment in general, and roads in particular, alter ecosystems processes through the modification of the species' interactions. Therefore, this thesis compiles the existing knowledge on how roads alter the interspecific relationships (Chapter 1), tackles the difficulties of assessing the impact roadkills have on the elusive carnivore community (Chapter 2), describes how dynamic the variables behind roadkill patterns can be and the implications that this variation can have on determining the places to implement mitigation actions (Chapter 3), and describes the variables that shape the presence of a carnivore community embedded in an intensely humanized landscape (Chapter 4).

- Chapter 1 serves as a good introductory chapter as we carried out a literature review on the existing knowledge about how roads may alter interspecific relationships. We aimed to identify knowledge gaps, and suggest avenues for future research and conservation management. We expected to find that most studies to be carried out on Europe and North America and to be focused on large mammals such as carnivores and ungulates. Therefore, we expected studies on predation to be overrepresented.
- Chapter 2 focused on the difficulties faced when trying to assess roadkill patterns, especially for elusive species such as carnivores. Using our own roadkill survey and the Spanish Atlas of Terrestrial Mammals, we tested whether opportunistic data such as those from atlases can be used to describe carnivore roadkill patterns. We expected discrepancy between both datasets due to biases in atlas data such as sampling effort and species-specific reporting probability, and the different sensibility of the studied species to be roadkilled.

- Chapter 3 digs deeper into the challenges present in describing roadkill patterns. Here we used the same roadkill survey but comparing it with another dataset separated by over a decade, to test if the variables explaining roadkill hotspots were consistent throughout space and time. We expected that the variables explaining roadkill hotspots would be the same, but the distribution of roadkill in space change between periods because of the spatial changes shown by these variables overtime.
- Chapter 4 aims to understand how human encroachment shapes the distribution and composition of the carnivore community in the intensely humanized landscape of central Spain. To test this, we conducted for three years an extensive trail camera survey covering half of the Toledo province and used it to fit state-of-the-art, spatial multispecies occupancy models. We aimed to understand how landscape composition and prey abundance influenced the presence of the carnivore community as a whole. We expected prey abundance to be a key positive factor while human activities to be a detrimental factor for carnivores. However, we expected species to show species-specific responses, reshaping the carnivore community across the space as landscape composition and prey abundance change.

Chapter 1: Interspecific interactions disrupted by roads

Abstract

Roads have pervasive impacts on wildlife, including habitat loss and fragmentation, road mortality, habitat pollution and increased human use of habitats surrounding them. However, the effects of roads on interspecific interactions are less understood. Here we provide a synthesis of the existing literature on how species interactions may be disrupted by roads, identify knowledge gaps, and suggest avenues for future research and conservation management. We conducted a systematic search using the *Web of Science* database for each species interaction (predation, competition, mutualism, parasitism, commensalism and amensalism). These searches yielded 2144 articles, of which 195 were relevant to our topic. Most of these studies focused on predation (50%) or competition (24%), and less frequently on mutualism (17%) or, parasitism (9%). We found no studies on commensalism or amensalism. Studies were biased towards mammals from high-income countries, with most conducted in the USA (34%) or Canada (18%). Our literature review identified several patterns. First, roads disrupt predator–prey relationships, usually with negative impacts on prey populations. Second, new disturbed habitats created in road corridors often benefit more competitive species, such as invasive species, although some native or endangered species can also thrive there. Third, roads degrade mutualistic interactions like seed dispersal and pollination. Fourth, roads can increase parasitism rates, although the intensity of the alteration is species specific. To reduce the negative impacts of roads on interspecific interactions, we suggest the following management actions: (*i*) verges should be as wide and heterogenous as possible, as this increases microhabitat diversity, thus enhancing ecosystem services like pollination and seed dispersal; (*ii*) combining different mowing regimes can increase the complexity of the habitat corridor, enabling it to act as a habitat for more species; (*iii*) the use of de-icing salts should be gradually reduced and replaced with less harmful products or maintenance practices; (*iv*) wildlife passes should be implemented in groups to reduce animal concentrations inside them; (*v*) periodic removal of carcasses from the road to reduce the use of this resource by wildlife; and (*vi*) implementation of traffic-calming schemes could enhance interspecific interactions like pollination and avoid disruption of predator–prey relationships.

Key words: competition, mutualism, parasitism, predation, road ecology, species interactions.

1. Introduction

Human development and the associated infrastructure (land-use transformations, industry, urbanisation, new energy developments) constitute one of the main drivers of ecological change and biodiversity loss (Visconti *et al.*, 2016). Regardless of the type of infrastructure, this encroachment on natural landscapes leads to habitat loss (Biasotto and Kindel, 2018; Borda-de-Água *et al.*, 2017; Marques *et al.*, 2020; van der Ree *et al.*, 2015). Linear infrastructure like roads, railways, pipelines, or powerlines all create more or less intense barrier effects (Borda-de-Água *et al.*, 2017; van der Ree *et al.*, 2015; Vistnes *et al.*, 2004). Mortality caused by collisions differs between static infrastructure like powerlines (Bernardino *et al.*, 2018), and those with mobile elements like windfarms (Marques *et al.*, 2014), and even more so for infrastructure used by vehicles, such as roads or railways (Borda-de-Água *et al.*, 2017; van der Ree *et al.*, 2015). The impact of vehicles differs according to traffic intensity or emissions of pollutants (Barrientos *et al.*, 2019). Consequently, whereas some mitigation actions can be applied to more than one infrastructure, many others are necessarily infrastructure specific (Bernardino *et al.*, 2018; Borda-de-Água *et al.*, 2017; van der Ree *et al.*, 2015). Roads are the most studied linear infrastructure, probably because they occupy the largest surface and are used daily by millions of people.

The road network is, indeed, the largest human infrastructure on Earth with over 21 million paved kilometres (Meijer *et al.*, 2018), a total length that triples when unpaved roads are included (van der Ree *et al.*, 2015). Moreover, this infrastructure is predicted to undergo an unprecedented expansion in the coming years, with an estimated 60% increase by 2050 (Dulac, 2013; Meijer *et al.*, 2018). Roads have several pervasive impacts on wildlife, including habitat loss and fragmentation, barrier effects, road mortality, pollution, facilitation of the expansion of invasive species and increased human access

(Benítez-López *et al.*, 2010; Forman, 2003; van der Ree *et al.*, 2015). The construction of a new road involves the destruction of habitat and allows human access to previously remote natural habitats (Dwinnell *et al.*, 2019; Olynyk *et al.*, 2021; Santos and Tabarelli, 2002; Selås *et al.*, 2010). Infrastructure corridors create separated habitat patches in formerly unified habitats (Cullen *et al.*, 2016; Sawaya *et al.*, 2019), and modify the habitat on both sides of the corridor, in a way that may attract some species – either native or alien – and deter others (Darlington *et al.*, 2022; McClure, 2021; da Silva *et al.*, 2019). Finally, road traffic causes wildlife–vehicle collisions and road-avoidance behaviours in response to road-associated pollution due to noise, light or particle emissions from the vehicles (Auerbach *et al.*, 1997; Hintz and Relyea, 2019; McClure, 2021). These impacts can ultimately threaten the long-term viability of animal populations, but only a handful of species (mainly carnivores and ungulates) concentrate most of the studies on this topic (Barrientos *et al.*, 2021).

While single-species studies in road ecology are limited for most taxa, we know even less on how roads may alter interspecific interactions. This may be key to evaluating the global impact of this infrastructure on biodiversity as several studies have shown that not all species are equally affected. There is evidence that roads have a higher negative impact on species with greater mobility, larger home ranges, lower reproductive rates, or late maturity age (Grilo *et al.*, 2020; Moore *et al.*, 2023; Rytwinski and Fahrig, 2012). On the contrary, some evidence shows that road effects on species with small territories and high reproductive rates can be neutral or even positive (Fahrig and Rytwinski, 2009; Rytwinski and Fahrig, 2013). Thus, we expect that some species interactions will be disrupted by road proximity because one or more of the species involved are differentially affected (either benefited or harmed).

Organisms live within an ecological community, which is defined as an assemblage of populations of more than one species that interact in a certain area (Ricklefs, 2008). Interspecific interactions form the basis for many ecosystem properties, processes such as nutrient cycling and food webs and are also the motor for evolutionary changes. For example, when a wolf pack hunts a deer, it contributes to nutrient cycles (e.g. the carbon cycle), and also forms part of an 'arms race' between these two species, in which survival depends on the individuals' phenotype (Begon and Townsend, 2021). The nature of interspecific interactions can vary depending on the evolutionary and environmental context, aspects that are often difficult to define and measure, and are frequently dependent on scale (Ricklefs, 2008). It is important to note that the intensity of these relationships may vary even within the lifetime of an individual. An approach generally adopted by the scientific community is to define interspecific interactions based on outcome (positive, negative or neutral) for the species involved (Begon and Townsend, 2021; Figure 1). The six commonly accepted interspecific interactions are: (*i*) mutualism, when both species benefit; (*ii*) predation and (*iii*) parasitism, when one species feeds on the other, killing it (predation) or extracts resources from its host (parasitism); (*iv*) competition, when two species compete for the same resources, such as food or space; (*v*) commensalism, when one species takes advantage of the other but without costs for the latter; and (*vi*) amensalism, when a species is harmed by interacting with another that remains unaffected. Since interspecific interactions are the basis of ecosystems, cascading effects can modify ecosystem functioning.

Figure 1: Species interactions based on the outcome for the species involved. Percentages indicate the proportion of articles identified in our literature search documenting each interaction.

We provide a synthesis of the existing literature on the species interactions disrupted by roads. We aimed to identify current knowledge gaps, and potential road-mediated cascade effects, as such information is needed to be able to mitigate the impacts caused by this largest form of human construction. We used the studies identified in our searches to synthetize and exemplify what we know to date on how roads disrupt interspecific interactions, to describe common patterns among interactions, as well as to identify avenues for future research and to recommend best practices for road management. We expect to find most of studies carried out in North America and Europe, as well as focused on large mammals like carnivores and ungulates (Barrientos *et al.*, 2021; Bennett, 2017). As many large mammals are predators, we expect an important proportion of studies approaching how roads disrupt predation-prey dynamics.

2. Materials and Methods

Our aim was not to identify all road studies in which biological interactions are mentioned (i.e. to generate an annotated list), but rather to define the current understanding of interspecific interactions disrupted by roads, and to identify patterns and knowledge gaps. For this purpose, we searched the literature for articles relating to the effects of roads on the six interspecific interactions listed above (Begon and Townsend, 2021), which are based on positive, negative, or neutral outcomes for the species involved.

We conducted a systematic review of the literature to identify studies that describe how roads interfere with interspecific interactions on October 2nd, 2023. We used the *Web of Science* database for six different searches. Each search used the string ("highway" OR "highways" OR "motorway" OR "motorways" OR "parkway" OR "parkways" OR "road" OR "roads") AND "interaction", for the following six interactions: predation, competition, mutualism, parasitism, amensalism and commensalism. We specified the domain as ‘science and technology’ and the research topic ‘environmental science and ecology’, within the Science Citation Index Expanded (SCI-EXPANDED) database for the timespan 1900 to present. This initial search returned 2144 articles. We first screened these articles based only on their titles, retaining 540 articles. We then conducted a second screening by reading the abstracts of the retained articles. Any studies for which inclusion remained uncertain were read in full. This screening process resulted in 195 articles (see online Supporting Information, Table S1). Within this hierarchical screening process, in each step we looked for articles that focused on species interactions, on species ecology disrupted by roads or ideally on both aspects at once. Note that some of the identified studies did not have a primary focus on the effect of roads on species interactions; however, after a critical reading, we could extract relevant information. Finally, we read in full all selected papers, extracted suitable information regarding our topics, and classified each article according to the study taxa, country and main type of road impact. Our searches were intended to enable a quantitative approach to the current knowledge of roads as disruptors of interspecific interactions. Nevertheless, the variety of studied topics (and, consequently, the large diversity of variables reported) prevented a meta-analysis of the patterns found.

3. Results

Of the 195 articles located by our literature search, 50% focused on predation, 24% on competition, 17% on mutualism, and 9% on parasitism. We found no studies addressing road effects on commensalism or amensalism (Figure 1). Most of the studies were carried out in the USA (34%), followed by Canada (18%), Spain (7%), Australia (5%) China (4%), and South Africa (4%). Mammals (46%), plants (27%), arthropods (23%), birds (23%) and amphibians (5%) were the most studied taxa, with several works studying more than one taxon. The most studied road impacts were landscape changes (39%), edge effect (39%) and road pollutants (20%), with several studies reporting more than one impact. Our review provides a useful starting point to clarify the research topics already investigated, and to identify knowledge gaps for future research.

(1) Predation

Of the 97 studies that recorded effects of roads on predation, most focused on how roads affected habitat selection and movements of predators and prey (35%), followed by those focused on the influence of roads on nest predation (26%). Less common were studies focused on how roads altered predatory and anti-predator behaviours (18%), those that tested predator release and prey trap hypotheses (9%), those investigating how road dust and salt pollution influenced predation rates (7%), and those focused on how roads alter herbivory rates (5%) (Figure 2).

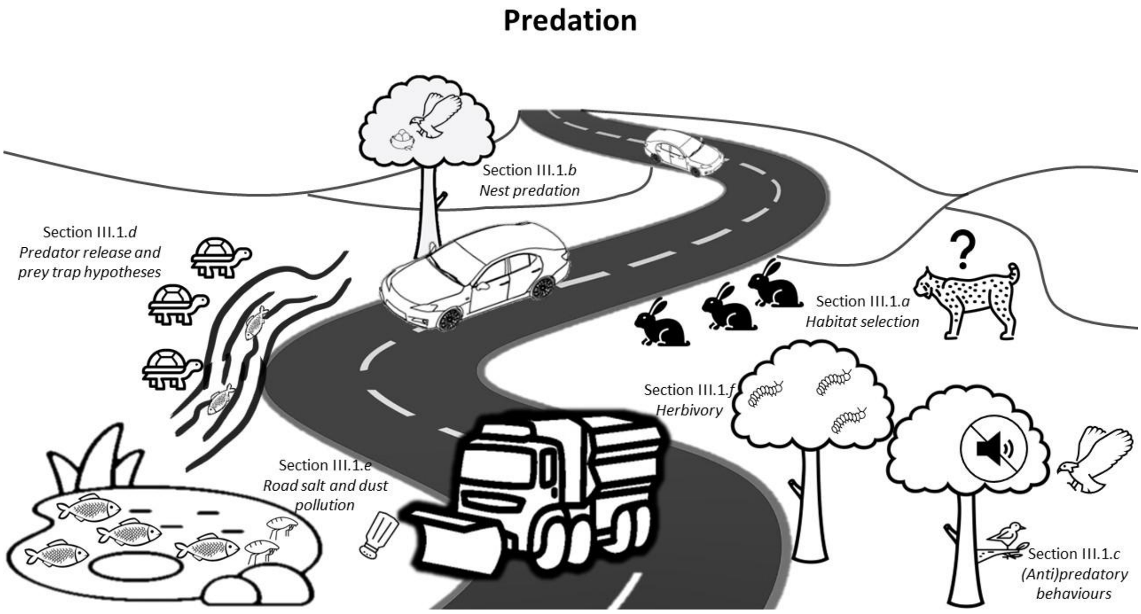

Figure 2: Representation of potential impacts of roads on predation interactions (see Section 3.1 for details).

(*a*) *Effects on habitat selection and animal movements*

Roads and passing vehicles modify the adjacent habitat in several ways; for instance, by changing soil composition or increasing chemical, noise, or light pollution. All these modifications may alter habitat selection by animals, but also create barriers in otherwise continuous habitats that filter animal movements across the road corridor. The mowing of road verges is a common maintenance activity aimed at avoiding wildlife–traffic collisions. This practice has several advantages: (*i*) it reduces the attractiveness of verges as feeding grounds for many species (Andreassen *et al.*, 2005; Jaren *et al.*, 1991); (*ii*) animals perceive these cleared areas as more dangerous, and so spend less time in them (Jaren *et al.*, 1991); and (*iii*) they provide a clear view for both the animal and the driver to avoid a collision (Jaren *et al.*, 1991).

We found several examples of how the new habitat created in road verges can alter habitat selection by both predators and prey and affect the interactions between them. The outcome of such interactions depends primarily on whether the predator or prey avoids or uses the roadside, and at what cost. Most relevant studies were focused on ungulates and their predators (wolves and, to a lesser extent, bears) in North America.

Sometimes, predators avoid roads while prey species use the roadside as it offers a relatively favourable habitat with abundant resources and an easy-to-dig soil (Meunier *et al.*, 1999; Planillo and Malo, 2013; Stapp and Lindquist, 2007). However, the costs of using these habitats vary depending on the degree of road avoidance by their predators. For example, Planillo and Malo (2013) found the highest European rabbit (*Oryctolagus cuniculus*) densities at medium distances (450 m) from the road, whereas predator abundance was higher at 850 m. Thus, in this case the road alleviated predator pressure to some extent, but the habitat close to the road was not fully optimal. This could be related to the fact that predator tolerance towards roads is commonly species-specific. Mata *et al.* (2017) investigated the carnivore guild in the same region, and showed that most species made more intensive use of the motorway verges (likely to patrol their territory boundaries), although some were indifferent or avoided these areas. The potential benefits associated with road verges (easy to dig, allow dust baths, larger seed banks than the surrounding habitat) can exceed the costs associated with higher mortality risk. Some prey species use these resources, despite an increased predation risk, often mitigating this risk by modulating their activity patterns in time and space. For example, kangaroo rats (*Dipodomys ordii*) will inhabit road verges, where predator pressure is higher (Stapp and Lindquist, 2007). By using live-trapping and foraging experiments, these researchers showed that kangaroo rats reduced their foraging intensity near the road during moonlit nights when predation risk was highest (see Section 3.1.*c*). Loosen *et al.*

(2021) found that mowing of road verges offered good foraging opportunities for moose (*Alces alces*), but they only used this habitat along secondary roads, which were used less by wolves (*Canis lupus*) than primary roads. By contrast, Kunkel and Pletscher (2000) found higher moose mortality was higher at lower road densities; in this case wolf activity was higher in those areas. Moose also selected birth sites close to paved roads to avoid traffic-averse brown bears (*Ursus arctos*) (Berger, 2007). White-tailed deer (*Odocoileus virginianus*) strongly selected road corridors, despite a potential increase in wolf encounters, as road verges provide good foraging opportunities in landscapes dominated by intensive agriculture (Darlington *et al.*, 2022).

In other cases, prey species avoid roads in order to reduce predation risk (Fryxell *et al.*, 2020; Mumma *et al.*, 2017) because predators actively use them (Bradley and Fagre, 1988; Rondinini *et al.*, 2006) for faster movement through their territory (James and Stuart-Smith, 2000; Vanlandeghem *et al.*, 2021) and to increase their hunting success (Dickie *et al.*, 2017; Johnson-Bice *et al.*, 2023; Newton *et al.*, 2017). Most such studies were focused on the dynamics between wolves and woodland caribou (*Rangifer tarandus caribou*), elk (*Cervus elaphus*) or white-tailed deer. Roads usually increased predation rates (Courbin *et al.*, 2009; Lendrum *et al.*, 2018; Whittington *et al.*, 2011). Prey migration behaviour can affect the likelihood of predators using roads to move faster through their territory (Nelson *et al.*, 2012). In particular, caribou mothers with calves actively avoid road surroundings to improve offspring survival (Leclerc *et al.*, 2014), however this avoidance resulted in increased calf predation by black bear (*Ursus americanus*), which are more abundant further from roads (Dussault *et al.*, 2012). (Mumma *et al.*, 2019) and (Vanlandeghem *et al.*, 2021) studied a predator–multi-prey system involving the wolf, woodland caribou and moose. Both prey usually avoided areas with higher road densities, while wolves used roads as corridors. However, prey habitat selection varied between the sexes (road avoidance was higher for females) and seasons (avoidance was higher during calving and absent during winter).

Some generalist predator species benefit from scavenging roadkill. For example, the pied crow (*Corvus alba*) is an invasive species in South Africa (Joseph *et al.*, 2017) and its range expansion has been linked to the availability of road carcasses. Populations of generalist predators like this corvid that are maintained at high levels by scavenging roadkill will likely exert increased predation pressure on local small vertebrate populations, especially in areas where predator presence is novel.

(*b*) *Effects on nest predation*

New habitats created by road corridors (see Section 3.1.*a*) can act as ecological traps if animals that breed there experience higher predation or parasitism (Section 3.4.*a*) rates. Road proximity is usually negatively related to bird nest survival in temperate regions (Falk *et al.*, 2011; Newsome and Hunter, 2022; Yoo and Koper, 2017) as edge-associated predators use these new habitats for hunting (Dijak and Thompson, 2000; Fraser and Whitehead, 2005; Lahti, 2001; Newmark and Stanley, 2011; Small and Hunter, 1988; Thogmartin, 1999). By contrast, some studies have found no effect (Bechet *et al.*, 1998; Huhta, 1995; Mettenbrink *et al.*, 2006; Svobodová *et al.*, 2007) or a positive effect of road proximity on nest survival (Angkaew *et al.*, 2019; Delgado García *et al.*, 2005; da Silva *et al.*, 2019). Nest predation on road verges involves a complex interaction among: (*i*) the type of infrastructure, with nest predation higher near dirt roads (DeGregorio *et al.*, 2014); (*ii*) roadside structure (Bergin *et al.*, 1997; Shochat *et al.*, 2005), with perches such as trees increasing nest predation and tall grass reducing it (Depalma and Mermoz, 2019); (*iii*) traffic volume, with higher traffic loads decreasing nest predation relative to birds breeding close to medium-to-low-traffic roads (Pescador and Peris, 2007); and (*iv*) predator traits, with human-tolerant or bold predators showing increased foraging activity along road corridors (Khamcha *et al.*, 2018; Pedersen *et al.*, 2011). However, it is necessary to point out that literature on nest predation is largely dominated by studies on birds, with only two studies focused on another taxon (turtles). Both these studies found that the population viability of turtles improved when nesting near roads, with higher roadkill rates compensated by reduced nest predation (Marchand and Litvaitis, 2004; Murphy *et al.*, 2022).

(*c*) *Effects on predatory and anti-predator behaviours*

Roads and traffic may alter the behaviour of both predators and prey in several ways. First, road noise can reduce the hunting efficiency of acoustically based predators like bats and owls. For the greater mouse-eared bat (*Myotis myotis*) in Europe (Siemers and Schaub, 2011), road noise decreased their foraging efficiency by a factor of five. As these bats predate other predators like carabid beetles, hunting spiders and centipedes, this reduction in bat foraging performance may have complex effects on the food web. Second, roads can result in changes to activity patterns: human disturbance influences the ratio of daytime to nighttime activity in carnivores, which may become more nocturnal to avoid the periods when traffic volume is highest (Watabe and Saito, 2021). Third, roads can lead to modifications in microhabitat use. Camacho *et al.*, (2017) showed that red-necked nightjars (*Caprimulgus ruficollis*) sense overall predator pressure and modulate their microhabitat use of surrounding vegetation as cover from roads patrolled by predators. Fourth, roads can result in dietary modifications. Ruiz-Capillas *et al.* (2021) found that carnivore scats near a road included 10–20% more biomass from small mammals, likely related to increased numbers of micromammals along road verges (see Section 3.1.*a*). Fifth, road proximity may force small mammals to reduce their time spent foraging (Giordano *et al.*, 2022) the increased predation risk perceived due to the proximity of the road (Gonzalez-Olimon *et al.*, 2016). These road-mediated changes in predatory or anti-predatory behaviours may vary within a population, as individual characteristics such as age or social status can also alter risk tolerance. This was the case for brown bears that usually avoid areas with human activity (i.e. fishing paths and houses and their dirt roads) while foraging on sockeye salmon (*Oncorhynchus nerka*). Socially subordinate subadults exhibited a significantly higher tolerance to humans, allowing them to increase their foraging efficiency (Kilfoil *et al.*, 2023).

Passing vehicles produce noise that reduces the distance over which other sounds can be heard; it is usually sustained and its frequency overlaps that of biological sounds (McClure, 2021). It therefore has the potential to influence antipredator behaviours by altering predator detection and perceived risk (Shannon *et al.*, 2014). This may happen by: (*i*) masking biologically relevant sounds like those of an approaching predator (Francis and Barber, 2013); (*ii*) increasing vigilance time, with observed negative impacts on foraging time in both mammals (Morris-Drake *et al.*, 2017; Shannon *et al.*, 2014) and birds (Grade and Sieving, 2016; Owens *et al.*, 2012), and associated reductions in fitness (Dominoni *et al.*, 2020); or (*iii*) causing perception errors, when road noise is misinterpreted as a predation risk and triggers inappropriate responses (Dominoni *et al.*, 2020).

Traffic noise can also hinder interspecific communication by disrupting, or blocking alarm calls and responses to them (Grade and Sieving, 2016), as well as increasing distances between neighbouring forest birds (Owens *et al.*, 2012). However, prey species can become habituated to road noise, with an associated reduction in negative effects (Pettinga *et al.*, 2016). In an urban population of songbirds, anti-predator behaviours were unchanged when road noise overlapped their predator calls, likely because these urban species can differentiate road noise from natural sounds (Pettinga *et al.*, 2016).

Even unused roads can alter prey behaviour, as their construction inevitably involves changes in the surrounding habitats, such as the clearing of road verges (see Section 3.1.*a*). In an ungulate, the guanaco (*Lama guanicoe*), the number of vigilant individuals decreased when foraging in large groups close to roads, probably due to the increased visibility provided by the road corridor for this visually oriented species (Cappa *et al.*, 2017).

(*d*) *Testing the predator release and prey trap hypotheses*

Mammals with greater mobility, lower reproductive rates and larger body sizes are predicted to be more vulnerable to the negative effects of roads because they usually have larger home ranges, and thus higher encounter rates with roads (Barthelmess and Brooks, 2010; Grilo *et al.*, 2020; Rytwinski and Fahrig, 2013). Thus, the predation release hypothesis (Fahrig and Rytwinski, 2009; Rytwinski and Fahrig, 2013) predicts population increase in species whose predators are negatively affected by roads (Muhly *et al.*, 2011; Rogala *et al.*, 2011). To test this hypothesis, (Downing *et al.*, 2015) placed caged mice at sites with different road densities. They found little support for the predator release hypothesis, although as 87% of the recorded predation attempts were by racoons (*Procyon lotor*), being, the experiment provided limited evidence regarding the predator community as a whole (Downing *et al.*, 2015). Planillo and Malo (2013) reported higher prey than predator abundance close to a highway, potentially supporting the predation release hypothesis. In a theoretical study, Rytwinski and Fahrig (2013) developed an individual-based model with several combinations of species traits for both predators and prey regarding their behaviour in proximity to roads, body size, territory size and reproductive rate. These simulations showed positive effects of roads on both small- and large-bodied prey, mediated by reduced predation by generalist and road-affected predators. However, for large-bodied prey species the effect of roads was overall negative.

Their models worked well for small-bodied mammals but failed to replicate observed patterns for amphibians and reptiles (Rytwinski and Fahrig, 2013).

Road-crossing structures, either specifically designed wildlife passages or incidental (culverts), are common road elements that increase permeability and reduce barrier effects (Grilo *et al.*, 2008; Rodriguez *et al.*, 1996; Yanes *et al.*, 1995). Wildlife passages are usually associated with road fences, intended to funnel wildlife through these crossing points. The prey trap hypothesis argues that when prey are conducted into predictable confined spaces where predator pressure is concentrated (see also Section III.4.*c* for parasitism hotspots). This hypothesis has been tested several times and a literature review (Little *et al.*, 2002) concluded that there was little supporting evidence. Alcott *et al.* (2020) described how culverts at road–stream crossings can increase fish density by reducing stream width and fish movement, which can be exploited by predators such as the snapping turtle (*Chelydra serpentina*) to improve their hunting success on migratory river herring (*Alosa* spp.). By contrast, Martinig *et al.* (2020) found no support for the prey trap hypothesis, using co-occurrence data from camera trapping in wildlife passages for both terrestrial mammal predator and prey. Similarly, there was no support in a study of crossing sequences in a wildlife passage over a highway in India, with prey crossing followed by predator crossing sequences rarely recorded by trail cameras (Saxena and Habib, 2022).

(*e*) *Effects of salt and dust pollution on predator activity*

The use of de-icing salts on roads for driver safety is a common practice, especially in northern Europe and North America, with almost five million tonnes of road salts employed annually in Canada alone (Canada Environmental, 2001; Sanzo and Hecnar, 2006). This pollutant often ends up in aquatic habitats when the snow melts, increasing the salinity of freshwater bodies near roads by a factor of 33 compared with rural lakes (Sanzo and Hecnar, 2006). This increased salinity has negative effects on vertebrates (particularly amphibians), macroinvertebrates, algae and protozoa, and can impact the whole community inhabiting these freshwater bodies (Findlay and Kelly, 2011). For example, it can disrupt predator–prey interactions, affecting energy flow through freshwater food webs. Hintz and Relyea (2017) and Hintz *et al.* (2017) found an additive negative effect of increased salinity and predation on zooplankton (water flea *Daphnia pulex*) populations, 85% of that population reduction was due to increased salinity (1300 mg Cl^-/l) and 11% was due to predatory stress. Huber *et al.* (2023) reported antagonistic effects of increased salinity and predation on *Daphnia* vertical movement and abundance. Moreover, they described how the reduction in zooplankton populations led to a phytoplankton bloom and triggered a trophic cascade, with reduction of periphyton *via* shading, reduction of populations of grazers that depend on periphyton, and reduced fish body condition due to food scarcity. Such impacts can also modify competition dynamics (see Section 3.2), as well as the overall energy flow through freshwater food webs.

There is little information related to the effects of road dust on predator–prey systems, but Oi and Barnes (1989) did investigate effects on mite predation rates. They described predation by the western predatory mite (*Typhlodromus occidentalis*) on Pacific spider mite (*Tetranychus pacificus*) in dusty habitats, but did not find a detrimental effect of dust on the abundance of any of the species studied.

(*f*) *Effects on herbivory rates*

Gas emissions from cars include oxides of nitrogen, at concentrations more than 16 times higher than those in clean air (Mansfield, 1979). NO and NO_2 are absorbed by plants though their leaves, making them more attractive to herbivorous insects. The increased activity of herbivores in the vicinity of roads represents a limiting factor for plant growth and reproduction rates (Port and Thompson, 1980). A recent laboratory experiment demonstrated that caterpillars detected leaf damage on oak trees arising from exposure to vehicle emissions and selected them preferentially for foraging, resulting in increased caterpillar performance (mass gain) (Meineke *et al.*, 2023).

By contrast, herbivorous birds tend to associate road traffic with higher predation risk, reducing their foraging efficiency and vegetation biomass consumption per unit time (Gill *et al.*, 1996). Nonetheless, herbivores can adapt to traffic by modifying their activity patterns, for example pink-footed geese (*Anser brachyrhynchus*) increased foraging in fields closer to roads at night (Madsen, 1998).

(2) Competition

Of the 48 studies that investigated competition, most focused on how differences in species tolerance towards roads, and their adaptability to the new resources these infrastructures provide, altered competition dynamics (54%). A smaller number of studies described invasions by alien plants on road verges (21%) or the effects of road salt pollution on equilibria in freshwater communities (13%). A few studies used theoretical modelling of competition dynamics to investigate fragmentation and habitat degradation (6%), or studied the beneficial effects of road verges on disturbance-tolerant insects (6%) (Figure 3).

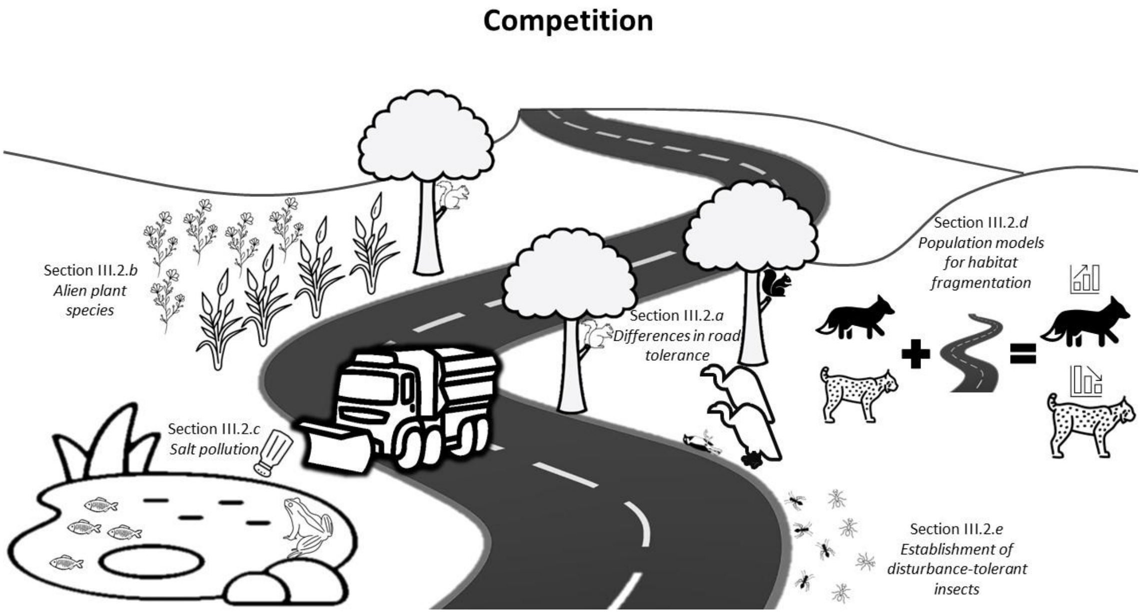

Figure 3: Representation of potential impacts of roads on competition interactions (see Section 3.2 for details).

(*a*) *Differences in species tolerance towards roads alter competition dynamics*

Roads can have many direct and indirect impacts on wildlife, but the tolerance to these impacts will be taxon specific with some species actively avoiding roads while others take advantage of the new habitats created by road corridors (see Sections 3.1.*a* and 3.1.*d*).

Chen and Koprowski (2016) radio-tracked squirrels to study how territory use was affected by road presence, and how this infrastructure impacts competition dynamics between native forest-dependent Mount Graham red squirrel (*Tamiasciurus hudsonicus*) and the introduced Abert’s squirrel (*Sciurus aberti*). Roads acted as a barrier to the movements of *T. hudsonicus*, impeding access to food or mates on the other side of the road. On the contrary, roads provided additional habitat for the non-native, edge-tolerant *S. aberti*, which would even cross the road. This study demonstrated that species with similar body size, but different road tolerance, responded in different ways, altering their competition dynamics.

Rød-Eriksen *et al.* (2020) described how roads facilitated the access of red foxes (*Vulpes vulpes*) into alpine areas in Norway, affecting endangered Artic fox (*V. lagopus*) populations. Similarly, (Kolbe *et al.*, 2007) described how snowmobile tracks allowed coyotes (*Canis latrans*) to invade the hunting grounds of Canada lynx (*Lynx canadensis*), outcompeting them for the same prey (snowshoe hare, *Lepus americanus*). (Lombardi *et al.*, 2020) found lower competence (i.e. co-occurrence) of carnivores close to roadways, with the only road-tolerant species being the ocelot (*Leopardus pardalis*). Rodríguez *et al.* (2020) described how, within the same habitats, domestic cats (*Felis catus*) preferred areas close to paved roads, while European wildcats (*Felis silvestris*) and red foxes selected areas close to streams and forest edges. These differences in road tolerance can lead to altered patterns of spatial, temporal, and dietary segregation. For example, herbivores like the white-tailed deer or the red deer (*Cervus elaphus*) gain a competitive advantage by occupying and exploiting resources closer to roads than their competitors moose and roe deer (*Capreolus capreolus*), respectively (Hinton *et al.*, 2022; Torres *et al.*, 2012). A similar pattern has been described for predators: black bear and pampas fox (*Pseudalopex gymnocercus*) tend to use habitat closer to paths or dirt roads, gaining an advantage in terms of the spatial partitioning arising from their competition with grizzly bears (*Ursus arctos horribilis*) and crab-eating fox (*Cerdocyon thous*), respectively.

One of the main impacts of roads is vehicle–wildlife collisions (Forman and Alexander, 1998), which lead to the persistence of carrion on the road surface for variable periods, depending on carcass size and taxon (Barrientos *et al.*, 2018). This resource can be a crucial factor modifying competition dynamics of scavenger communities, as not all species use them to the same extent. Use of this resource represents a trade-off between energy intake and mortality risk (Knight and Kawashima, 1993). The risk of feeding directly on the road surface is higher for large raptors, which usually do not exploit this resource, as their lower manoeuvrability makes them more vulnerable to collision with incoming vehicles (Lambertucci *et al.*, 2009; Speziale *et al.*, 2008). (Lambertucci *et al.*, 2009) found that smaller raptors took less time between detecting and feeding on a carcass near roads, because they perched close to them and are more tolerant to road disturbance (see also Benítez-López *et al.,* 2010). Another example is provided by the study conducted by Selås *et al.* (2010) testing whether the increased food availability associated with roads favoured red fox populations to the detriment of those of the Artic fox. They found that habitat selection of Artic foxes was negatively related to road coverage, and that increased food availability at the habitat interface between the two fox species did indeed benefit populations of the generalist red fox (Selås *et al.*, 2010).

(*b*) *Road verges favour establishment of alien plant species*

Roads affect plant community composition in many ways beyond habitat loss and fragmentation. Road verges can alter plant communities *via* pollutants like road salt (see Section 3.1.*e*) and dust, and maintenance actions like mowing of road verges (see Section 3.1.*a*). Roads can also act as barriers for seed dispersal (see Section 3.3.*b*) as well as corridors for the colonisation of new species, including alien invasives.

Gravel and dust from roads can spread into the surrounding environment. Auerbach *et al.* (1997) found that dust from gravel roads in Alaska increased soil pH and bulk density, reduced soil moisture, favoured earlier melting of the snowpack, increased active-layer thaw and reduced soil nutrient availability in tundra ecosystems. Consequently, many tundra-adapted plant species disappeared, and nitrophilous pioneer species of grasses, forbs, and bryophytes became more abundant, impoverishing the plant community diversity. A reduction in abundance of some key species, such as *Sphagnum* mosses was particularly significant, as they regulate competitive regimes and perform key ecosystems functions (Auerbach *et al.*, 1997).

The new habitats created by road verges can act as surrogate habitat for native plants (Von Holle and Simberloff, 2005), but unfortunately, in most cases road verges are colonised, and eventually dominated, by disturbance-adapted alien invasives, which readily establish in disturbed habitats and have high seed production rates (Hansen and Clevenger, 2005; Kelly *et al.*, 2009; Khattak *et al.*, 2024). In alpine habitats, alien plant species can thrive despite their presumed lack of adaptation to this ‘specialist’ niche (Alexander *et al.*, 2009), a phenomenon that some authors attribute to the lack of biotic resistance (high native species richness, that allow those to compete with alien species) in higher altitudes, which at lower altitudes hampers plant invasions (Popp and Kalwij, 2021). Zeeman *et al.* (2018) described how grasslands surrounded by dense road networks tended to have higher richness of non-native plants. However, Zielinska *et al.* (2016) found that road verges represent a last refuge for spring pasque flower (*Pulsatilla vernalis*) populations, a relict mountain plant from open habitats. Some studies report that scrub vegetation can facilitate survival of native plant populations along roadsides to the detriment of alien plant species (Perea *et al.*, 2019).

(*c*) *Effects of salt pollution on freshwater communities*

De-icing products like salt used in road maintenance can pollute aquatic habitats (Section 3.1.*e*). This often results in a decline in zooplankton abundance, which depending on the community composition and other environmental factors, may lead to changes in competition among species. Jones *et al.* (2017) found that zooplankton decline led to elevated phytoplankton abundance. However, increased salinity did not interact with biotic stressors in their wetland communities, highlighting the independent effects of road salts and biotic stressors on such communities. Petranka and Doyle (2010) found a reduction in zooplankton abundance, in particular cladocerans and copepods, in response to increased salinity. This reduction of zooplankton led to a reduction in wood frog (*Lithobates sylvaticus*) abundance, which reduced predator pressure on white-dotted mosquito *Culex restuans*, dramatically increasing the abundance of this latter. Contrary to Jones *et al.* (2017), Van Meter *et al.* (2011) showed that as the zooplankton community declined in response to increased salt levels, largely due to the loss of adult copepods, tadpoles experienced a release of competition for algal resources, which led to a dramatic decrease in phytoplankton and periphyton abundance. Some amphibians are more susceptible to increased salinity than others, potentially altering competition dynamics. Increased salinity has stronger negative effects on spotted salamanders (*Ambystoma maculatum*) that on wood frogs, giving the latter a competitive advantage in these habitats. A combination of increased salinity and altered competition dynamics reduced salamander survival by 80% more than salinity changes alone (Ocampo *et al.*, 2022).

Competition processes are key for plant species colonising degraded environments and can facilitate the settlement of other species. Miklovic and Galatowitsch, (2005) demonstrated that, for native marsh plants, the detrimental effects of competition with lesser bulrush (*Typha angustifolia*) were greater at high salt concentrations, where *T. angustifolia* gained a competitive advantage over the native species. Moreover, the responses to salt and *T. angustifolia* presence were species specific within the community of native plants, exemplifying how salt impacts vary with plant species assemblage (McKee and Mendelssohn, 1989).

(*d*) *Modelling of competition dynamics with habitat fragmentation and degradation*

Roads are an important factor driving habitat fragmentation, which can trigger population declines of species living in their surroundings (Benítez-López *et al.*, 2010; Fahrig and Rytwinski, 2009). This can result in remnant patches of natural habitat surrounded by disturbed patches. Cantrell *et al.* (1998) developed a mathematical framework in which they simulated the competition dynamics of two coexisting species in a natural patch habitat and how external degradation affected their competition dynamics. They demonstrated that increasing external hostility led either to a greater competitive advantage or to reversal of the competitive advantage of one species. Whether this competitive reversal took place was dependent on the intensity of the competitive interactions, rates of reproduction and dispersal inside the preserved habitat, and geometry of the preserved habitat (Cantrell *et al.*, 1998). When one of the species is a generalist in terms of habitat selection, it is likely to have a competitive advantage against specialists. Consequently, maintaining undisturbed and unfragmented habitat is a cost-effective defence against invasive species (Marvier *et al.*, 2004).

(*e*) *Road verges allow the establishment of disturbance-tolerant insects*

Road verges can be colonised by many insect species, but the vast majority of the studies identified in our search focused on ants. Keals and Majer, (1991) found that the number of ant species that colonised road verges was directly related to the proportion of native vegetation retained and verge width, due to the greater number of available microhabitats. Road verges constitute a disturbed habitat, and the ant assemblages there differ from those present in natural habitats, with some species being indicators of disturbance (Majer *et al.*, 1994; Tschinkel, 1988). Samways *et al.* (1997) found that one species, *Pheidole megacephala*, dominated most assemblages near roads, and modulated the abundance of the remaining species. Nonetheless, ant species abundance, richness and diversity were higher close to the road, which the authors associated with the high availability of insect carcasses due to massive roadkill (Baxter-Gilbert *et al.*, 2015). We also found one study on butterflies, which related the expansion of the road network in a region in Korea to population declines in all butterfly species except one, whose populations are increasing because it is relatively unaffected by habitat loss and reduction of ecosystem functioning (Kim *et al.*, 2019).

(3) Mutualism

Most of the 34 articles studying mutualism focused on the effects of roads on pollinators (59%) or seed dispersal (35%) and on how tread particles from vehicle tyres alter microbiome interactions (6%) (Figure 4).

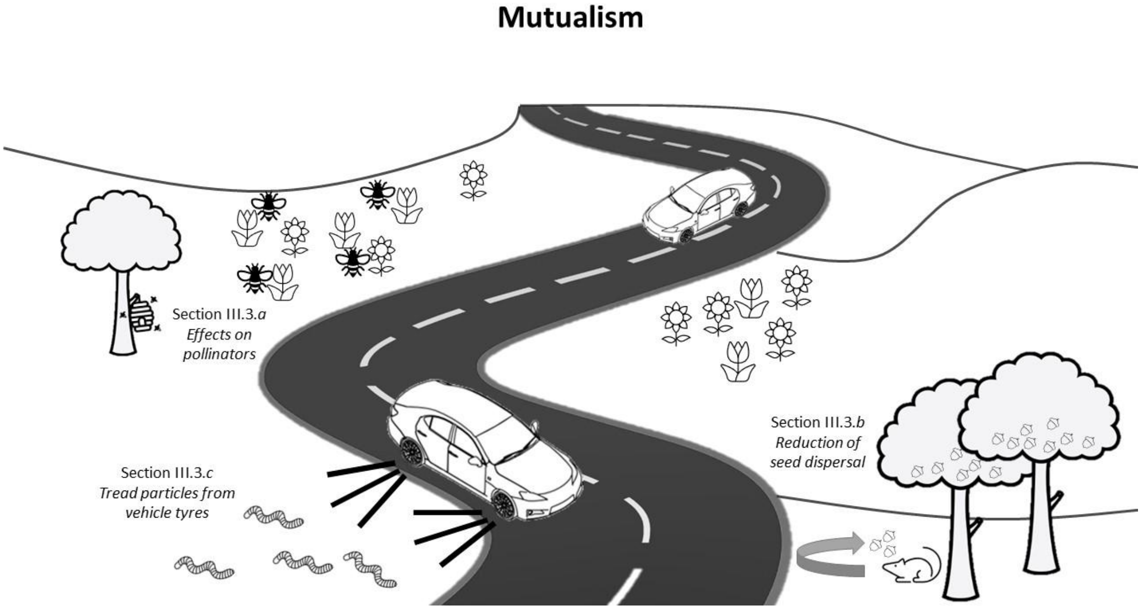

Figure 4: Representation of potential impacts of roads on mutualism interactions (see Section 3.3 for details).

(*a*) *Effects on pollinators*

Pollination is a key ecosystem service necessary for the reproduction of plant species. This sensitive process is present in virtually all Earth ecosystems, of which animal-mediated pollination is mainly provided by insects, although other taxa, such as nectar-feeding birds and bats contribute as well (Geerts and Pauw, 2011). Roads can impose a movement barrier even to flying pollinators like insects (Fitch and Vaidya, 2021) and birds (Geerts and Pauw, 2011). For some taxa like bumblebees, more than physical barriers, roads can act as landmarks that help individuals orient themselves and recognise foraging sites (e.g. Bhattacharya *et al.*, 2002). Roadkill of pollinators is a commonly overlooked impact of roads on these mutualistic relationships (Baxter-Gilbert *et al.*, 2015), potentially contributing to the severe declines of pollinators affecting the ecological functioning of many ecosystems around the globe. High traffic speed negatively affects pollination by reducing the frequency and duration of insect visits (Dargas *et al.*, 2016), and by shaping the pollinator community in the vicinity of the road (Phillips *et al.*, 2019). Habitat loss (including edge effect) caused by roads can also reduce pollinator populations (Olynyk *et al.*, 2021). Pollutants from vehicles can alter how bees detect volatile organic compounds. When those compounds are polluted, it takes longer to remember them and are easier for them to forget them more easily, which implies impaired pollinator efficiency and impacts on colony health (Leonard *et al.*, 2019). Nonetheless, pollinators can benefit from the presence of road verges as they use them for navigation (Bhattacharya *et al.*, 2002; Brebner *et al.*, 2021), or forage in these habitats with often less-intensive mowing regimes (Chaudron *et al.*, 2020; Hanula *et al.*, 2016; see also Section 3.1.*a*). Changes to mowing regimes of roadsides can boost floral resources and overall pollinator abundance, however, there is little consensus on ideal mowing regimes, with research conducted in very different environments and under different road management practices. Some authors advocate adding a late mowing at higher vegetation height (Chaudron *et al.*, 2020), while others advocate for a reduction in overall mowing frequency (Halbritter *et al.*, 2015). Thus, although new habitats created by road verges can benefit the expansion of alien plant species (see Section III.2.*b*), several authors agree that the benefits of new pollination relationships created outweigh the costs (Monasterolo *et al.*, 2020; Phillips *et al.*, 2020).

(*b*) *Roads limit seed dispersal*

Roads act as a barrier to animal movements when wildlife is reluctant to cross them or when they die while attempting to cross (Auerbach *et al.*, 1997; Barrientos *et al.*, 2021; Grilo *et al.*, 2020; Hintz and Relyea, 2019; McClure, 2021). Seed dispersal is a key ecosystem service that animals provide (zoochory) to many plant species (Jansen *et al.*, 2014; Levine and Murrell, 2003). In some cases, zoochory is the only mechanism by which plants disperse their seeds and avoid inbreeding (Gómez *et al.*, 2019; LaManna *et al.*, 2017).

Several studies have shown that roads can act as barriers for zoochory provided by small mammals, diminishing seed dispersal. Most studies detected: (*i*) null seed removal from road surfaces (Kikuzawa, 1988); (*ii*) asymmetric seed dispersal, with seeds not carried to the other side of roads despite the ability of dispersers to exceed that distance in the absence of roads (Chen *et al.*, 2019a; Lambert *et al.*, 2014; Niu *et al.*, 2018, 2021); and (*iii*) a reduction in seed-dispersal distances (Chen *et al.*, 2019b, 2019a; Cui *et al.*, 2018). Niu *et al.* (2021) described how road presence changed the species involved in this interaction, with urban or farmland rodents carrying out most of the seed dispersal close to roads, due to their greater tolerance of this infrastructure than forest–shrub rodent species. Regarding seed dispersal effectiveness (i.e. proportion of dispersed seeds that germinate; Schupp *et al.*, 2010), studies show contrasting results. Chen *et al.* (2019a) found a reduction in this key parameter close to roads, whereas Cui *et al.* (2018) found an increase in this and other dispersal parameters such as seed removal rates. Chen *et al.* (2019b, 2019a) described how the road impact on seed dispersal faded away around 200 m from the road. Some large mammals, such as primates, serve as seed dispersers in tropical forests. However, this key ecosystem service they provide can be diminished by human activity: (*i*) by reduced consumption of natural resources due to human provisioning close to roads; and (*ii*) by reduced effective seed dispersal, when seeds fall onto paved roads (Sengupta *et al.*, 2015). In many cases, seed dispersal by small mammals can compensate to some extent, however some plant species are reliant solely on large frugivores (Coutant *et al.*, 2022).

Changes in salinity and pH or chemical pollution of soil can affect seed dispersal mediated by ants (myrmecochory) in road verges (Palfi *et al.*, 2020), a mutualism that is a significant driver of plant diversity and population dynamics (Lengyel *et al.*, 2010). Palfi *et al.* (2017b) found that soil disturbance is more intense in narrow road verges (see also Section 3.2.*e*), with resulting poorer biotic and abiotic conditions and, consequently, lower abundance of seed disperser ants. Palfi *et al.* (2017a) reported that more disturbed road verges were correlated with higher seed dispersal distances, possibly due to simplification of the foraging landscape for ants. However, these results applied mainly to a single ant species, the meat ant (*Iridomyrmex purpureus*), with no effect observed for the other species.

(*c*) *Tread particles from vehicle tyres alter microbiome interactions*

Tread particles are lost from tyres due to friction against the road surface. These non-airborne emissions can deposit on road verges, and are widely distributed in soil and aquatic ecosystems (Rillig, 2012; Wagner *et al.*, 2018). Researchers have found that these microplastics alter the microbiota of soil worms (*Enchytraeus crypticus*), negatively affecting their fitness, with more opportunistic and pathogenic species thriving when tread particles are present (Ding *et al.*, 2020). O'Brien *et al.* (2022) found a negative effect of tread particles on mutualisms between plants and microbes: pollution increased microbial growth but reduced that of duckweed (*Lemna minor*).

(4) Parasitism

Most of the 17 studies on parasitism focused on avian brood parasitism in road margins (47%), followed by studies focused on how road salt altered parasitism rates in freshwater species (41%), and on how road underpasses may act as parasitism hotspots (12%) (Figure 5).

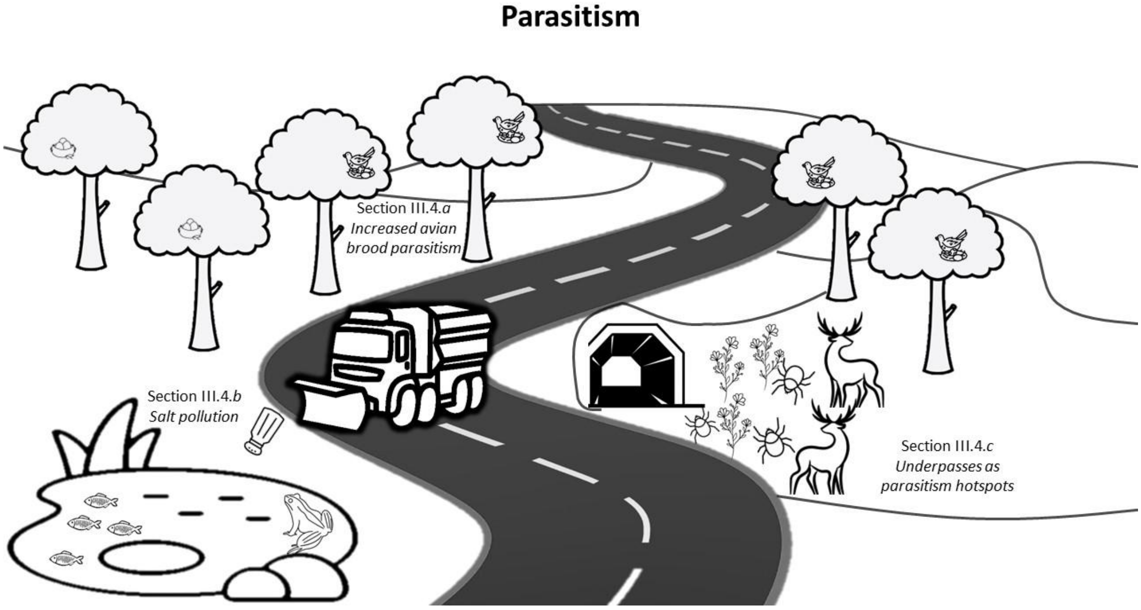

Figure 5: Representation of potential impacts of roads on parasitism interactions (see Section 3.4 for details).

(*a*) *Increased avian brood parasitism close to roads*

Mowing road verges is a common practice in several road networks (see Sections 3.1.*a* and 3.3.*a*). These habitats can therefore provide breeding grounds for grassland birds (see also Section 3.1.*b*), and new opportunities for generalist brood parasites like the brown-headed cowbird (*Molothrus ater*). This species is widely distributed in North American plains (Chace *et al.*, 2003), where it can parasite two-thirds of the bird species breeding there (Shaffer *et al.*, 2003). Increased brown-headed cowbird abundance in road verges has been described across multiple habitats, such as reclaimed surface-mined land (Dixon *et al.*, 2008), urban areas (Chace *et al.*, 2003) and oil and natural gas infrastructure

(Bernath-Plaisted *et al.*, 2017). Patten *et al.* (2006) described how nests close to roads had between two and five times higher parasitism rates compared to those far away (but see Datta and Begum, 2021). Brown-headed cowbirds are attracted to woody vegetation on road verges, which they use as perches to scan for host nests (Shaffer *et al.*, 2003). Clotfelter and Yasukawa (1999) found parasitism rates by this bird to decrease with distance to a road, however there was no effect of road proximity on the number of eggs laid by brown-headed cowbirds in each parasitised nest or on the overall reproductive success of the hosts. Etterson *et al.* (2014) found road density to be positively correlated with parasitism rates by brown-headed cowbird, with landscape fragmentation proposed as a driving force that alters community composition, and therefore predation and parasitism rates.

(*b*) *Road salt alters parasitism rates in freshwater species*

The application of de-icing products can alter predation and competition dynamics (see Sections 3.1.*e* and 3.2.*c*), and potentially also parasitism, although few studies specifically tested this. Milotic *et al.* (2017) exposed wood frog and northern leopard frog (*Lithobates pipiens*) tadpoles to low, medium, and high concentrations of road salt representative of rural and urban environments. The frog anti-parasite response against infection by trematode parasites (helminths) consists of maintaining elevated swimming activity with rapid tail movements to avoid these parasites (Koprivnikar *et al.*, 2014); this behaviour was reduced at medium and high salt concentrations, translating into higher parasitisation rates in wood frog tadpoles. However, for northern leopard frogs, the intermediate salt treatment had the lowest infection rate.

Road de-icing salts may alter the way the fungal parasite *Metschnikowia bicuspidate* infests water fleas (*Daphnia dentifera*), a common freshwater zooplankton species (Merrick and Searle, 2019). These authors designed two experiments with four treatments to explore how salinity affected the demography of both the host and the parasite. At an individual level, they found that increased salinity led to higher mortality of *D. dentifera*, but with no change in infection prevalence. At a population level, *D. dentifera* densities decreased when salt concentration increased, but infection prevalence remained similar. This could be explained because the higher salinity killed both hosts and parasites, reducing potential contacts between them (Merrick and Searle, 2019).

Distance to roads can also modify parasitism prevalence by trematodes in both amphibian and odonate larvae (Koprivnikar *et al.*, 2010). However, infection prevalence showed opposite trends for these taxa, increasing in amphibians and reducing in odonates. These contrasting results were probably driven by the abundance of potential vertebrate final hosts for adult trematodes. Trematodes infecting amphibians have canids as final hosts, which are relatively reluctant to use roads (Hartson *et al.*, 2011; Koprivnikar and Redfern, 2012). On the contrary, trematodes infecting odonates have a variety of birds and mammals as final hosts which are more tolerant to roads (King *et al.*, 2007; Koprivnikar and Redfern, 2012).

Road salt can also increase parasitism rates of species outside freshwater environments. In a series of studies in Switzerland, researchers described how de-icing salt and, to a lesser extent, drought, increased aphid (*Aphis pomi*) population on motorway verges, where they are parasites of hawthorns (*Crataegus* spp.) (Braun and Flückiger, 1984). Air pollution altered this host plant–parasite relationship by: (i) increasing aphid population more than four times; and (ii) increasing the susceptibility of hawthorn to this parasite (Braun and Flückiger, 1985).

(*c*) *Road underpasses as parasitism hotspots*

Road-crossing structures, such as wildlife passages and culverts, concentrate wildlife in certain points, facilitating interactions that require close contact between individuals (see also Section 3.1.*d*). McEnroe (1971) described dog tick (*Dermacentor variabilis*) attraction to roads, potentially contributing to increased prevalence of ticks and tick-borne diseases (Buskirk and Ostfeld, 1998). However, few studies have considered this interaction. One valuable exception is a survey carried out by Delgado *et al.* (2017) which found higher tick abundance close to roads and inside underpasses (culverts). Similarly, Payne *et al.* (2020) found that sleepy lizards (*Tiliqua rugose*) living close to a road tended to have four times more ticks than those living 500 m away.

4. Implications for road management

Some patterns arise across species interactions that can guide environmental policies, as only by careful planning, design, and management will we be able to reduce the impacts of roads on biodiversity interactions. We therefore make the following recommendations.

(1) Wider and structurally heterogeneous verges maximise the diversity of microhabitats, allowing roadside colonisation by both plants and insects. For example, plants attract pollinators, and insects like ants increase seed dispersal. Wider verges can act both as a refugia for threatened species and enhance key ecosystem services, outweighing the costs (i.e. insect roadkills or establishment of alien plants).

(2) The mowing of road verges creates new, homogeneous habitat in the road corridor, different from the habitat surrounding it. The standard mowing regimen (i.e. a single annual event at short height) exacerbates predation and parasitism rates of ground-nesting

birds, favours the establishment and expansion of non-native plants, and negatively impacts flower pollination. Nonetheless, other mowing regimes (less frequent and less intense), or even a combination of several of them aiming to increase verge heterogeneity could help the road corridor to act as a surrogate, safe habitat for more species (and their interactions).

(3) The use of de-icing salts alters several species interactions (predation, competition, and parasitism), and negatively affects several freshwater taxa such as zooplankton, amphibians and fishes living in nearby waterbodies. Moreover, cascade effects can alter food webs, leading to demographic changes. We suggest a gradual reduction of the use of these salts and their replacement by other products or maintenance practices less harmful to the environment.

(4) Both seed dispersal and pollination can be disrupted by roads. To maintain these key ecosystem services, human-assisted revegetation plans (e.g. with native plants) of road verges are probably needed. The presence of native plants can, in turn, limit the expansion of invasive species.

(5) Wildlife passages are built to enable safe road crossings but inevitably concentrate animals in these structures. Thus, to avoid effects on predator–prey or host–parasite (and, likely, others) interactions, ideally many passes should be provided in a single mitigation planning.

(6) Carcasses on the road surface represent an easy-to-access and relatively predictable source of food that can alter habitat selection and competition equilibria in scavenger communities, both of vertebrates and invertebrates. Furthermore, foraging on road carcasses can end with the roadkill of the scavengers themselves. Therefore, periodic removal of carcasses from the road should be implemented across major road networks.

(7) High traffic flow and speed can hinder anti-predator responses and reduce pollinator visitation rates to plants on road verges, although they also reduce nest predation rates. Traffic-calming schemes should be implemented in sensitive habitats, such as where roads bisect nature reserves.

5. Conclusions

Although studies specifically designed to explore the impact of roads on interspecific relationships (e.g., monitoring these interactions before and after road construction) are scarce, some broad patterns arise from our literature review:

(1) Most studies exploring the impact of roads on interspecific interactions were conducted in high-income countries of North America and Europe and were focused on large mammals. Alarmingly for among conservation planners and governments, we have little information on taxa and countries from the Global South, a region that is likely to see large increases in road network coverage in the coming years. Some interactions (parasitism, amensalism and commensalism) have been little studied, or not studied at all. The same happened and with certain road impacts (e.g., dust pollution, barrier effect, roadkills or overexploitation of resources), which is again concerning and unexpected for well-known impacts such as barrier effect or roadkills.

(2) Most studies focused on how roads disrupt predator–prey relationships: (*i*) by having a negative influence on prey, forcing them to avoid roads frequented by predators, altering their anti-predator behaviours or experiencing increased nest predation rates, although small mammals and human-tolerant species may be exceptions; (*ii*) although roads modify the behaviour and habitat selection of predators, there are no obvious negative effects on their fitness, other than for acoustically oriented species which show reduced

hunting success in the presence of road noise; (*iii*) the effect of roads depends on the road type (primary and tertiary roads having opposite effects), traffic volume, and pollution intensity; (*iv*) even though the prey trap hypothesis and predator release hypothesis are widely cited in road ecology literature, they have little empirical support.

(3) Disturbed habitats created in road corridors alter competition by usually benefiting alien species (both plants and insects) due to their greater competitiveness (e.g. colonisation abilities). For some small mammals, the ability to thrive along road corridors determines community composition, however some native or even endangered species can also establish in road margins. Road impacts like roadkills increase the competitive advantages of smaller or bolder scavengers, and the use of salt as de-icer increases the salinity of nearby freshwater habitats, reducing zooplankton abundance and therefore amphibian populations, leading to cascading effects at a community level.

(4) Roads usually degrade mutualistic interactions like seed dispersal and pollination, which are key ecosystem processes. Roads can reduce both interaction rates due to barrier effects, or can alter the behaviour and habitat selection of the species involved through habitat alteration and pollutants.

(5) Roads usually result in increased parasitism rates, although the pattern is species specific. Road characteristics and maintenance practices also modulate the intensity of this interaction. The scarce information on parasitism is especially worrying, as it has deep implications on population dynamics and co-evolution.

(6) To understand better how roads disrupt species interactions we first need to unify how we measure their effects. We suggest establishing common metrics for certain interactions, such as effective seed dispersal for mutualism, infection rates for parasitism or percentage of land use at different distances from the road for both prey and predators.

This would also allow future meta-analyses with higher inference power, especially where common metrics are measured before and after road construction.

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7. Author contributions

P.Q.: Conceptualisation, Methodology, Software, Formal analysis, Investigation, Writing - Original Draft and Visualisation. **R.B.**: Conceptualisation, Methodology, Investigation, Resources, Writing - Original Draft, Writing - Review & Editing, Supervision, Project administration and Funding acquisition.

8. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Final set of articles identified in the systematic search and key data extracted from them.

Interaction	Road impact	Country	Mammals	Birds	Amphibians	Reptiles	Fish	Arthropods	Invertebrates no arthropods	Plants	Fungi	Bacteria	Taxa 1	Taxa 2	Taxa 3	Taxa scope	n taxa	Topic	Authors	DOI	Publication Year
Predation	Edge effect	UK	0	0	0	0	0	1	0	1	0	0	Plants	Invertebrates	0	Multiple	2	Alteration of herbivory rates	Port, GR; Thompson, JR	10.2307/2402643	1980
Predation	Edge effect	USA	1	1	0	0	0	0	0	0	0	0	Birds	Mammals	0	Multiple	2	Road influence on nest predation	Small, MF; Hunter, ML	10.1007/BF00379601	1988
Predation	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Bradley, LC; Fagre, DB	10.2307/3899388	1988
Predation	Road pollutants	USA	0	0	0	0	0	1	0	0	0	0	Invertebrates	0	0	Single	1	Road salt and dust pollution influencing predator activity	Oi, DH; Barnes, MM	10.1093/ee/18.5.892	1989
Predation	Landscape changes	Finland	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Huhta, Esa	10.2981/wlb.1995.0012	1995
Predation	Road pollutants	UK	0	1	0	0	0	0	0	1	0	0	Birds	Plants	0	Multiple	2	Alteration of herbivory rates	Gill, JA; Sutherland, WJ; Wat	10.2307/2404948	1996
Predation	Landscape changes	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Yahner, RH; Mahan, CG		1997
Predation	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Bergin, TM; Best, LB; Freema		1997
Predation	Landscape changes	France	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Bechet, A; Isenmann, P; Gau	10.1016/S1146-609X(98)80011-8	1998
Predation	Road pollutants	Denmark	0	1	0	0	0	0	0	1	0	0	Birds	Plants	0	Multiple	2	Alteration of herbivory rates	Madsen, J		1998
Predation	Edge effect	France	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Meunier, FD; Corbin, J; Verhe	10.1139/cjz-77-1-108	1999
Predation	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Thogmartin, WE	10.2307/4089671	1999
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Kunkel, KE; Pletscher, DH	10.1139/cjz-78-1-150	2000
Predation	Edge effect	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	James, ARC; Stuart-Smith, A	10.2307/3802985	2000
Predation	Edge effect	USA	1	1	0	0	0	0	0	0	0	0	Birds	Mammals	0	Multiple	2	Road influence on nest predation	Dijak, WD; Thompson, FR	10.2307/3802992	2000
Predation	Landscape changes	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Bergin, TM; Best, LB; Freema	10.1023/A:1008112825655	2000
Predation	Landscape changes	Spain	1	1	0	0	0	0	0	0	0	0	Birds	Mammals	0	Multiple	2	Road influence on nest predation	Delgado, JD; Arevalo, JR; Fe	10.1034/j.1600-0587.2001.d01-209.x	2001
Predation	Barrier effect	Australia	1	0	0	0	0	0	0	0	0	0	Mammals	All	0	Multiple	all	Testing predator release and prey trap hypotheses	Little, SJ; Harcourt, RG; Clev	10.1016/S0006-3207(02)00059-9	2002
Predation	Landscape changes	USA	1	0	0	1	0	0	0	0	0	0	Reptiles	Mammals	0	Multiple	2	Road influence on nest predation	Marchand, MN; Litvaitis, JA	10.1016/j.biocon.2003.07.003	2004
Predation	Landscape changes	Spain	1	1	0	0	0	0	0	0	0	0	Birds	Mammals	0	Multiple	2	Road influence on nest predation	Garcia, JDD; Arevalo, JR; Fe	10.1080/00222930500104427	2005
Predation	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Shochat, E; Wolfe, DH; Patte	10.1016/j.biocon.2004.05.012	2005
Predation	Edge effect	Italy	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Rondinini, C.; Ercoli, V.; Boita	10.1111/j.1469-7998.2006.00073.x	2006
Predation	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Mettenbrink, Christian W.; Dr	10.1894/0038-4909(2006)51[191:NSOMPF	2006
Predation	Landscape changes	USA	1	0	0	0	0	0	0	1	0	0	Mammals	Plants	0	Multiple	2	Alteration of herbivory rates	Ripple, William J.; Beschta, R	10.1016/j.foreco.2006.04.023	2006
Predation	Edge effect	Czech Republic	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Svobodova, Jana; Salek, Mir		2007
Predation	Edge effect	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Stapp, Paul; Lindquist, Mark	10.3398/1527-0904(2007)67[368:RFBKRI]	2007
Predation	Edge effect	Spain	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Pescador, Moises; Peris, Sal	10.1016/j.landurbplan.2007.01.017	2007
Predation	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Berger, Joel	10.1098/rsbl.2007.0415	2007
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Courbin, Nicolas; Fortin, Dan	10.1007/s10980-009-9389-x	2009
Predation	Road pollutants	Belgium	0	0	1	0	0	0	0	0	0	0	Amphibians	0	0	Single	1	Road salt and dust pollution influencing predator activity	Denoel, Mathieu; Bichot, Mari	10.1016/j.aquatox.2010.05.007	2010
Predation	Edge effect	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Testing predator release and prey trap hypotheses	Ford, Adam T.; Clevenger, A	10.1111/j.1523-1739.2010.01564.x	2010
Predation	Landscape changes	Norway	1	1	0	0	0	0	0	0	0	0	Birds	Mammals		Multiple	2	Road influence on nest predation	Pedersen, Ashild O.; Asmyhr	10.1071/WR11031	2011
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Testing predator release and prey trap hypotheses	Rogala, James Kimo; Hebble	10.5751/ES-04251-160316	2011
Predation	Edge effect	China	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Lian, Xinming; Zhang, Tongz	10.1071/WR10158	2011
Predation	Landscape changes	Canada	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Falk, Karla J.; Nol, Erica; Bur	10.1007/s10980-010-9543-5	2011
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Testing predator release and prey trap hypotheses	Muhly, Tyler B.; Semeniuk, C	10.1371/journal.pone.0017050	2011
Predation	Road pollutants	Germany	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Siemers, Bjoern M.; Schaub,	10.1098/rspb.2010.2262	2011
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Whittington, Jesse; Hebblewh	10.1111/j.1365-2664.2011.02043.x	2011
Predation	Road pollutants	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Owens, Jessica L.; Stec, Cou	10.1016/j.beproc.2012.05.010	2012
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Dussault, Christian; Pinard, V	10.1098/rspb.2012.1700	2012
Predation	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Nelson, Abigail A.; Kauffman,	10.1890/11-1829.1	2012
Predation	Edge effect	Spain	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Planillo, Aimara; Maio, Juan	10.1016/j.mambio.2012.11.001	2013
Predation	Landscape changes	Canada	0	0	0	0	0	0	0	0	0	0	Theorical	0	0	Multiple	all	Testing predator release and prey trap hypotheses	Rytwinski, Trina; Fahrig, Len	10.1007/s00442-013-2684-x	2013
Predation	Landscape changes	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	DeGregorio, Brett A.; Weathe	10.1002/ece3.1049	2014
Predation	Road pollutants	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Shannon, Graeme; Angeloni,	10.1016/j.anbehav.2014.06.004	2014
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Leclerc, Martin; Dussault, Ch	10.1007/s00442-014-3012-9	2014
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Testing predator release and prey trap hypotheses	Downing, Richard J.; Rytwins	10.1007/s11284-015-1264-4	2015
Predation	Edge effect	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Popp, Jesse N.; Donovan, Vi	10.1163/15707563-00002500	2016
Predation	Road pollutants	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Pettinga, D.; Kennedy, J.; Pr	10.1007/s11252-015-0498-9	2016
Predation	Road pollutants	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Grade, Aaron M.; Sieving, Ka	10.1098/rsbl.2016.0113	2016
Predation	Road pollutants	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Shannon, Graeme; Crooks, K	10.1093/beheco/arw058	2016
Predation	Landscape changes	France	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Tissier, Mathilde L.; Jumeau,	10.1016/j.ecoleng.2016.07.012	2016
Predation	Edge effect	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Gonzalez-Olimon, Gabriella;	10.1674/0003-0031-176.2.282	2016
Predation	Edge effect	South Africa	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on habitat selection and animal movements	Joseph, Grant S.; Seymour,	10.1016/j.biocon.2016.11.026	2017
Predation	Landscape changes	Spain	1	1	0	0	0	0	0	0	0	0	Birds	Mammals	0	Multiple	2	Road influence on habitat selection and animal movements	Camacho, Carlos; Saez-Gom	10.1002/ecs2.1611	2017
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Dickie, Melanie; Serrouya, R	10.1111/1365-2664.12732	2017
Predation	Landscape changes	Canada	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on habitat selection and animal movements	Yoo, Jenny; Koper, Nicola	10.1371/journal.pone.0174243	2017
Predation	Road pollutants	USA	0	0	0	0	1	1	0	1	0	0	Invertebrates	Fish	0	Multiple	3	Road salt and dust pollution influencing predator activity	Hintz, William D.; Mattes, Bri	10.1002/eap.1487	2017
Predation	Road pollutants	South Africa	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Morris-Drake, Amy; Bracken,	10.1016/j.envpol.2017.01.049	2017
Predation	Edge effect	Spain	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Mata, Cristina; Ruiz-Capillas,	10.1007/s10344-017-1118-1	2017
Predation	Road pollutants	USA	0	0	0	0	1	1	0	0	0	0	Invertebrates	Fish	0	Multiple	2	Road salt and dust pollution influencing predator activity	Hintz, William D.; Relyea, Ri	10.1007/s00442-017-3925-1	2017
Predation	Edge effect	Argentina	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Cappa, Flavio M.; Giannoni,	10.1016/j.anbehav.2017.07.020	2017
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Newton, Erica J.; Patterson,	10.1371/journal.pone.0186525	2017
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Mumma, Matthew A.; Gillingh	10.1002/ece3.3563	2017
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Lendrum, Patrick E.; Northru	10.1007/s10980-017-0590-z	2018
Predation	Edge effect	Spain	1	1	0	0	0	1	0	1	0	0	All	0	0	Multiple	4	Road alteration of predatory and anti-predator behaviours	Suarez-Esteban, Alberto; Deli	10.1111/avsc.12349	2018
Predation	Road pollutants	USA	0	0	0	0	0	1	0	0	0	0	Invertebrates	0	0	Single	1	Road salt and dust pollution influencing predator activity	Schuler, Matthew S.; Relyea,	10.1111/oik.04837	2018
Predation	Edge effect	Thailand	1	1	0	0	0	0	0	0	0	0	Birds	Mammals	0	Multiple	2	Road influence on nest predation	Khamcha, Daphawan; Powell	10.1016/j.gecco.2018.e00450	2018
Predation	Edge effect	Australia	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Raiter, Keren G.; Hobbs, Rich	10.1016/j.biocon.2018.10.011	2018
Predation	Edge effect	Thailand	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Angkaew, Rongrong; Sankar	10.1093/condor/duy013	2019
Predation	Road pollutants	Canada	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Ng, Christoph S.; Des Brisay,	10.1016/j.anbehav.2018.12.001	2019
Predation	Road pollutants	USA	0	0	1	0	1	1	1	1	0	0	Invertebrates	Fish	0	Multiple	5	Road salt and dust pollution influencing predator activity	Hintz, William D.; Relyea, Ri	10.1111/fwb.13286	2019
Predation	Edge effect	Brazil	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	da Silva, Gleidson Ramos; D	10.1002/ece3.5158	2019
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Spangenberg, Matthias C.; S	10.1002/ecs2.2904	2019
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Mumma, Matthew A.; Gillingh	10.1007/s10980-019-00905-9	2019
Predation	Edge effect	Argentina	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Road influence on nest predation	Maria Depalma, Daniela; Emi		2019
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Fryxell, John M.; Avgar, Tal;	10.1002/jwmg.21829	2020
Predation	Edge effect	China	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Wang Mu-yang; Ji Sheng-nar	10.13292/j.1000-4890.202003.014	2020
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Testing predator release and prey trap hypotheses	Martinig, April Robin; Riaz, M	10.1038/s41598-020-67340-8	2020
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Hill, Jacob E.; De Vault, Travi	10.1111/mam.12222	2021
Predation	Landscape changes	USA	0	0	0	1	1	0	0	0	0	0	Reptiles	Fish	0	Multiple	2	Testing predator release and prey trap hypotheses	Alcott, Derrick; Long, Michael	10.1098/rsbl.2020.0218	2020
Predation	Landscape changes	Norway	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Loosen, Anne E.; Devineau,	10.1002/ecs2.3358	2021
Predation	Road pollutants	Japan	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Watabe, Ryoga; Saito, Masa	10.1007/s11355-020-00434-7	2021
Predation	Road pollutants	China	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Xu, Feng; Yang, Weikang; M	10.17582/journal.pjz/20190222070230	2021
Predation	Edge effect	Spain	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Ruiz-Capillas, Pablo; Mata, C	10.3390/d13040173	2021
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Vanlandeghem, Virginie; Dra	10.1002/ecs2.3550	2021

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Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Darlington, Siobhan; Ladle, A	10.1038/s41598-022-05018-z	2022
Predation	Edge effect	Canada	0	0	0	1	0	0	0	0	0	0	Reptiles	0	0	Single	1	Road influence on nest predation	Murphy, Rowan E.; Martin, A	10.1002/ecs2.3946	2022
Predation	Road pollutants	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Giordano, A.; Hunninck, L.; S	10.1111/jzo.12968	2022
Predation	Barrier effect	India	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Testing predator release and prey trap hypotheses	Saxena, Akanksha; Habib, Bi	10.3390/d14050312	2022
Predation	Edge effect	USA	1	1	0	0	0	0	0	0	0	0	Birds	Mammals	0	Multiple	2	Road influence on nest predation	Newsome, Corina D.; Hunter,	10.1093/ornithapp/duac023	2022
Predation	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Lacerte, Rebecca; Leblond, M	10.1016/j.jnc.2022.126256	2022
Predation	Road pollutants	USA	0	0	0	0	0	1	0	1	0	0	Plants	Invertebrates	0	Multiple	2	Alteration of herbivory rates	Meineke, Emily K.; Eng, Davi	10.1111/1365-2664.14328	2023
Predation	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Barker, Kristin J.; Cole, Eric;	10.1111/1365-2656.13900	2023
Predation	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road alteration of predatory and anti-predator behaviours	Kilfoil, James P.; Quinn, Tho	10.1016/j.gecco.2023.e02407	2023
Predation	Road pollutants	USA	0	0	0	0	0	1	0	0	0	0	Invertebrates	0	0	Single	1	Road salt and dust pollution influencing predator activity	Huber, Eric D.; Wilmoth, Bay	10.1016/j.envpol.2023.121767	2023
Predation	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road influence on habitat selection and animal movements	Johnson-Bice, Sean M.; Gabl	10.1002/eap.2911	2023
Competition	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Briese, LA; Smith, MH	10.2307/1379092	1973
Competition	Edge effect	USA	0	0	0	0	0	1	0	0	0	0	Invertebrates	0	0	Single	1	Road verges allow the establishment of disturbance−tolerant insec	Tschinkel, WR	10.1093/aesa/81.1.76	1988
Competition	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Thurber, JM; Peterson, RO;	10.1139/z92-335	1992
Competition	Edge effect	USA	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	Auerbach, NA; Walker, MD;		1997
Competition	Edge effect	South Africa	0	0	0	0	0	1	0	0	0	0	Invertebrates	0	0	Single	1	Road verges allow the establishment of disturbance tolerant insect	Samways, MJ; Osborn, R; C	10.1023/A:1018355328197	1997
Competition	Landscape changes	USA	0	0	0	0	0	0	0	0	0	0	Theorical	0	0	Multiple	all	Theoretical competition dynamics affected by habitat fragmentatio	Cantrell, RS; Cosner, C; Fag	10.1007/s002850050139	1998
Competition	Landscape changes	USA	0	0	0	0	0	0	0	0	0	0	Theorical	0	0	Multiple	all	Theoretical competition dynamics affected by habitat fragmentatio	Marvier, M; Kareiva, P; Neub	10.1111/j.0272-4332.2004.00485.x	2004
Competition	Landscape changes	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Ingelfinger, F; Anderson, S		2004
Competition	Edge effect	USA	0	0	1	0	0	0	0	0	0	0	Amphibians	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Marsh, DM; Beckman, NG	10.1890/03-5179	2004
Competition	Road pollutants	USA	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Disturbance in freshwater communities caused by road salt polluti	Miklovic, S; Galatowitsch, S	10.1672/16	2005
Competition	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	0	Differences in species tolerance towards roads alter competition dy	Apps, Clayton D.; McLellan,	10.1111/j.0906-7590.2006.04564.x	2006
Competition	Landscape changes	Brazil	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Vieira, E. M.; Port, D.	10.1111/j.1469-7998.2006.00237.x	2007
Competition	Edge effect	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Kolbe, Jay A.; Squires, John	10.2193/2005-682	2007
Competition	Edge effect	South Africa	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	Kalwij, Jesse M.; Milton, Suz	10.1007/s10980-008-9201-3	2008
Competition	Edge effect	Denmark	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Damgaard, Christian; Mathia	10.1897/07-267.1	2008
Competition	Edge effect	Australia	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Maron, Martine	10.1071/MU08064	2009
Competition	Edge effect	USA	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	Alexander, Jake M.; Naylor,	10.1111/j.1600-0587.2008.05605.x	2009
Competition	Landscape changes	Argentina	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Lambertucci, Sergio A.; Spez	10.1007/s10531-008-9573-3	2009
Competition	Landscape changes	China	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Theoretical competition dynamics affected by habitat fragmentatio	Qi, Dunwu; Hu, Yibo; Gu, Xia	10.1007/s10531-009-9577-7	2009
Competition	Edge effect	UK	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	Kelly, Alice B.; Small, Christi	10.3159/09-RA-007.1	2009
Competition	Landscape changes	Uganda	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Averbeck, Christiane; Apio, A	10.1111/j.1365-2028.2009.01076.x	2009
Competition	Road pollutants	USA	0	0	1	0	0	1	0	0	0	0	Amphibians	Invertebrates	0	Multiple	2	Disturbance in freshwater communities caused by road salt polluti	Petranka, James W.; Doyle,	10.1007/s10452-009-9286-z	2010
Competition	Landscape changes	Norway	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Selas, Vidar; Johnsen, Borge	10.2981/09-023	2010
Competition	Road pollutants	USA	0	0	1	0	0	1	0	0	0	0	Amphibians	Invertebrates	0	Multiple	2	Disturbance in freshwater communities caused by road salt polluti	Van Meter, Robin J.; Swan, C	10.1007/s13157-011-0199-y	2011
Competition	Landscape changes	Portugal	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Torres, Rita T.; Virgos, Emili	10.1163/157075612X631213	2012
Competition	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Benson, John F.; Patterson,	10.1007/s00442-013-2730-8	2013
Competition	Landscape changes	Sweden	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Ordiz, Andres; Milleret, Cyril;	10.1890/ES15-00243.1	2015
Competition	Landscape changes	Poland	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	Zielinska, Katarzyna M.; Kied	10.1038/srep31913	2016
Competition	Landscape changes	Sweden	0	0	0	0	0	1	0	0	0	0	Invertebrates	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Herbertsson, Lina; Lindstrom	10.1016/j.baae.2016.05.001	2016
Competition	Road pollutants	USA	0	0	1	0	0	1	0	1	0	0	Invertebrates	Amphibians	0	Multiple	3	Disturbance in freshwater communities caused by road salt polluti	Jones, Devin K.; Mattes, Bria	10.1016/j.envpol.2016.11.060	2017
Competition	Barrier effect	Australia	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Johnson, Christopher D.; Eva	10.3389/fevo.2017.00036	2017
Competition	Landscape changes	Canada	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Ladle, Andrew; Steenweg, R	10.1371/journal.pone.0191730	2018
Competition	Edge effect	Spain	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Luzuriaga, Arantzazu L.; San	10.1016/j.baae.2018.03.008	2018
Competition	Landscape changes	Australia	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	Zeeman, Ben J.; Minden, Va	10.1007/s10530-018-1756-6	2018
Competition	Landscape changes	Korea	0	0	0	0	0	1	0	0	0	0	Invertebrates	0	0	Single	1	Road verges allow the establishment of disturbance tolerant insect	Kim, Do-Sung; Cho, Youngh	10.1111/1748-5967.12386	2019
Competition	Edge effect	Brazil	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	Perea, Ramon; Cunha, Jessi	10.1016/j.ecoleng.2019.06.024	2019
Competition	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Lombardi, Jason V.; MacKen	10.1002/ece3.6242	2020
Competition	Landscape changes	Norway	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Rod-Eriksen, Lars; Skrutvold,	10.1111/1365-2664.13668	2020
Competition	Edge effect	Japan	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	Oshima, Katsumi; Takahashi	10.1007/s10530-020-02283-9	2020
Competition	Landscape changes	Spain	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Rodriguez, Alberto; Urra, Fer	10.3390/d12070268	2020
Competition	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Manlick, Philip J.; Windels, S	10.1007/s10980-020-01077-7	2020
Competition	Landscape changes	Poland	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Zawadzki, Grzegorz; Zawadz	10.1186/s40663-020-00271-y	2020
Competition	Edge effect	South Africa	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	Popp, Manuel R.; Kalwij, Jes	10.1007/s11258-021-01116-6	2021
Competition	Landscape changes	USA	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Hinton, Joseph W.; Hurst, Je	10.1371/journal.pone.0273707	2022
Competition	Landscape changes	Italy	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Differences in species tolerance towards roads alter competition dy	Fedele, Ettore; Mori, Emilian	10.1007/s42991-022-00313-8	2022
Competition	Road pollutants	USA	0	0	1	0	0	0	0	0	0	0	Amphibians	0	0	Single	1	Disturbance in freshwater communities caused by road salt polluti	Ocampo, Melissa; Chuirazzi,	10.1016/j.envpol.2022.120349	2022
Competition	Edge effect	Brazil	0	0	0	0	0	0	0	1	0	0	Plants	0	0	Single	1	Road verges favouring alien plant species establishment	de Oliveira Junior, Neil Dama	10.1007/s42974-023-00136-8	2023
Mutualism	Barrier effect	Japan	1	0	0	0	0	0	0	1	0	0	Mammals	Plants	0	Multiple	2	Road limits seed dispersal	Kikuzawa, K	10.1016/0378-1127(88)90129-6	1988
Mutualism	Edge effect	French Guiana	1	0	0	0	0	0	0	0	0	0	Mammals	0	0	Single	1	Road limits seed dispersal	Delaval, Marguerite; Charles-		2006
Mutualism	Edge effect	Netherlands	0	0	0	0	0	1	0	0	0	0	Insects	0	0	Single	1	Road influence on pollinators	Wynhoff, Irma; van Gestel, R	10.1007/s10841-010-9337-8	2011
Mutualism	Landscape changes	USA	0	0	0	0	0	1	0	0	0	0	Insects	0	0	Single	1	Road influence on pollinators	Watson, J. C.; Wolf, A. T.; A	10.1603/EN10231	2011
Mutualism	Edge effect	South Africa	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Geerts, Sjirk; Pauw, Anton	10.1111/j.1442-9993.2010.02201.x	2011
Mutualism	Edge effect	Spain	1	0	0	0	0	0	0	1	0	0	Mammals	Plants	0	Multiple	2	Road limits seed dispersal	Suarez-Esteban, Alberto; Del	10.1016/j.biocon.2013.07.022	2013
Mutualism	Landscape changes	Panamá	1	0	0	0	0	0	0	1	0	0	Mammals	Plants	0	Multiple	2	Road limits seed dispersal	Lambert, Thomas D.; Sumpt		2014
Mutualism	Edge effect	Spain	1	0	0	0	0	1	0	1	0	0	Plants	Insects	Mammals	Multiple	3	Road influence on pollinators	Suarez-Esteban, Alberto; Del	10.1016/j.baae.2014.08.001	2014
Mutualism	Road kills	Canada	0	0	0	0	0	1	0	0	0	0	Insects	0	0	Single	1	Road influence on pollinators	Baxter-Gilbert, James H.; Ril	10.1007/s10841-015-9808-z	2015
Mutualism	Edge effect	India	1	0	0	0	0	0	0	1	0	0	Mammals	Plants	0	Multiple	2	Road limits seed dispersal	Sengupta, Asmita; McConke	10.1371/journal.pone.0140961	2015
Mutualism	Edge effect	USA	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Halbritter, Dale A.; Daniels, J		2015
Mutualism	Road pollutants	Brazil	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Dargas, J. H. F.; Chaves, S.	10.1111/plb.12437	2016
Mutualism	Edge effect	Spain	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Hevia, Violeta; Bosch, Jordi;	10.1016/j.agee.2016.08.021	2016
Mutualism	Edge effect	USA	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Hanula, James L.; Ulyshen,	10.3375/043.036.0409	2016
Mutualism	Edge effect	Estonia	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Kutt, Laura; Lohmus, Kertu;	10.1016/j.ecolind.2016.06.009	2016
Mutualism	Edge effect	Australia	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road limits seed dispersal	Palfi, Zsofia; Spooner, Peter	10.1007/s00442-016-3767-2	2017a
Mutualism	Edge effect	Australia	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road limits seed dispersal	Palfi, Zsofia; Spooner, Peter	10.3389/fevo.2017.00132	2017b
Mutualism	Edge effect	USA	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Vinchesi, Amber; Walsh, Dou	10.1093/ae/tmy011	2018
Mutualism	Road pollutants	Australia	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Leonard, Ryan J.; Vergoz, Va	10.1111/oik.05405	2019
Mutualism	Edge effect	China	1	0	0	0	0	0	0	1	0	0	Mammals	Plants	0	Multiple	2	Road limits seed dispersal	Chen, Wenwen; Xie, Zongqia	10.1016/j.foreco.2018.11.029	2019a
Mutualism	Edge effect	UK	0	0	0	0	0	1	0	0	0	0	Insects	0	0	Single	1	Road influence on pollinators	Phillips, Benjamin B.; Gaston	10.1111/1365-2664.13470	2019
Mutualism	Road pollutants	China	1	0	0	0	0	0	0	1	0	0	Mammals	Plants	0	Multiple	2	Road limits seed dispersal	Chen, Wenwen; Zhong, Jie;	10.1111/1365-2745.13221	2019b
Mutualism	Road pollutants	China	0	0	0	0	0	0	1	0	0	1	Invertebrates	Bacteria	0	Multiple	2	Tread particles from vehicle tyres alter microbiome interactions	Ding, Jing; Zhu, Dong; Wang	10.1021/acs.est.0c00917	2020
Mutualism	Road pollutants	South Africa	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Grobler, B. Adriaan; Campbe	10.1086/708385	2020
Mutualism	Edge effect	Australia	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road limits seed dispersal	Palfi, Z.; Robinson, W.; Spoo	10.1007/s00040-020-00778-1	2020
Mutualism	Edge effect	UK	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Phillips, Benjamin B.; Wallac	10.1016/j.biocon.2020.108687	2020
Mutualism	Edge effect	Argentina	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Monasterolo, Marcos; Poggio	10.1016/j.agee.2020.107084	2020
Mutualism	Edge effect	Canada	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Olynyk, Marika; Westwood, A	10.1093/ee/nvaa186	2021
Mutualism	Edge effect	China	1	0	0	0	0	0	0	1	0	0	Mammals	Plants	0	Multiple	2	Road limits seed dispersal	Niu, Hongyu; Peng, Chao; C	10.1007/s10342-020-01345-w	2021
Mutualism	Road pollutants	USA	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Fitch, Gordon; Vaidya, Chatu	10.1111/1365-2664.13884	2021

Mutualism	Landscape changes	UK	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road influence on pollinators	Brebner, Joanna S.; Makinso	10.1016/j.anbehav.2021.07.003	2021
Mutualism	Road pollutants	Canada	0	0	0	0	0	0	0	1	0	1	Bacteria	Plants	0	Multiple	2	Tread particles from vehicle tyres alter microbiome interactions	O'Brien, Anna M.; Lins, Tiag	10.1016/j.envres.2021.111727	2022
Mutualism	Edge effect	French Guiana	1	0	0	0	0	0	0	1	0	0	Mammals	Plants	0	Multiple	2	Road limits seed dispersal	Coutant, Opale; Boissier, Oli	10.3389/fevo.2022.805376	2022
Mutualism	Edge effect	South Africa	0	1	0	0	0	0	0	1	0	0	Birds	Plants	0	Multiple	2	Road influence on pollinators	Grobler, B. Adriaan; Campbe	10.1016/j.sajb.2021.11.056	2022
Parasitism	Road pollutants	Switzerland	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road salt alters parasitism rates on freshwater species	Braun, S; Fluckiger, W	10.1016/0143-1471(84)90007-2	1984
Parasitism	Road pollutants	Switzerland	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road salt alters parasitism rates on freshwater species	Braun, S; Fluckiger, W	10.1016/0143-1471(85)90016-9	1985
Parasitism	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Increased avian brood parasitism close to roads	Chace, JF; Cruz, A		1999
Parasitism	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Increased avian brood parasitism close to roads	Clotfelter, ED; Yasukawa, K;		1999
Parasitism	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Increased avian brood parasitism close to roads	Chace, JF; Walsh, JJ; Cruz,	10.1016/S0169-2046(02)00220-7	2003
Parasitism	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Increased avian brood parasitism close to roads	Patten, MA; Shochat, E; Rein	10.1890/1051-0761(2006)016[0687:HELM	2006
Parasitism	Edge effect	Netherlands	0	0	0	0	0	1	0	1	0	0	Insects	Plants	0	Multiple	2	Road underpasses as parasitism hotspots	Harvey, J. A.; Wagenaar, R.	10.1111/j.1439-0418.2006.01093.x	2006
Parasitism	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Increased avian brood parasitism close to roads	Dixon, Thomas P.; Lopez, R	10.1016/j.landurbplan.2008.01.001	2008
Parasitism	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Increased avian brood parasitism close to roads	Etterson, Matthew A.; Green	10.1650/CONDOR-13-045.1	2014
Parasitism	Edge effect	USA	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Increased avian brood parasitism close to roads	Bernath-Plaisted, Jacy; Nenn	10.1098/rsos.170036	2017
Parasitism	Landscape changes	Canada	0	0	0	0	0	1	1	0	0	0	Insects	Invertebrates	0	Multiple	2	Road salt alters parasitism rates on freshwater species	Koprivnikar, J.; Urichuk, T. M	10.1139/cjz-2016-0210	2017
Parasitism	Road pollutants	Canada	0	0	1	0	0	0	1	0	0	0	Amphibians	Invertebrates	0	Multiple	2	Road salt alters parasitism rates on freshwater species	Milotic, Dino; Milotic, Marin;	10.1016/j.aquatox.2017.05.015	2017
Parasitism	Road pollutants	USA	0	0	0	0	0	1	0	0	1	0	Insects	Fungi	0	Multiple	2	Road salt alters parasitism rates on freshwater species	Merrick, Abigail M.; Searle, C	10.1111/fwb.13245	2019
Parasitism	Landscape changes	USA	0	0	1	0	0	0	1	0	0	0	Amphibians	Invertebrates	0	Multiple	2	Road salt alters parasitism rates on freshwater species	VanAcker, Meredith C.; Lam	10.1007/s10393-019-01427-1	2019
Parasitism	Landscape changes	New Zeland	0	0	0	1	0	1	0	0	0	0	Reptiles	Insects	0	Multiple	2	Road underpasses as parasitism hotspots	Payne, Eric; Sinn, David L.;	10.1111/oik.06670	2020
Parasitism	Landscape changes	Bangladesh	0	1	0	0	0	0	0	0	0	0	Birds	0	0	Single	1	Increased avian brood parasitism close to roads	Datta, Ashis Kumar; Begum,	10.1007/s43388-021-00069-8	2021
Parasitism	Road pollutants	Canada	0	0	0	0	0	1	0	0	0	0	Insects	0	0	Single	1	Road salt alters parasitism rates on freshwater species	Zhang, Vicki M.; Martin, Ros	10.1093/ee/nvac014	2022

Chapter 2: Are road-kills representative of wildlife community obtained from atlas data?

Abstract

Systematic road-kill surveys are useful to study the impact of roads on wildlife. However, they are time-and budget-consuming, so the use of non-systematic data in road ecology is currently gaining popularity (for instance, by environmental consultants). Some data sources such as atlases (i.e., compilations of species records from a given region), which can include non-systematic and citizen-science data, can entail several intrinsic biases, mostly due to uneven sampling effort and uneven species detectability. Here, we tested this prediction by verifying if data from the Spanish Atlas of Terrestrial Mammals mirror the road-kill patterns obtained from our own systematic road-kill surveys. We focused on the Mediterranean mesocarnivore guild due to its easy identification by citizens involved in atlas-data collection. We tested if the relative abundance of each species, their richness and diversity obtained from Atlas and our systematic surveys were related, using linear models, while controlling for human population and road density (potentially confounding effects). We further compared the patterns of species abundance obtained from both sources. Our results highlight that road-kill patterns do not mirror the Atlas patterns for the three metrics evaluated. This is probably due to survey biases in typical data from wildlife atlases. When analysing species individually, we found that some species are road-killed more (or less) than expected in relation to their abundance in atlas records. These results are probably due to species-specific ecological or behavioural traits such as species morphology or species behaviour when facing the road. We suggest that abundance from atlas data should not be used as a proxy for road-kill rates.

Keywords: Atlas data; carnivores; citizen science; Road Ecology; wildlife-vehicle collisions

1. Introduction

Anthropic structures, such as roads, have several impacts on wildlife, including different kinds of disturbance, habitat loss and fragmentation (reviewed by Benítez-López *et al.*, 2010; Forman, 2003; van der Ree *et al.*, 2015). Road-kills are one of the most noticeable traffic impact for the public, because carcasses remain on the road visible to drivers (Hobday and Minstrell, 2008; Santos *et al.*, 2011a). Road-kills can have a considerable impact on population viability, causing population crashes in some species (Beaudry *et al.*, 2008; Roger *et al.*, 2011; Row *et al.*, 2007). Furthermore, wildlife-vehicle collisions implying large species, such as ungulates or large carnivores, can compromise driver safety (Conover *et al.*, 1995; Seiler, 2005). For all these reasons, road-kill is the most studied impact in road ecology (D'Amico *et al.*, 2018; Forman, 2003; Pinto *et al.*, 2020; van der Ree *et al.*, 2015).

Typical road-kill surveys are performed by car, driving slowly along a given itinerary, implementing a certain survey periodicity (for example, daily or weekly), and recording any road-killed individual of the target species (Canal *et al.*, 2019; Costa *et al.*, 2015). This kind of survey is time consuming and usually implies relatively high economic costs (Costa *et al.*, 2015). In order to reduce these costs, in the last decades several road ecologists investigated road-kill patterns using other sources of data, such as for example the data included into wildlife atlases.

A wildlife atlas is the result of a data-gathering effort on a certain taxon in a certain area (usually an administrative region). In an atlas, all occurrence records (from a variety of sources) of a species are compiled and structured in a geographical net (sometimes also providing information on seasonal presence, or even abundance and long-term population changes; see for example the Southern African Bird Atlas Project or the European Bird

Census Council). Atlas have been used for studying demographical trends (Fuller *et al.*, 1995; Lee *et al.*, 2017; Telfer *et al.*, 2002) and the factors behind these trends (Allan *et al.*, 1997; Gil-Tena *et al.*, 2007; Pascual-Hortal and Saura, 2008; Trzcinski *et al.*, 1999). Other studies used atlas to assess changes in species distribution (Kouba *et al.*, 2014), and species range projections for future scenarios (Morueta-Holme *et al.*, 2010; Virkkala *et al.*, 2008). The popularity of atlas as a source of data relies on their data-gathering nature, usually focused on a specific taxon in a certain region. However, this typical data collection for wildlife atlases usually implies a mixture of data sources (Ozolins and Pilats, 1995; Palomo *et al.*, 2007), such as specific surveys carried out by professionals, contributions from expert knowledge, voluntary surveys, questionnaires to authorities of protected areas, bibliographic search, specimens from collections and museums, or citizen-science projects. Consequently, this variety of sources may imply low data quality and uneven sampling effort especially in case of specimens from museums, voluntary surveys or citizen-science projects (Crall *et al.*, 2011). Furthermore, data from wildlife atlases are typically represented at a large scale and, for this reason, they should not be implemented for investigating patterns at a lesser scale, as downscaling may produce some errors, especially in poorly sampled regions (Araujo *et al.*, 2005; Böhning-Gaese, 1997). Nevertheless, this kind of data has been used for investigating road-kill patterns, both employing the occurrence of road-kills (Battisti *et al.*, 2012) and developing road-kill risk models from atlas datasets (Visintin *et al.*, 2016). Whereas some authors have found a positive association between species abundance and road-kills (Canova and Balestrieri, 2019; D'Amico *et al.*, 2015; Gehrt, 2002; Visintin *et al.*, 2016), this relationship seems to blur when abundance is based on atlas data (Battisti *et al.*, 2012). As publicly available atlas data are being used, for example, by environmental consultants and stakeholders to select the least impacting alternative among those competing for the construction of a new road, we think the relationship between atlas data and field-based road-kill patterns deserves further exploration.

The aim of this study is to test if datasets from wildlife atlases are suitable for investigating road-kill patterns. Considering that both species occurrence and abundance have been described as some of the main drivers of road-kill risk (Canova and Balestrieri, 2019; D'Amico *et al.*, 2015; Gehrt, 2002; Visintin *et al.*, 2016), we tested if road-kills are representative of the wildlife community based on the atlas data for a given species guild. For this purpose, we compared the data accumulated until 2016 in the Spanish Atlas of Terrestrial Mammals (Palomo *et al.*, 2007) in an area of central Spain with our own road-kill survey. We selected carnivores as the study group because they are relatively more reported than other species in citizen-science platforms (Kosmala *et al.*, 2016), and their medium-large carcasses are easier to detect and persist for longer times on the road than smaller ones (Barrientos *et al.*, 2018). Also, this guild undergoes high road-kill rates in Mediterranean road networks (Grilo *et al.*, 2009, 2015). We expect that road-kills are not representative of the wildlife community obtained from Atlas data (Battisti *et al.*, 2012), mainly due to the intrinsic limitations of Atlas data regarding survey biases (Isaac *et al.*, 2014; Vercayie and Herremans, 2015); but also due to the existence of species traits affecting differential road-kill risk among species (D'Amico *et al.*, 2015; Jacobson *et al.*, 2016). Consequently, we also expect that some species are road-killed above or below their occurrence in Atlas data.

2. Materials and Methods

2.1 Study area

We selected a homogeneous Mediterranean cropland mixed with abandoned fields where we could find a large and diverse carnivore guild, exposed to different road densities. The study area covers a total of 26 10x10 km UTM squares in the Tagus Valley, central Spain (Figure 1). The altitude ranges between 350m and 850m above sea level, and the climate is Mediterranean with 340 mm of average annual rainfall, and average daily maximum temperatures between 27.1°C (August) and 3.6°C (December). Most of the surface is dedicated to dry crops (55%), including cereals and olive groves, but also fallow lands. Whereas 14% is occupied by irrigated lands, non-cultivated areas (dominated by xerophytic shrubs such as the broom *Retama sphaerocarpa* and the tussock grass *Stipa tenacissima*) cover 23% of the area. The remaining 8% is occupied by different land uses, including urban settlements. In terms of road infrastructure, secondary roads are the main type of road, with densities that range from 0.12 km to 0.74 km per km^2 (mean = 0.4 km/ km^2), a medium road density compared to the rest of Spain. We focused on secondary (i.e., regional) roads because they are the most representative road type in our study area (Barrientos and Bolonio, 2009).

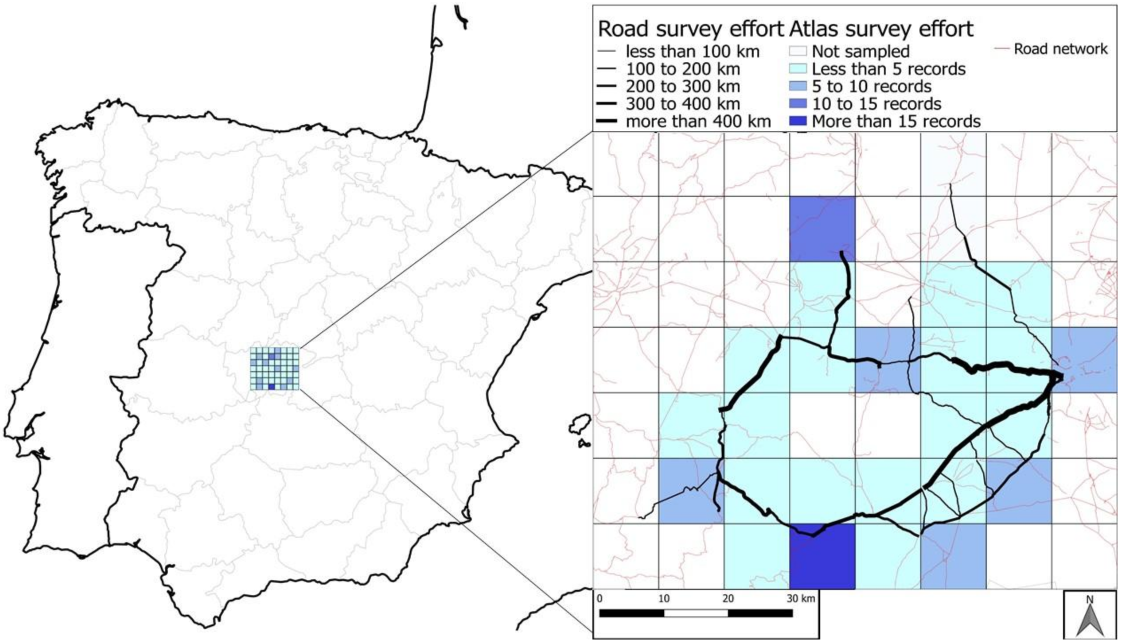


Figure 6: Survey effort in the study area, both for the road-kill survey and the Atlas. Black lines thickness represents the number of kilometres surveyed in a particular road segment. The blue gradient in the UTM squares represent the number of Atlas records in each one.

The study area hosts a rich community of medium-sized carnivores, including most common species of the Mediterranean landscapes of Iberian Peninsula (e.g., (Grilo *et al.*, 2009; Soto and Palomares, 2015). This carnivore guild is composed by one canid (red fox *Vulpes vulpes*), one felid (European wildcat *Felis silvestris*), one viverrid (small-spotted genet *Genetta genetta*), one herpestid (Egyptian mongoose *Herpestes ichneumon*), and four mustelids (European badger *Meles meles*, Eurasian otter *Lutra lutra*, Stone marten *Martes foina* and European polecat *Mustela putorious*). As they have similar body masses, carcass detectability and persistence rates are expected to be homogeneous (Barrientos *et al.*, 2018).

2.2 Data collection

The road-kill surveys were carried out between September 2014 and August 2016, by repeating exactly the same sampling schema carried in a previous work (Barrientos and Bolonio, 2009), in the framework of a long-term research project. We worked on the same 330 km-long road network during the two years, in which we carried out a total of 41 biweekly samplings (Barrientos and Bolonio, 2009). However, the distance covered in each survey was variable within those 330 km, and totalled ~5300 km (Figure 1). We drove at 40–50 km/h searching for carcasses on the road surface. Once a carcass was detected, we stopped the car to identify the species and locate it with a GPS device. This method has proven to be highly cost-effective for carnivore carcass detection, as the survey could be performed by just one researcher (Barrientos and Bolonio, 2009). Recorded carcasses were removed from the road in order to avoid re-sampling in successive surveys.

We obtained species occurrence data from the database of the Spanish Society of Mammalogists (Sociedad Española para la Conservación y Estudio de Mamíferos, SECEM). The SECEM compiled this database with the aim of generating the Spanish Atlas of Terrestrial Mammals (Palomo *et al.*, 2007), in collaboration with the Atlas of European Mammals (Mitchell-Jones *et al.*, 1999). Data incorporated into the Atlas is a heterogenous set of sources (both systematic and opportunistic) which includes regional atlas, bibliographic data, museum collections, technical reports or information provided by local administrations, data from collaborators and citizen-science data, which is the only source of the constant updates carried from 2007 to date. We used the original database employed to draw the maps, not the maps themselves (based on presence/absence outputs). So, every occurrence (positive UTM cell) could be composed of more than one record, similar to a standard census.

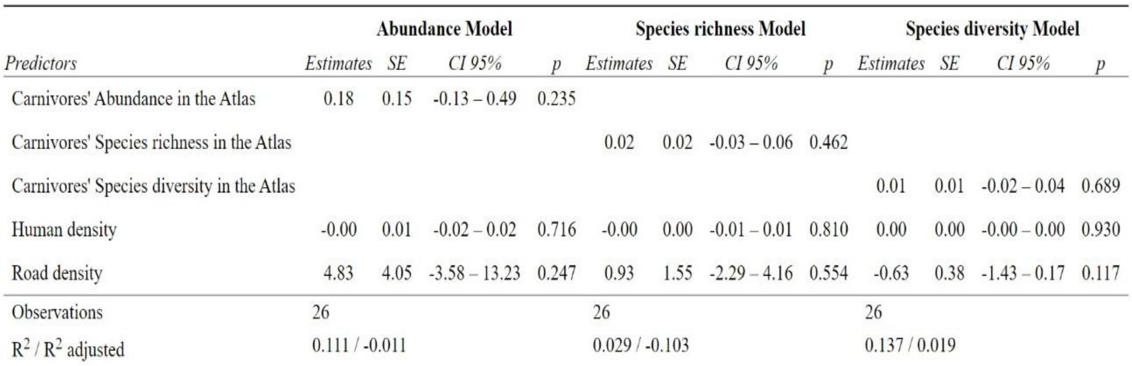
Our study units were those UTM squares (26) in which we performed road-kill surveys (Figure 1). We extracted all the Atlas data (any carnivore record of any kind since the beginning of the Atlas) from those squares and weighted both the atlas and the roadkill dataset to control for the sampling effort, in order to make them comparable. Namely, we divided the Atlas metrics (abundance of records, species richness and species diversity) of all carnivore species combined in every square by the total number of mammal records in that square. By controlling for sampling effort, we tried to mitigate one of the most important bias related to the Atlas data (Isaac *et al.*, 2014; Vercayie and Herremans, 2015). Similarly, we divided the road-kill figures (road-kill abundance, species richness and species diversity) of all carnivore species combined in each square by the accumulated km surveyed in that square. Note that road-kill abundance by km is usually denominated *road-kill ratio*, but in this work we will keep it as *abundance*, in order to preserve the analogy between *abundance of road-killed carnivores* and *carnivores' abundance in the Atlas*.

We further collected information on *human density* (inhabitants per square) and *road density* (kilometres of roads per square) as these variables can influence data-gathering in citizen science projects as *human density* determines the potential number of collaborators and *road density* determines how accessible is the landscape for those potential collaborators (Geldmann *et al.*, 2016). Finally, we confirmed that none of the final explanatory variables we used in our linear models were correlated by using the function "cor" in R (package "stats").

2.3 Data analyses

We fitted three Lineal Models (Table 1) using the "lm" function in R. In our first model, the response variable was the *abundance of road-killed carnivores*, and the explanatory variables were: *carnivores' abundance in the Atlas*, *human density* and *road density*. In our second model, the response variable was the *species richness of road-killed carnivores*, and the explanatory variables were: *carnivores' species richness in the Atlas*, *human density* and *road density*. In our third model, the response variable was the *species diversity of road-killed carnivores* (assessed with Shannon index), and the explanatory ones were: *carnivores' species diversity in the Atlas*, *human density* and *road density*.

Table 1: Carnivores' Abundance Model (in which we tested if the abundance in the Atlas is a potential predictor of the abundance of road-kills), Species richness model (in which we tested if the species richness in the Atlas is a potential predictor of the species richness of road-kills) and Species diversity model (in which we tested if the species diversity in the Atlas is a potential predictor of the species diversity of road-kills). Each model had Human and Road densities as additional predictors. Coefficient Estimates, Standard Error (SE), 95% Confidence interval (CI 95%) and p-value (p) are provided, and "Observations" represent the number of our 10X10 Km study units.



	Abundance Model				**Species richness Model**				**Species diversity Model**			
Predictors	*Estimates*	*SE*	*CI 95%*	*p*	*Estimates*	*SE*	*CI 95%*	*p*	*Estimates*	*SE*	*CI 95%*	*p*
Carnivores' Abundance in the Atlas	0.18	0.15	-0.13 – 0.49	0.235								
Carnivores' Species richness in the Atlas					0.02	0.02	-0.03 – 0.06	0.462				
Carnivores' Species diversity in the Atlas									0.01	0.01	-0.02 – 0.04	0.689
Human density	-0.00	0.01	-0.02 – 0.02	0.716	-0.00	0.00	-0.01 – 0.01	0.810	0.00	0.00	-0.00 – 0.00	0.930
Road density	4.83	4.05	-3.58 – 13.23	0.247	0.93	1.55	-2.29 – 4.16	0.554	-0.63	0.38	-1.43 – 0.17	0.117
Observations	26				26				26			
R^2 / R^2 adjusted	0.111 / -0.011				0.029 / -0.103				0.137 / 0.019			

As we expected that density-independent species traits (e.g., hunting behaviour, habitat selection, etc.) of some species may influence road-kill rates, we also analysed the differences in the observed proportion of road-kills compared to their expected occurrence from Atlas data with species-specific 2x2 chi-squares with the Yates correction. Statistical analyses were performed with R (R Core Team, 2017), and SIG analyses with Quantum GIS (Quantum GIS Development Team, 2018).

3. Results

In our 26 UTM study units, we found 146 carcasses during our two-year road-kill survey (Table 2): 29 foxes, 12 wildcats, 3 genets, 13 mongooses, 1 stone marten and 88 polecats, whereas no badgers or otters were found. On the other hand, the Atlas contained

119 records (Table 2): 24 foxes, 5 wildcats, 3 genets, 5 mongooses, 5 stone martens, 42 polecats, 3 badgers and 32 otters.

Table 2: Table with the number and percentage of road-kills and Atlas record for each species. Chi squared statistics are also shown (Chi square value; χ2 and p-value), with significance differences between road-kills and Atlas data for European otter and European polecat in bold.

Species	Road-kills (%)	Road-kills (n)	% Atlas	Atlas	χ2	df	p-value
Stone marten *(Martes foina)*	0,68	1	4,20	5	2,25	1	0,13
European wildcat *(Felis silvestris)*	8,22	12	4,20	5	1,16	1	0,28
Small-spotted genet *(Genetta genetta)*	2,05	3	2,52	3	0,03	1	0,87
Egyptian mongoose *(Herpestes ichneumon)*	8,90	13	4,20	5	1,61	1	0,2
Eurasian otter *(Lutra lutra)*	0,00	0	26,89	32	42,16	1	< 0,0001
European badger *(Meles meles)*	0,00	0	2,52	3	1,81	1	0,17
European polecat *(Mustela putorius)*	60,27	88	35,29	42	15,39	1	< 0,0001
Red fox (*Vulpes vulpes)*	19,86	29	20,17	24	0,01	1	0,93

First, none of the explanatory variables used in the linear models were correlated. Most importantly, in the three Linear Models comparing road-kill survey data and Atlas data, we did not find any significant predictor (Table 1). However, we found hints of a negative relation between road density and the diversity of road-killed carnivores in our third model, which we further analysed with a correlation test between both variables (t = -1.89, df = 24, p-value = 0.07).

Species-specific comparisons showed that whereas some species are road-killed more than expected given the Atlas data, others are road-killed less than expected (Table 2). Namely, polecats were road-killed more often (25 %) than expected from their abundance, whereas otters were road-killed less than expected. Foxes, wildcats, genets, mongooses, stone martens and badgers were road-killed on average to their occurrence in the Atlas records.

4. Discussion

The present findings suggest that road-kills were not representative of abundance, species richness and species diversity obtained from Atlas data. This is likely due to two factors: i) limitations of the Atlas data; ii) the fact that some species are intrinsically more (or less) prone to be road-killed than expected regarding their abundance.

In regard to wildlife-atlas data, (Isaac *et al.*, 2014) pointed out the potential of non-systematic data to swamp trends or to produce spurious patterns and described the types of biases inherent to citizen science data: (i) uneven recording intensity over time, (ii) unequal spatial coverage, (iii) heterogeneous sampling effort in every visit, and (iv) different detectability of the sampled species. Moreover, both the spatial and temporal scales of wildlife atlases may influence their suitability to be mirrored by road-kill patterns. Furthermore, Atlases spatial scale can affect how useful atlases are as conservation tools, as their scale could have a profound effect on model predictions based on them (Araujo *et al.*, 2005; Böhning-Gaese, 1997) and could, therefore, affect conservation planning (Bombi *et al.*, 2012). On the other hand, temporal scale is usually overlooked or poorly controlled, which could affect road-kill risk assessment, as wildlife populations are not static over the time (Carminatto *et al.*, 2020; Delibes-Mateos *et al.*, 2008; Gaüzère *et al.*, 2020).

Factors mismatching road-kill probability with species occurrence are likely influenced by morphological, ecological, life-history or behavioural traits. For example, Mata *et al.* (2017) found that foxes, stone martens and genets usually used the road proximities during foraging, whereas badgers and wildcats tended to avoid roads. In this sense, we found a negative trend of road density on road-killed species diversity. This could suggest that when road-kill risk is low (i.e., lower road density), no species is particularly affected as they all have low road-kill rates. On the contrary, when such risk increases, more susceptible species are disproportionately road-killed (Jacobson *et al.*, 2016). However, further investigations are needed to confirm this pattern.

The most road-killed species, relative to its occurrence in the Atlas data, was the European polecat (Table 2). Polecats in the Iberian Peninsula are specialists in European rabbit (*Oryctolagus cuniculus*) hunting, with lagomorphs (mainly rabbits) forming up to 87% of consumed biomass in Mediterranean habitats (Santos *et al.*, 2009). Polecat distribution overlaps with that of rabbits (Barrientos and de Dios Miranda, 2012; Santos *et al.*, 2009), and rabbit abundance is the most important driver of polecat road mortality (Barrientos and Bolonio, 2009; Barrientos and de Dios Miranda, 2012), because this predator searches for rabbits breeding in road embankments. Thus, repeated visits to road embankments, together with its particular body morphology (poorly-adapted to run), could increase the road-kill rates of polecats (Barrientos and Bolonio, 2009).

The higher-than-expected road-kill rates of the polecat is a good example of how density-independent species traits (such as hunting behaviour) can affect road-kill risk of certain species and makes road-kills do not reflect atlas data. In this sense, the polecat could be classified as a non-responder in the framework that Jacobson *et al.* (2016) developed, as they do not recognize or detect the threat of a moving vehicle, regardless of traffic volume. Thus, species like the polecat may have their road-kill rates affected not only by their local abundance, but also by their behavioural response to roads and traffic. Moreover, polecats are especially elusive, and they may had been underdetected in the Atlas data, which would help to explain the deviation from road-kill figures.

On the other hand, otters were road-killed less than expected from Atlas data (Table 2). Otters are semi-aquatic carnivores that feed in and displace by water courses, only rarely leaving them (Quaglietta *et al.*, 2012, 2013, 2014), so they are expected to be less impacted than terrestrial carnivores (e.g., Grilo *et al.*, 2009). However, they are not safe from being road-killed; for instance, their risk increases when they cannot cross the road under bridges or culverts because of high river flows (Guter *et al.*, 2006; Philcox *et al.*, 1999). Nevertheless, we think that the differences we found are associated to important biases in Atlas data. Our study area is a dry (annual rainfall of only 340 mm) Mediterranean area where otters are likely associated to the few rivers that have water throughout the year. Nonetheless, otter presence is easily detected by searching for their scats in protruding stones or in bridge foundations when infrastructures cross the rivers. In fact, there is a standardized method to detect this species in Europe (i.e., searches in 600 meters long surveys; (Jefferies, 1986; Manson and McDonald, 1986)), which has been employed in up to three national surveys in Spain (Jiménez *et al.*, 2008), which has been able to train many amateur samplers to detect otters. Moreover, the Atlas 10 x10 km square scale is known to overestimate otter abundance (Sales-Luís *et al.*, 2012). Otter case is a clear example of how citizen-science data biases, such those described by Isaac *et al.* (2014), can make this source unsuitable to investigate road-kill patterns.

The remaining species in our study underwent road-kills rates on average to their abundances in the Atlas data, although in some cases the number of occurrences was low to obtain sound patterns. Nevertheless, some of these remaining species are known to be affected differently by the road. For example, the stone martens are known to suffer more road-kills is sinuous road sections (Grilo *et al.*, 2011), a road topology that is scarce in our study area (Barrientos and Bolonio, 2009). Furthermore, road impact on badgers depends on traffic volume, as high traffic loads may discourage them from attempting to cross major roads, causing barrier effects and intermediate traffic flows can road-kill to those who dare to cross (Clarke *et al.*, 1998). Therefore, research using more occurrences in both road-kills and Atlas data would be necessary in order to better understand how good of a predictor for road-kill patterns the Atlas is for the whole carnivore guild.

Although it falls out of the scope of present study, it is worth mentioning that some authors have tried to correct the limitations of citizen science-based data mainly by means of three ways: (i) by validating the species distribution models (SDMs) obtained with citizen science data using conventional fieldwork. For example, Bradsworth *et al.* (2017) and Coxen *et al.* (2017), found that the generated SDMs predicted with great success the fieldwork data; (ii) with methodological improvements applicable to citizen-science projects such as properly training the data collectors or assessing the scope of the given citizen-science project (Conrad and Hilchey, 2011; Dickinson *et al.*, 2012); and, finally, (iii) establishing new statistical approaches that allow a better use of citizen-science data, better controlling the lack of systematic sampling effort both in time and space (Bird *et al.*, 2014; Isaac *et al.*, 2014).

5. Conclusions

To summarize, our findings suggest that wildlife atlas data does not always mirror road-kill patterns, likely due to both biases in Atlas data (including uneven recording intensity and detectability) and to species-specific responses to roads (such as morphological, ecological, life-history or behavioural traits). This mismatch is important while considering if road-kill data can be used (or not) for monitoring, not just road-kill rates but also population trends in general, as there are now numerous projects starting or operating across the globe on road-kill monitoring (Schwartz *et al.*, 2020). Therefore, it is key to separate road-kill data (abundance and occurrence) from data obtained from other projects with less bias. Thus, to study road-kill rates and patterns, we suggest that classical road-kill surveys should be the first option, however, as these are time-and budget-consuming, other sources of data could be used as well, but always using correcting approaches to citizen-science datasets and other non-systematic data sources. Moreover, species' ecology and traits should be considered if the study aims to determine species' specific road-kill patterns.

6. Acknowledgements

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7. CRediT authorship contribution statement

Pablo Quiles: Conceptualization, Methodology, Software, Formal analyses, Investigation, Writing - Original Draft and Visualization. **Fernando Ascensão**, **Marcello D'Amico** and **Eloy Revilla**: Conceptualization and Writing - Review & Editing. **Rafael Barrientos**: Conceptualization, Methodology, Investigation, Resources, Writing - Original Draft, Writing - Review & Editing, Supervision, Project administration and Funding acquisition.

Chapter 3: Nothing lasts forever: on the importance of identifying the factors driving roadkills rather than simply mapping hotspots

Abstract

Roadkills are the most studied road impact on wildlife, as they lead to barrier effects and population declines, making it essential to minimize wildlife-vehicle collisions. However, there is a lack of long-term studies evaluating how roadkill hotspots and the key factors influencing them vary over space and time. Understanding the mechanisms driving these roadkill hotspots is important for proactive conservation planning and the optimal implementation of mitigation strategies. This research aimed to investigate how roadkill rates have varied between two distinct time periods and evaluate whether the factors influencing roadkill rates have shifted spatially. We assessed the factors that influence polecat (*Mustela putorius*) roadkills in the same area in two periods (2002–2004 and 2014-2016), and we measured variables related to rabbit abundance, road characteristics, and landscape features in both periods. We recorded a total of 195 polecat roadkills in both periods. We show that the spatial distribution and aggregation of roadkill patterns have changed over time. These changes are likely associated with changes in the abundance of rabbits and vehicle traffic volume. Furthermore, speed limit positively influenced roadkill likelihood. This study showcases how roadkill hotspots change over space and time, primarily due to fluctuations in rabbit populations, and highlights the challenges of implementing effective long-term mitigation measures to reduce wildlife-vehicle collisions. Our research emphasises the importance of continuous monitoring and the need to identify underlying variables causing roadkill hotspots rather than simply locating them. It also demonstrates the value of replicating studies to assess the temporal transferability of ecological models, addressing a common weakness in field-based research.

Keywords: roadkill hotspot, road ecology, roadkill aggregations, temporal transferability, polecat, wildlife-vehicle collision

1. Introduction

Roads have several pervasive impacts on wildlife, such as habitat loss -as the corridor occupies previously suitable habitats-, habitat impoverishment due to pollutants from vehicles (smoke, noise, light), connectivity reduction or roadkills (Benítez-López *et al.*, 2010; Forman, 2003; van der Ree *et al.*, 2015). These latter two impacts have been the most studied (Barrientos *et al.*, 2021; Bennett, 2017) as roadkills can cause both barrier effects since animals avoid crossing or die when trying to cross. This leads to population crashes, eventually threatening population persistence in the long run when this mortality is massive (Barrientos *et al.*, 2021; Borda-de-Água *et al.*, 2014; Holderegger and Di Giulio, 2010; Roger *et al.*, 2011). Furthermore, roadkills implying large animals like ungulates or carnivores can compromise driver’s safety (Malo *et al.*, 2004; Seiler, 2005).

The identification of mortality hotspots is a widespread approach in road ecology studies both to identify ecological patterns and to select priority locations for implementing mitigation measures. In risk assessment, a hotspot is defined as the concentration of high-risk probability or frequency of roadkills over a small area (Crawford *et al.*, 2014). To locate those hotspots, road ecologists often divide the road into segments and identify those where roadkill probability is significantly higher than expected by chance. However, when this methodology is applied without considering corrections for multiple testing, the probability of identifying false hotspots (i.e., making Type I errors) is high (Borda-de-Água *et al.*, 2019). Moreover, some studies have proved that this “static” line of thinking may be wrong, as population abundance in the road surroundings- a common driver of roadkills (e.g., Burgstahler *et al.*, 2023; Fernández-López *et al.*, 2022) can change over time. In this sense, low mortality rates can be due to low population abundance caused by past mortality (Ascensão *et al.*, 2019; Zimmermann

Teixeira *et al.*, 2017), or due to any other reason, so hotspot locations can be unstable over time.

Roadkill studies are usually carried out in limited timescales (van der Ree *et al.*, 2015), with approaches evaluating the temporal transferability of roadkill patterns lacking. For instance, in their review of twenty-four published manuscripts, Gunson et al. (2011) found that all the studies but one (Langen *et al.*, 2009) were focused on a single time period. The evaluation of temporal patterns in roadkill studies has been mainly limited to identify hot moments (like dispersal or mating seasons), or to re-analyse the same dataset from a phenological point of view (Grilo *et al.*, 2009; Inbar and Mayer, 1999; Naciri *et al.*, 2023), incurring in space-for-time substitution assumptions that may lead to erroneous conclusions (Damgaard, 2019). Indeed, there is a claim among experts for the need of roadkill 'monitoring' (defined as 'the repeated measuring of explanatory variables, usually over an extended period of time') in road ecology studies, as monitoring is needed to assess both the road impact and the effectiveness of mitigation measures over time (van der Ree *et al.*, 2015). Few studies have explored whether roadkill patterns are repeatable over time. For example, Santos *et al.* (2017) found that hotspots and hot moments are generally more consistent at larger temporal and spatial scales in their 5-year study, suggesting that uncertainty appears at small scales (when used 500 m-long road sections or fortnightly samplings). For their part, Rendall *et al.* (2021) compared how climatic and road-related variables influenced roadkill records in two sampling periods separated by 16 years, but with both varying sampling efforts and extensions of surveyed roads. These authors found that roadkill rates peaked at moderate speeds, likely mediated by species abundance, although they did not took this latter measure (Rendall *et al.*, 2021). A three-year study in southern Portugal, Medinas *et al.* (2021) found that most of the bat roadkill hotspots identified by means of the Kernel Density Estimation

(KDE) approach vanished in consecutive years. This temporality was associated with decreasing vegetation production and increasing water stress on road surroundings expressed by the NDVI (Medinas *et al.*, 2021). However, remote sensing techniques have limitations as several variables influencing roadkill locations need to be measured on the field (Gunson *et al.*, 2011).

When models are intended to be used beyond the areas and time periods over which they were calibrated, one critical characteristic is their transferability, that is, the predictive ability of the model in other scenarios (Barrientos and Miranda, 2012; Seiler, 2005). The above-mentioned studies on the repeatability of roadkill patterns rarely identified the variables underlying such patterns, which hinders the model transferability. However, the lack of research on model performance in new scenarios is not a singularity of roadkill models but the contrary, it is a common weakness of ecological models, especially regarding field-based studies (Randin *et al.*, 2006; Tuanmu *et al.*, 2011; Wenger and Olden, 2012; Werkowska *et al.*, 2017). In the case of roadkill studies, rather than identifying roadkill concentrations in space and time (i.e., hotspots), the truly important question is to identify the variables and mechanisms drawing such roadkill hotspots. This was sharply evident during the COVID-19 pandemic, when the reduction in road traffic (a key variable in countless models; reviewed in Gunson *et al.* (2011), see also (Burgstahler *et al.*, 2023; Rendall *et al.*, 2021) led to dramatic changes in roadkill patterns at a global scale, but with some species more affected than others depending on their ecological traits (Pokorny *et al.*, 2022; Raymond *et al.*, 2023), thus modifying the spatial distribution of roadkills.

Animals can be killed when crossing roads in their displacements or when they visit this infrastructure searching for resources, such as those related to foraging (Hill *et al.*, 2021). Two major types of variables influence roadkills: those related to the road itself (traffic flow and speed, road characteristics such as width, presence of embankments or other barriers, etc) and ecological factors either offered by the road itself or because the road bisects species' favourable habitats (reviewed in Gunson *et al.*, 2011). Including variables of these two types, we explored the spatial distribution of hotspots in two 2-year surveys separated by 12 years. With a 'question-driven monitoring' (*sensu* Lindenmayer and Likens, 2010), i.e., a monitoring guided by a conceptual framework and a rigorous experimental design), we repeated exactly the same survey carried out in 2002-2004 by Barrientos and Bolonio (2009) to investigate how roadkill hotspots may have temporally and spatially shifted due to these variable changes. In particular, we assessed these changes for roadkill from the Mediterranean polecat (*Mustela putorious*), a carnivore whose roadkills concentrate in those road sections with the highest densities of rabbits (*Oryctolagus cuniculus*) (Barrientos and Bolonio, 2009; Carmona *et al.*, 2024), its main prey (Santos *et al.*, 2009). However, rabbits undergo marked population fluctuations due to diseases and game-oriented management, with local extinctions and recoveries (Delibes-Mateos *et al.*, 2008; Delibes-Mateos *et al.*, 2009). Since it has been shown that polecats spatially track the local abundance of rabbits (Santos *et al.*, 2009), and that polecat abundance is positively related to its roadkill rates (Barrientos and Miranda, 2012), we aim to: i) test if the distribution of polecat roadkill hotspots have changed in 2014-2016 with respect to 2002-2004, which would prove the instability of roadkill hotspots, and the need of continuous monitoring of roadkills; ii) identify the spatial and temporal factors influencing roadkill patterns and how those change through time. We predict these influences would remain constant through time but their effect may vary spatially.

2. Material and Methods

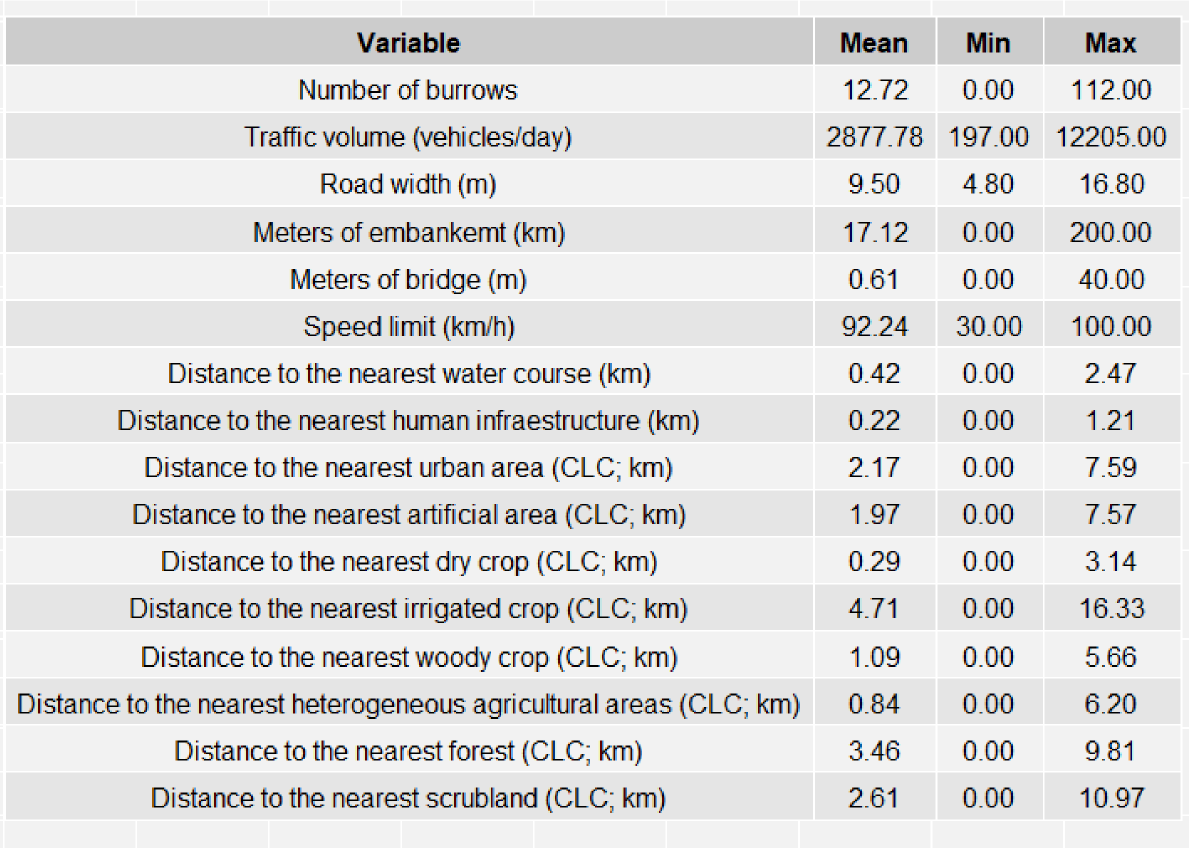
(a) Sampling design

The study area is a typical Mediterranean agrosystem dominated by dry crops (cereal, olive fields; summing 54.6% of land surface, based on 104 random points; see Barrientos and Bolonio 2009) with some remains of natural vegetation dominated by scrublands of *Retama sphaerocarpa* and *Stipa tenacissima* (33.2%). The remaining land uses are urban areas (10.1%) and irrigated crops (2.1%). All the sampled roads were two-line, with traffic flow ranging 197-9445 (average, 2354) vehicles per day for 2014-2016.

We replicated the study carried by Barrientos and Bolonio (2009) during 2002-2004 twelve years later. Using the same methodology as the original survey, we sampled a total of 4830 km of roads from October 2014 to September 2016. We sampled exactly the same routes, and in the same (±7) calendar days. However, we concentrated our efforts into the Tajo valley, and we excluded from the original scheme some areas with low representativeness due to the few number of surveys (<10% of total survey length). The surveys were conducted driving at 40-50 km/h mainly on a fortnightly basis (Barrientos and Bolonio, 2009). Despite smaller intervals between surveys have been proposed as more accurate for carnivore sampling (Santos *et al.*, 2011a), our scheme has the advantage of allowing for fully comparison of the two study periods, since the methodology was identical, and potential biases are expected to be the same between study periods. We thus assume that the ratio of carcass removal by scavengers or carcasses being overlooked by researchers (the two main biases; see Barrientos *et al.*, 2018) were similar between periods. Besides recording roadkill events, we revisited the same 104 random points as in the previous survey, measuring the same variables as in roadkill points. Moreover, roadkill points from 2004-2006 were also revisited in 2014-2016 and we took the same measurements.

We measured the same variables as in the previous work (Barrientos and Bolonio, 2009) for every roadkill as they were geo-referred. Two variables related to rabbit abundance (distance to the nearest burrow and number of burrows in a radius of 50 m from the roadside on both sides of the road) were measured in the field. We also included nine road-related variables, including traffic flow, meters of embankment, speed limit and percentage of unbroken line (See Table 1). We obtained the monthly traffic flow and the percentage of heavy vehicles from local government website (Junta de Comunidades de Castilla - La Mancha, 2024). The only difference in our methods between studies is that whereas in the first study we measured all habitat variables in the field, in present study we used both Spanish Instituto Geográfico Nacional (Ministerio de Transportes y Movilidad Sostenible, 2024) and the Corine Land Cover (CLC; European Environment Agency, 2000, 2019) 2000 and 2012 databases to calculate habitat variables for both periods. Specifically, we used those databases to measure the distance between each roadkill and relevant landscape features (e.g. human infrastructures, water courses dry crops, irrigated crops, forest, etc.). As we used two different time periods, we used the 2000 CLC database for the "first" period (2002-2004) and the 2012 CLC database for the "second" period (2014-2016) (see Russo *et al.*, 2020 for a similar approach). The large-scale landscape variables were calculated using the `sf` (Simple Features) package for R (Pebesma, 2018; R Core Team, 2022).

Table 3: Roadside and landscape variables summary. Roadside variables were measured on the field in a radius of 50 m from the roadside on either side of the road. Traffic data was obtained from the local government website. Landscape variables (distances to) were measured using R (sf package) and both the Spanish Instituto Geográfico Nacional and the Corine Land Cover databases.



Variable	Mean	Min	Max
Number of burrows	12.72	0.00	112.00
Traffic volume (vehicles/day)	2877.78	197.00	12205.00
Road width (m)	9.50	4.80	16.80
Meters of embankemt (km)	17.12	0.00	200.00
Meters of bridge (m)	0.61	0.00	40.00
Speed limit (km/h)	92.24	30.00	100.00
Distance to the nearest water course (km)	0.42	0.00	2.47
Distance to the nearest human infraestructure (km)	0.22	0.00	1.21
Distance to the nearest urban area (CLC; km)	2.17	0.00	7.59
Distance to the nearest artificial area (CLC; km)	1.97	0.00	7.57
Distance to the nearest dry crop (CLC; km)	0.29	0.00	3.14
Distance to the nearest irrigated crop (CLC; km)	4.71	0.00	16.33
Distance to the nearest woody crop (CLC; km)	1.09	0.00	5.66
Distance to the nearest heterogeneous agricultural areas (CLC; km)	0.84	0.00	6.20
Distance to the nearest forest (CLC; km)	3.46	0.00	9.81
Distance to the nearest scrubland (CLC; km)	2.61	0.00	10.97

(b) Data analyses

Continuous explanatory variables were scaled using the `scale` function from the R base package. We created a dummy linear model with our explanatory variables and used the `vif` function from the car package (Fox and Weisberg, 2019) to calculate their variance inflation factors (VIF). With that information, we eliminated those variables with VIF values above 2.5, to minimize multicollinearity (Johnston *et al.*, 2018). We fitted a saturated generalized additive model (GAM) with a binomial distribution to investigate the relationship between our response variable (presence/absence of roadkill) and our explanatory variables. GAMs were constructed using the `mgcv` package in R (Wood, 2017). For model selection, we created a saturated model and a series of models that combined variables related to road characteristics, landscape and rabbit abundance. Then we compared them using a corrected Akaike Information Criterion (AICc) and selected the model that offered the lowest value of AIC (Wood, 2017; Table S1). We determined that the number of rabbit burrows may have heterogeneous effects on roadkill presence between periods and that there may be spatial autocorrelation in our data (Figure S2). Furthermore, we also hypothesise that the abundance of rabbits has non-linear relationships with polecat roadkill probability. The assumption of linearity was then relaxed, and binomial generalized additive models (GAMs) were utilized to detect potential non-linearities in associations between the *number of rabbit burrows* and polecat roadkill probability. The *number of rabbit burrows* included in the GAMs was smoothed using thin plate regression splines, as they offer a solution to the challenges associated with knot placement and have lower mean squared errors compared to knot-based splines in a pure regression context (Wood, 2003). We include an interaction between the smoothed *number of rabbit burrows* and the factor of two levels depending on when the survey was done (first and second). As GAM models allowed to do so, for the rest of the selected variables we tested whether the smoothed term was significant over a linear model, which led us to replace non-significant smooths with linear terms on all variables besides *number of rabbit burrows* to prevent over-fitting to the data. To control for spatial autocorrelation, we included Gaussian process spatial smooths using geographical coordinates of grid cells, allowing them to interact with the factor of two levels depending on when the survey was done (first and second). We also included spatial autocorrelation in the model as a spatial process as a tensor product between a two-dimensional smooth term (lat-long). We utilized maximum likelihood (ML) for smoothing parameter selection. Therefore, our final model looked like this:

Roadkill probability ~ s(n burrows, by= first/second) + first/second + traffic + speed limit + road width +
m embankment + m bridge + distance to human + distance urban +
distance to irrigated crops + distance to scrubland +s(longitude ,latitude, by= first/second)

Diagnostics were performed using residual plots and tests on the deviance residuals. In particular, we look at quantile-quantile plots and residual versus fitted values plots to see if there are any patterns unexplained by the model. We also check the autocorrelation in the residuals using the again function mgcv package in R (Figure S2). All the analyses described were performed in R (ver R-4.4.1; R Core Team, 2022).

3. Results

We recorded 195 polecat roadkills, 107 (in 85 locations) during the 2002-2004 period and 88 (in 82 locations) during the 2014-2016 period. While revisiting the roadkill locations form the “first” period, we only found polecat roadkills in 3 of those. Whereas the main polecat hotspots during 2002-2004 period appeared in roads CM-4013, CM-401 and CM-4102, during 2014-2016 hotspots were concentrated in CM-4000, CM-401 (but further west) and CM-4011 (Figure 1).

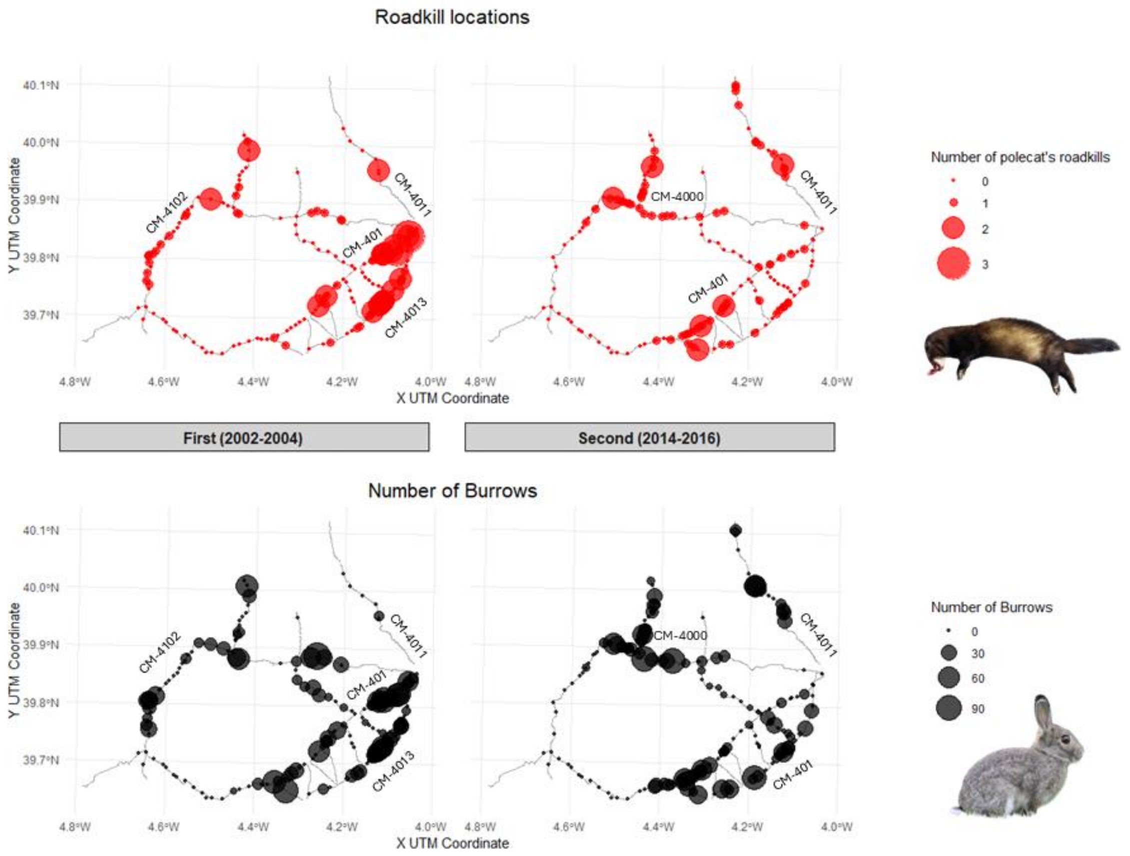
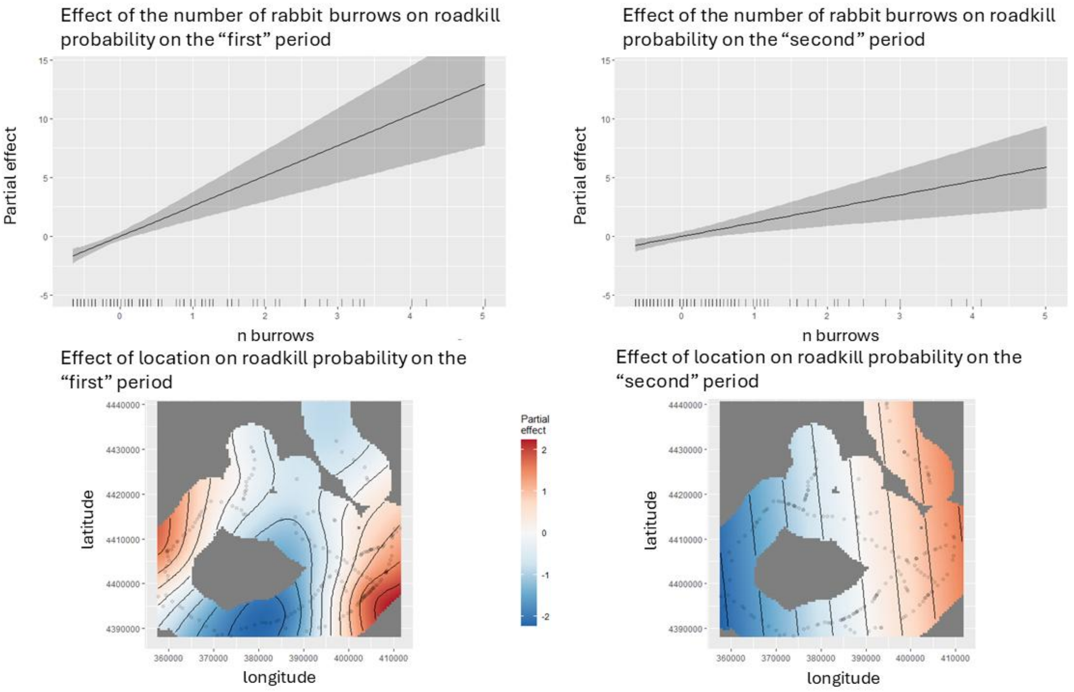


Figure 7: Distribution of polecat roadkills and number of rabbit burrows at random points in the "first" and the "second" periods.

The number of rabbit burrows close to the road has a positive effect on roadkill probability, although its effect is stronger in the “first” period than in the in the “second” period (Table 2; Figure 2). Our model describes a positive relation between polecat roadkill probability and speed limit. Increasing distance to irrigated crops has a negative effect on roadkill probability (i.e., irrigated crops abundance increases roadkill probability), while increasing distance to scrubland has the opposite effect (Table 2). Moreover, our model shows that there was a significant clustering of polecat’s roadkill locations; it is significant during the “first” period, but not significant during the “second” period (Table 2; Figure 2).



Effect of the number of rabbit burrows on roadkill probability on the "first" period

Effect of the number of rabbit burrows on roadkill probability on the "second" period

Effect of location on roadkill probability on the "first" period

Effect of location on roadkill probability on the "second" period

Figure 8: Plots of the partial effect of the variables with different effect in the first and second period: Number of rabbit burrows and Coordinates

Table 2. Results of the gam model that describes polecat roadkill probability. Estimates, Confident interval and p-values are shown. Number of rabbit burrows and X and Y coordinates have separate effects for each time period; "first" and "second".

	Polecat roadkill probability		
Predictors	*Log-Odds*	*CI*	*p*
Intercept	-0.61	-1.28 – 0.06	0.075
First/Second	0.49	-0.36 – 1.34	0.261
Traffic	0.33	-0.12 – 0.78	0.148
Speed Limit	0.69	0.23 – 1.15	**0.003**
Road Width	0.44	-0.01 – 0.89	0.056
Meters of Embankment	0.02	-0.32 – 0.36	0.911
Meters of Bridge	-0.13	-0.45 – 0.20	0.452
Distance to Human infrastructure	0.04	-0.30 – 0.39	0.802
Distance to Urban areas	0.12	-0.26 – 0.50	0.531
Distance to Irrigated Crops	-0.60	-1.09 – -0.12	**0.014**
Distance to Scrubland	0.47	0.11 – 0.84	**0.011**
Smooth: n rabbit burrows - First/Second: First			**<0.001**
Smooth: n rabbit burrows - First/Second: Second			**0.001**
Smooth: longitude, latitude - First/Second: First			**0.036**
Smooth: longitude, latitude - First/Second: Second			0.712
Observations	375		
R^2	0.477		

4. Discussion

We replicated the roadkill survey conducted by Barrientos and Bolonio (2009) and found that polecat roadkill hotspots shifted significantly between 2002 and 2014, highlighted by the fact that only 3.5% of the “first” period hotspots happened in the “second” period, indicating low temporal repeatability (Figure 1). However, when examining the underlying mechanisms driving polecat roadkill over time, the survey period itself was not significant. Instead, changes in rabbit abundance and speed limits between 2002 and 2014 emerged as the primary factors influencing the spatiotemporal shifts in polecat roadkill hotspots (Table 2). This change in the distribution of polecat roadkills (Figure 1) highlights the need for longitudinal studies to understand wildlife road mortality better. Without such studies, implementing effective mitigation measures is challenging, as actions may quickly become obsolete or inadequate over time.

One of the main reasons for this shift in hotspot locations seems to be the temporal-spatial changes in the abundance of rabbits breeding in the road embankments (Figure 1), as previous studies identified this variable as the most influential for polecat roadkills (Barrientos and Bolonio, 2009; Barrientos and Miranda, 2012; Carmona *et al.*, 2024). Rabbits have been identified as the polecat’s main prey in Mediterranean regions (Santos *et al.*, 2009), making up to 87% of polecat’s consumed biomass. In this sense, the abundance of feeding resources probably leads polecats to repeatedly visit road margins, where these lagomorphs concentrate their burrows, which ends with the predator’s roadkill. We found a stronger relationship between the probability of a polecat roadkill event and the number of rabbits in 2002-2004. Although we acknowledge that our monitoring is not the best approach to census alive polecats, road mortality is usually related to the abundance of the species in the road surroundings (Burgstahler *et al.*, 2023; Fernández-López *et al.*, 2022). Since we recorded 12% less roadkilled polecats during

2014-2016, and road mortality is usually related to the abundance of the species in the road surroundings (Burgstahler *et al.*, 2023; Fernández-López *et al.*, 2022), it is possible that the relationship with rabbit abundance in road embankments was less pronounced just because there were fewer polecats in this period. Whatever the intensity of this relationship in the future, it does not seem risky to predict that rabbit abundance will mark the points where its predator has more probability to be roadkilled. This makes the implementation of mitigation measures a tremendously complex task, as rabbit densities are highly variable at mid-term due to disease cycles such as myxomatosis or haemorrhagic disease virus, as well as to game management (Delibes-Mateos *et al.*, 2008; Delibes-Mateos *et al.*, 2009).

In concordance with previous studies in road ecology, speed limit was correlated with polecat roadkill probability. This variable increases in first class roads, which jeopardizes safe crossings for polecats. Usually, this variable effect decreases at higher values, likely because it deters animal from attempting to cross, decreasing the roadkill probability again (Russo *et al.*, 2020; Seiler, 2005). However, in our study area, speed limit upper ceiling was limited by the roads it includes, masking the drop off expected in this effect at higher vehicle speeds. Roadkill patterns depend on the individual response towards oncoming cars, and polecats can be classified as "speeders" (as described in (Jacobson *et al.*, 2016). This category represents animals that avoid roadkill by running, but it is only effective when traffic volume or vehicle speed is low.

Relative abundance of irrigated crops and scrubland near roadkill locations have opposite effect, as the first one increased roadkill probability while the latter decreased it. This could be a matter of space availability for rabbits to dig their burrows, where polecats hunt them. When highly mechanized, intensive irrigated crops (e.g., corn, rapeseed, alfalfa) are close to the road, the surface available for rabbit burrows is constrained to the plot borders, that commonly coincide with the side of the road. On the contrary, scrublands offer a land use where rabbits can dig their burrows (often under granite boulders) everywhere, alleviating the risk of roadkill for polecats when the visit them.

Finally, we show a temporal change in the spatial clustering of roadkill locations, but the effect differed between periods, as it was clustered in the “first” and more diluted in the “second” (Figure 2). This pattern is similar to that of the relative abundance of rabbit has on polecat roadkill probability. This change between periods suggests that spatial clustering of roadkills occurs in different places between survey periods, probably associated with changes in the landscape characteristics or food resource availability. Our results highlight the importance of continued monitoring of factors related to roadkill probabilities.

We must acknowledge that our work has some limitations. First, we did not follow a fixed route for searching for carcasses, which may have created certain biases. Also, our biweekly schedule is less frequent than that recommended for carcasses of similar size. For both limitations we think that repeating exactly the same sampling scheme may have minimized them. Nevertheless, we recognize that as important ecological variables for roadkills (rabbit abundance, land uses) change over time and space, the density of scavengers may also have done so. Data wise, we think a finer scale timing (i.e., three or four periods instead of two) and landscape abundance data for both the roadkilled species and their prey, could improve our ability to describe the factors behind roadkill hotspots. Although polecat roadkills are usually the only viable option to monitor this cryptic species in Mediterranean habitats, we understand that our study depicts a “narrow” image focus on the road.

5. Conclusions

Roadkill patterns are dynamic both in space and time, so rather than to simply geo-reference roadkill hotspots, we need to know both ecological and road-related factors that determine their appearing. This also means implementing continuous monitoring of those factors and moving into a dynamic approach for applying mitigation measures. Improving cost-effectiveness of mitigation actions is essential, as funding is limited and these measures tend to be expensive. For polecats, roadkill risk is related to speed limit, distance to irrigated crops and scrubland, which are fairly static factors, whose effects need to be restudied if these factors change (i.e., road retrofitting or land use changes). Monitoring rabbit abundance, on the contrary, is quite challenging due to the fluctuating nature of this variable. However, it is a key factor in polecat roadkill probability, therefore it is worth doing it. In parallel, as a mitigation action we suggest fencing those embankments in rabbit-rich landscapes that can be colonized by this lagomorph, providing rabbits with alternative emplacements for their burrows away from roads (e.g., in scrubland-dominated landscapes).

6. Acknowledgements.

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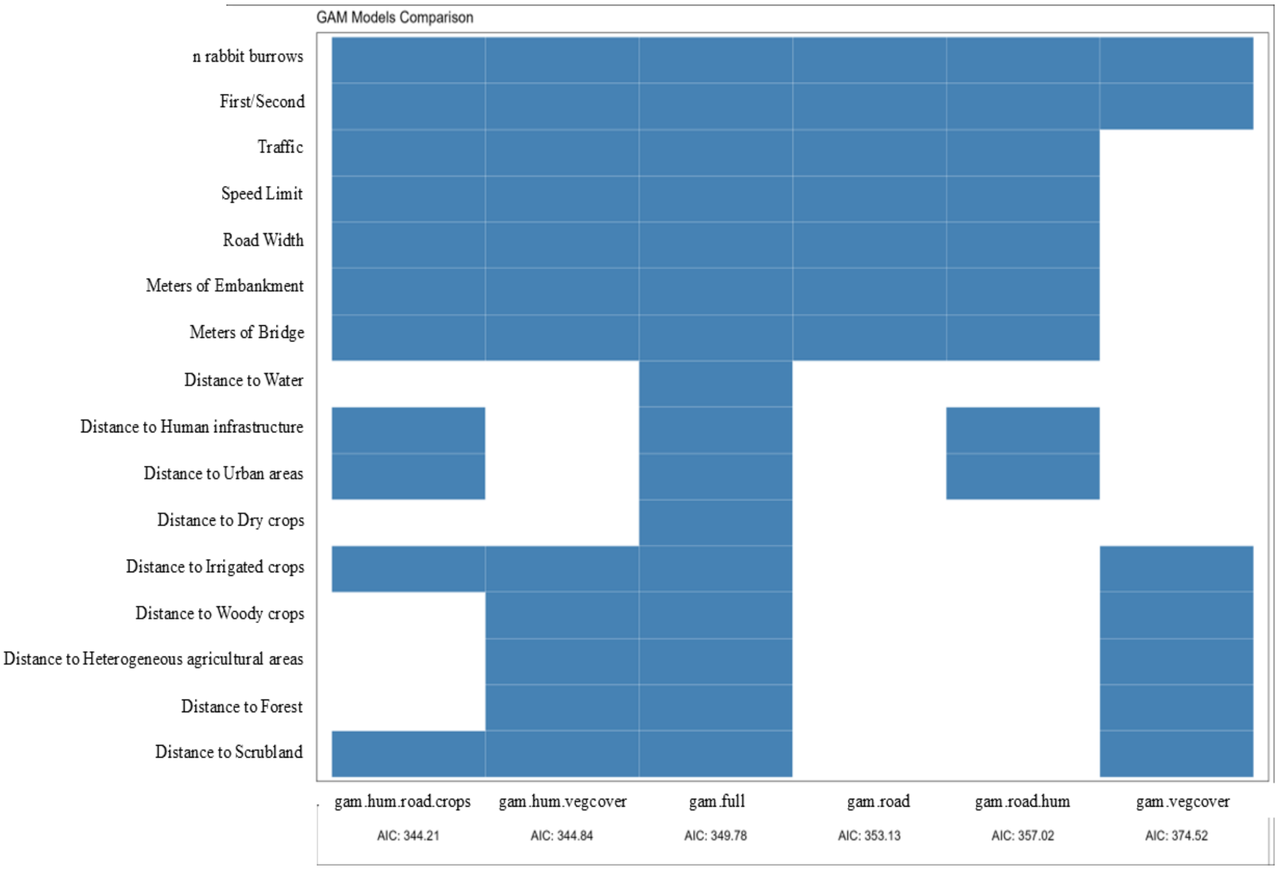
7. Authors contributions.

P. Q.: conceptualisation, methodology, software, formal analysis, investigation, writing – original draft and visualisation. G. F.: software, formal analysis. R. B.: conceptualisation, fieldwork, methodology, investigation, resources, writing – original draft, writing – review and editing, supervision, project administration and funding acquisition.

8. Supplementary material.

Table S1: Explanatory variables selection process by AIC, different hypothesis represented by different models and their AIC values are shown.



GAM Models Comparison

	gam.hum.road.crops AIC: 344.21	gam.hum.vegcover AIC: 344.84	gam.full AIC: 349.78	gam.road AIC: 353.13	gam.road.hum AIC: 357.02	gam.vegcover AIC: 374.52
n rabbit burrows	■	■	■	■	■	■
First/Second	■	■	■	■	■	■
Traffic	■	■	■	■	■	
Speed Limit	■	■	■	■	■	
Road Width	■	■	■	■	■	
Meters of Embankment	■	■	■	■	■	
Meters of Bridge	■	■	■	■	■	
Distance to Water			■			
Distance to Human infrastructure	■		■		■	
Distance to Urban areas	■		■		■	
Distance to Dry crops			■			
Distance to Irrigated crops	■	■	■			■
Distance to Woody crops		■	■			■
Distance to Heterogeneous agricultural areas		■	■			■
Distance to Forest		■	■			■
Distance to Scrubland	■	■	■			■

Figure S1: Variogram. X axis: distance between pair of locations. Y axis: semivariance; half the average squared difference between values at pairs of locations.

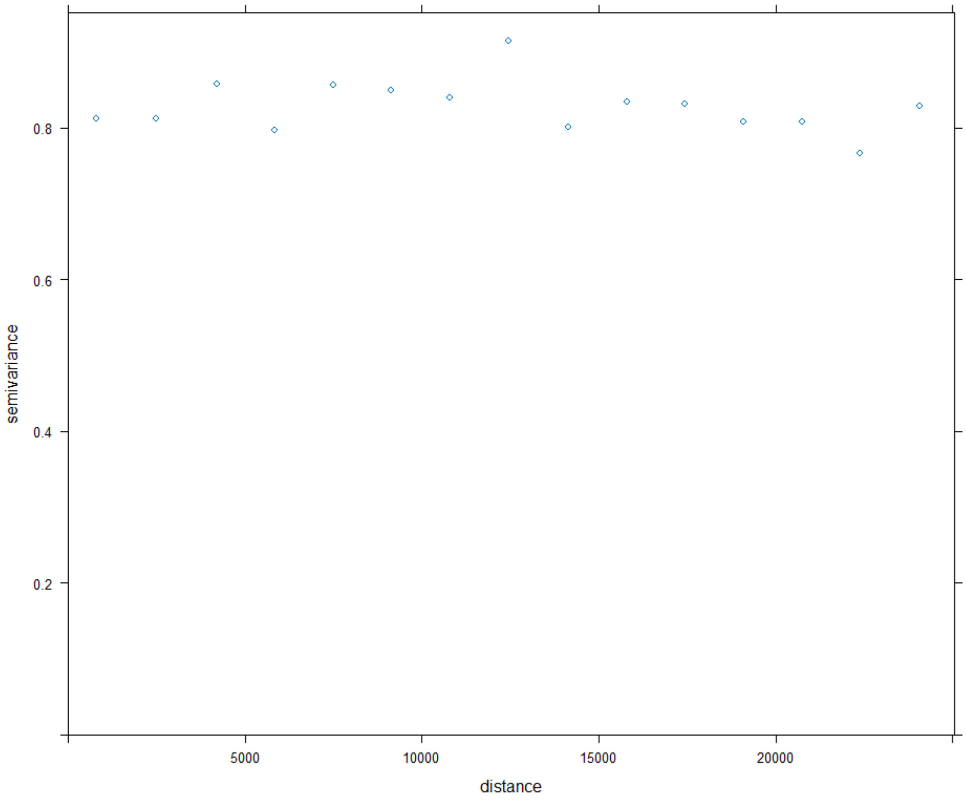
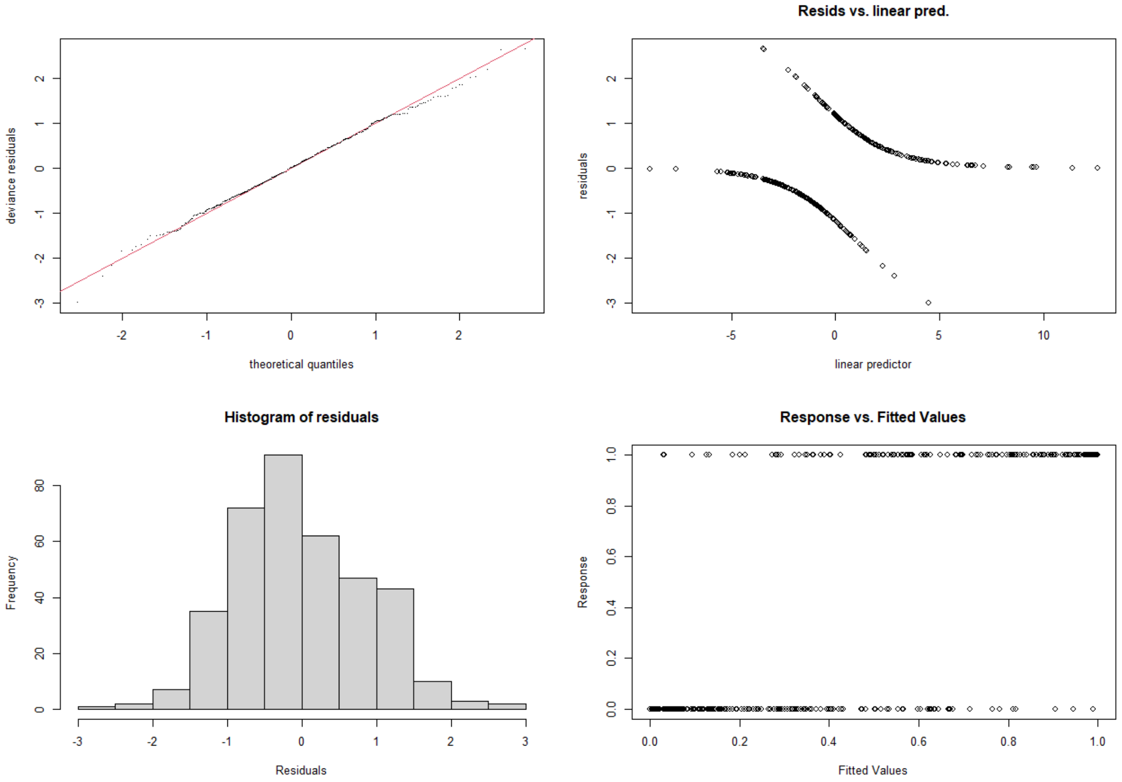


Figure S2: Plots used for gam model validation



Chapter 4: Human encroachment shapes the diversity patterns of a carnivore guild in a Mediterranean agrosystem

Abstract

As human development continues so do agricultural and urban expansion, industrialization, and their associated infrastructure. This development leads to human encroachment in natural habitats, threatening biodiversity conservation, which is an effect that has been especially sound in the Mediterranean basin. Despite human pressures, mesocarnivores persist in these habitats, maintaining vital roles in ecosystem dynamics. Therefore, this study focuses on understanding how human encroachment, prey abundance, vegetation cover, and agricultural activities affect the mesocarnivore community in the centre of the Iberian Peninsula. To test this, we conducted for three years an extensive trail camera survey covering half of the Toledo province and used it to fit state-of-the-art, spatial multispecies occupancy models. Despite European rabbits being a key prey for the carnivore community in the area, high rabbit abundance had a general negative effect on the community occurrence, likely due to intensive predator control practices in areas with high small-game hunting activities. However, our model described spatial variability in the effect of rabbit abundance, with positive effects on some localities. Despite their described adaptability, red foxes, Egyptian mongooses, and stone martens showed lower occurrence ratios around humanized areas while domestic cats were naturally present around human settlements. On this mostly deforested landscape, rivers and seasonal streams where positively related to the occurrence of Egyptian mongooses, genets, stone martens and badgers, as these species frequent riparian forests for food, water, and cooler temperatures. Road presence was positively related to the occurrence of domestic cats and polecats, with domestic cats linked to human settlements and polecats benefiting from rabbit burrows on road embankments. Finally, our model let us identify two groups of species based on co-occurrence probabilities: one group consisting of red foxes, stone martens, badgers, and genets, and another of domestic cats and polecats. These groups share the landscape probably through differences in trophic niches and activity patterns. The study highlights the complex interactions between carnivore species, prey abundance, human infrastructure, and habitat characteristics, emphasizing the need to consider spatial variability and species-specific responses in conservation efforts.

Key words:

mesocarnivores; camera trapping; occupancy models; predator–prey relationships; coexistence.

1. Introduction

Human development usually implies urban expansion, industrialization, land-use changes, overexploitation of animal resources (e.g., overhunting), and the growth of associated infrastructure. This development generates deep changes in ecosystems and is a primary driver of biodiversity loss (Visconti *et al.*, 2016). These human impacts emerge from complex socio-economic scenarios and alter ecosystem processes in complex and usually synergistic ways, such as land use changes and expansion of invasive species, or climate change and habitat degradation (Brook *et al.*, 2008; Didham *et al.*, 2007). So, understanding the future implications of these impacts is key to evaluate future trade-offs in conservation planning (Mace, 2010). As human population increases, the demand for food follows, with increasing consequences for biodiversity (Cozim-Melges *et al.*, 2024). Consequently, global changes in agricultural production have been described as the main driver of biodiversity loss (Campbell *et al.*, 2017), through intensification of its practices and the substitution of natural habitats by agricultural fields (Maxwell *et al.*, 2016). In the last decades, the Mediterranean basin has been one of the areas that has most suffered this intensification of agriculture (Sokos *et al.*, 2013), what has driven significant modifications in the structure and organisation of its ecosystems (Peñuelas *et al.*, 2017), and habitat losses for several wildlife species (Intergovernmental Panel On Climate Change, 2023; Valladares, 2007). Agricultural intensification in the Mediterranean region has led to the unification of small agricultural plots into large monocultures where field margins are destroyed. The resulting homogeneous landscape that allows the use of heavy machinery for more efficient production at lower economic costs (Brotons *et al.*, 2004).

Agricultural intensification requires infrastructure development to provide water and electricity for crops as well as the transportation of goods to and from consumption centres, while decreasing production costs (Alamgir *et al.*, 2017; Laurance *et al.*, 2014). The development of motorways, railways, roads, and power lines, among other infrastructure directly result in habitat loss for wildlife (Biasotto and Kindel, 2018; Borda-de-Água *et al.*, 2017; van der Ree *et al.*, 2015). Traffic also causes wildlife-vehicle collisions and road-avoidance behaviours in response to vehicle noise, light or particle emissions (Auerbach *et al.*, 1997; Hintz and Relyea, 2019; McClure, 2021). Finally, among the indirect impacts of infrastructure (including dirty roads) development, is the access that they allow to the entire territory, fueling secondary uses of agrosystems like hunting (Martín-Delgado *et al.*, 2022; Sánchez-García *et al.*, 2021) and ending roadless areas that could serve as a refuge for wildlife.

Due to the great pressure exerted by humans, top predators are practically absent in these agrosystems. However, mesocarnivores (i.e., species below 15 kg) still have important populations in these habitats (Monterroso *et al.*, 2020). This guild is remarkably more diverse, and more behaviourally and ecologically versatile than large carnivores (Roemer *et al.*, 2009). Mesocarnivores are relatively abundant and play vital roles in ecosystem dynamics such as carcass removing, disease dynamics, carbon storage, seed dispersal, and crop production (Draper *et al.*, 2022; Ripple *et al.*, 2014). Moreover, due to their role in trophic webs, their absence can create trophic cascades that reverberate through lower trophic levels (Beschta and Ripple, 2009; Estes *et al.*, 2011).

While the mesocarnivore community enjoys less pressure from large carnivores in agricultural landscapes (i.e., mesopredator release hypothesis; Prugh and Sivy, 2020), still some risks remain. Agricultural lands occupy most of the landscape (Intergovernmental Panel On Climate Change, 2023; Valladares, 2007), leaving little room for original or even semi-natural habitats. In this agriculture-dominated matrix, uncultivated lands, scrublands, or even planted pinewoods and riparian forests are key to maintain some protection and allow the mobility of these mesocarnivores (Palomares, 2001; Virgós, 2001). Arguably as important for carnivore persistence is prey abundance, as predators tend to choose areas with high prey abundance (Rabelo *et al.*, 2019). In this sense, the European rabbit (*Oryctolagus cuniculus*) has been described as the key component of Mediterranean carnivores diet (Delibes-Mateos *et al.*, 2007; Monterroso *et al.*, 2020). However, their populations fluctuate frequently at a local scale, due to disease cycles, such as myxomatosis or haemorrhagic disease virus, as well as to game management (Delibes-Mateos *et al.*, 2008; Delibes-Mateos *et al.*, 2009). In this agricultural areas, small game hunting is a popular activity and an important economic motor for the local community. For this activity, landowners and hunting properties make use of non-selective techniques such as snare traps and poisons to target mesocarnivores, with the aim of reducing the pressure they may apply on small game species in Mediterranean habitats such as the European rabbit and the red-legged partridge (*Alectoris rufa*) (Delibes-Mateos *et al.*, 2013; Virgós and Travaini, 2005).

Regardless of the perturbation, the consequent fluctuations in carnivore populations and their behaviour can disrupt the delicate balance of interactions and coexistence strategies among predator species (Quiles and Barrientos, 2024). In this sense, temporal, spatial, and diet partitioning are the main mechanisms facilitating coexistence among carnivores (Ferreiro-Arias *et al.*, 2021; Monterroso *et al.*, 2020). Disruptions to this equilibrium can have far-reaching consequences for prey populations and broader ecosystem dynamics (Palomares and Caro, 1999). The Iberian Peninsula's unique biogeographical context, supporting a diverse carnivore community, underscores the significance of understanding these interactions (Rosalino *et al.*, 2023). In order to understand how Mediterranean mesocarnivores responds to human perturbations, habitat loss, predator control, and fluctuations of their main prey we need a good understanding of species- and community-level processes, as it is essential for their conservation (Jiménez *et al.*, 2017). However, the impacts those perturbations on animal communities are not well understood for most taxa, primarily due to limitations in available data (Breiner et al., 2015; Kindsvater et al., 2018), as it is the case for cryptic species such as many mesocarnivores (Boitani and Powell, 2012). As biodiversity continues to decline, it becomes increasingly important to assess entire communities rather than focusing solely on well-studied or charismatic species (Ahumada *et al.*, 2013; Jiménez *et al.*, 2017).

Traditionally, studies of richness patterns have often assumed that species are perfectly detected at sites where they are present. However, species detectability can vary in space, time, and among taxa (Guillera-Arroita *et al.*, 2014; Iknayan *et al.*, 2014). Multispecies occupancy modeling offers a flexible solution by estimating both community- and species-level relationships with environmental variables while accounting for imperfect detection (Devarajan *et al.*, 2020; Dorazio and Royle, 2005) even in situations where data for rare species is limited. However, this method also faces challenges, including spatial autocorrelation (Banerjee *et al.*, 2014; Latimer *et al.*, 2009) and residual species correlations (Ovaskainen *et al.*, 2010), which can complicate accurate modeling. Incorporating spatial dependencies among observations is key to producing valid inferences about species distributions; which has led to the development of spatial occupancy models (Johnson *et al.*, 2013), while failure to account for interspecific interactions between co-occurring species can lead to biased inferences, especially when only abiotic and habitat associations are considered (Rota *et al.*, 2016). Recent advancements in multispecies occupancy models that account for both species interactions and spatial autocorrelation offer improved insights into occurrence patterns, helping researchers understand community dynamics across a range of spatial scales from local to continental (Doser *et al.*, 2023; Tobler *et al.*, 2019). Additionally, species-environment relationships may vary as a result of abiotic (e.g., historical disturbance regimes) and biotic processes (i.e., density-dependent habitat selection) interacting at multiple spatial scales (Rollinson *et al.*, 2021; Thorson *et al.*, 2023). Therefore, some studies may require the modeling to be flexible and account for the spatial variation in the effects the explanatory variables can have (i.e., spatially varying coefficient models (see Doser *et al.*, 2024).

As human population demands increase, and with it the rate of global change, the challenge is how to accommodate this human growth while maintaining biodiversity in agrosystems (Cozim-Melges *et al.*, 2024). In particular, we need to find ways to preserve the minimum requirements carnivore species need to exist in humanized habitats, as their complete disappearing could have major consequences (Estes *et al.*, 2011). For these reasons, we aimed to describe the distribution of the carnivore community as well as to understand the effects of prey abundance, human infrastructure, vegetation cover, and agrosystem activities on their occupancy probability. We argue that the use of multi-species occupancy models will provide both species-level and community-level assessments, ultimately yielding a more holistic approach to understanding the impact of agricultural lands and developing conservation actions. We expect higher occupancy probabilities of the community in areas where natural vegetation cover is still present, road infrastructure presence is low, and prey abundance is high. Although we expect this scenario to benefit all species, the ones more sensitive to human impact would select remnants of natural habitats (Virgós, 2001), while the ones more adapted to human presence would be present all around or even select human infrastructures (i.e., roads and human settlements) to exploit resources they provide (Barrientos and Bolonio, 2009; Recio *et al.*, 2015).

2. Material and methods

2.1 Study area and study species

We surveyed 41 10x10 km UTM squares, ranging from 40.28º to 39.66º in latitude and from -4.74º to -3.83º in longitude in the Spanish province of Toledo (i.e., some 4,500 km^2 sampled; see Figure 1). The altitude ranges 365-1,063 m. a. s. l., and the climate is Mediterranean with average daily maximum temperatures ranging between 36.7°C (August) and 11.6°C (January), with 350mm of average annual rainfall (data from easyclimate package (Cruz-Alonso *et al.*, 2023; Moreno and Hasenauer, 2016; Pucher, 2023; Pucher and Neumann, 2022). This area is dominated by Mediterranean croplands, namely 78% according to Corine Land Cover 2018 level 1 (European Environment Agency, 2019), followed by forests and semi natural areas (18%) and artificial surfaces (4%). In turn, these croplands are composed by arable lands (64%), heterogeneous agricultural areas (20%) and permanent crops (16%) in level 2. Non-cultivated areas are dominated by shrubs and/or herbaceous vegetation (69%). Forests (31%) only thrive around major rivers, in areas unsuitable for agriculture like hilly areas where some remnants of Mediterranean forests survive and in scattered pine plantations embedded in the agricultural matrix. Secondary roads are the most common road infrastructure in the area, with densities ranging from 0 km to 7.46 km per km^2 (mean = 0.46). Areas dedicated to small hunting very common in our study area, with 95% of our cameras embedded in some short of small hunting estate.

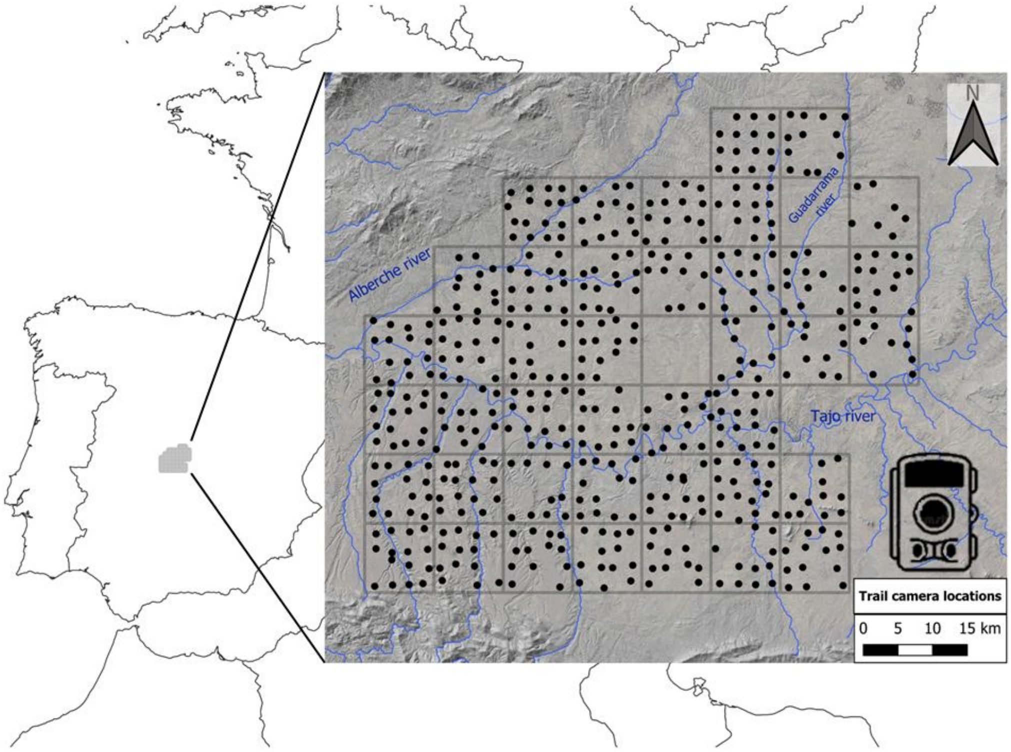


Figure 9: Study area and camera locations during the surveyed UTMs.

Our study area hosts the whole community of medium-sized carnivore species present in Mediterranean habitats from the Iberian Peninsula (e.g., Grilo *et al.*, 2009; Soto and Palomares, 2015). This guild is composed by eight species, four being mustelids (European badger *Meles meles*, Eurasian otter *Lutra lutra,* Stone marten *Martes foina* and European polecat *Mustela putorius*), one herpestid (Egyptian mongoose *Herpestes ichneumon),* one viverrid (small-spotted *genet Genetta genetta),* two felids (European wildcat *Felis silvestris* and domestic cat *F. catus*), and one canid (red fox *Vulpes vulpes*). The Iberian lynx (*Lynx pardinus*) is being reintroduced in the area, but it is still scarce (recorded in 3% of our cameras), and even more rare (it was not recorded by our cameras) is the Iberian wolf (*Canis lupus*), which is experiencing a natural expansion from the north.

2.2 Trail camera methodology

We sampled the carnivore community during autumn of 2020, 2021 and 2022 and during spring go 2021, 2022 and 2023. We selected these two seasons because the abundance of carnivores is stable between spring and autumn in our region (Ferreras *et al.*, 2017; Jiménez *et al.*, 2017). Each season was then divided into 3 camera traps deployments, where our 48 cameras covered 3 UTMs at the same time. After sampling, the cameras were moved to the next 3 UTMs. In this way each UTMs was only surveyed once in our 4-years study. It is important to note that although we aimed to survey 45 UTMs squares we missed 4 of them as several issues (too many cameras failed or were stolen) avoided us to representatively sampling these squares.

We employed 16 cameras per UTM that worked day and night for 21 days, a period long enough to record all the carnivores present in areas like ours (Ferreras *et al.*, 2017; Jiménez *et al.*, 2017). We tried to place the 16 cameras 2.5 km away from each other to sample all habitats according to their availability and to cover all carnivores' territories regardless of the species. Nonetheless, final distances between cameras ranged from 0.46 to 5.03 km (mean= 2.13 km) since sometimes it was difficult to find suitable locations for all of them and in others some cameras were missing because did not work or were stolen. We checked each camera around the 10-day to replace batteries and SD card and attractant. Three camera traps models were used: Browning-Command OPS Pro 14MP, Browning-Dark OPS HD Max Plus and Moultrie-A300i. All have high picture resolution (12 Megapixels or more), a Passive Infra-Red (PIR) detector that triggers the camera based on heat and movement, and no-glow infra-red flash for night photos, that does not disturb nocturnal animals. All cameras were programmed in the most sensitive sensor setting, to take a 3-photo burst when triggered (day or night) and with a 15 sec delay between bursts to preserve space in the SD cards. We placed the cameras on trees, around

0.3-1.2 m above the ground. We used urine from Iberian lynx as attractant, as it has been proved as one of the most effective and generalist attractants for mesocarnivores (Monterroso *et al.*, 2011). The urine was poured into a piece of cotton and secured under a rock 2 meters away from the camera.

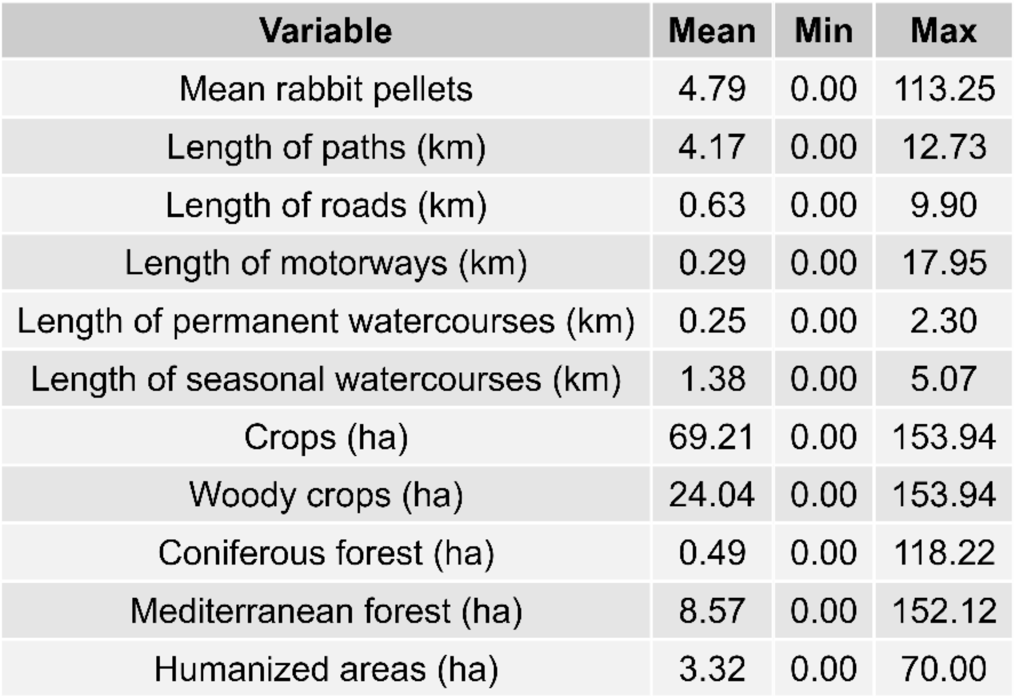
2.3 Images processing

As we successfully recovered 523 cameras, we obtained around 2.5 million images to review. We opted for MegaDetector (Beery *et al.*, 2019) which reduced the images needed to review by 80%. MegaDetector uses a two-stage process known as a Faster Region-based Convolutional Neural Network, which firstly searches and marks areas in the image different from the background, and secondly the model examines and assigns a classification to each object, along with a confidence value reflecting the model's certainty in the assigned class. MegaDetector has been trained on hundreds of thousands of images, which were manually reviewed and labelled by a human reviewer. It classifies objects into three categories: animal (any non-human animal), human (any person), or vehicle. With our pool of filtered images, we proceeded to identify the species that appeared on them. We used the software XnView, which allowed us to insert categorical information in the images metadata (e.g. camera ID, species, etc). Afterwards we extracted the metadata of each tagged image using R (R Core Team, 2022) in combination with ExifTool and obtained a database with all animal detections from our study, including species identification.

2.4 Habitat variables

During the mid-sampling visit to the cameras, we surveyed rabbit abundance by counting rabbit pellets in four 1x1m squares in the four cardinal points at 5 meters from the camera (Palomares, 2001). To evaluate the effects of infrastructure, humanized areas and land uses on species occupancy, and their interspecific co-occurrence, we extracted information about these variables in a buffer of 700 m around each camera location (Table 1). We selected this radius to reduce overlaps between contiguous cameras while also covering the known home range of our study species (Mata *et al.*, 2017; Ruiz-Capillas *et al.*, 2021; Soto and Palomares, 2015). We extracted the length of roads, motorways, railways, and transmission (high voltage) powerlines in our buffer, as well as length of permanent and seasonal water courses, using data Spanish Instituto Geográfico Nacional (Ministerio de Transportes y Movilidad Sostenible, 2024). We also extracted traffic data from roads, namely average daily traffic flow, publicly available in the Toledo province government website. To describe the landscape around each camera, we used data from Corine Land Cover 2018 (European Environment Agency, 2019) and extracted the surface corresponding to the different categories of land use at level 2 (see Table 1 for description and mean values) but with a couple of modifications. We divided forest into coniferous forest and oak forest, and combined together urban, industrial, mines, and parks into humanized areas.

Table 4: Mean and range of the variables used in the model.



Variable	Mean	Min	Max
Mean rabbit pellets	4.79	0.00	113.25
Length of paths (km)	4.17	0.00	12.73
Length of roads (km)	0.63	0.00	9.90
Length of motorways (km)	0.29	0.00	17.95
Length of permanent watercourses (km)	0.25	0.00	2.30
Length of seasonal watercourses (km)	1.38	0.00	5.07
Crops (ha)	69.21	0.00	153.94
Woody crops (ha)	24.04	0.00	153.94
Coniferous forest (ha)	0.49	0.00	118.22
Mediterranean forest (ha)	8.57	0.00	152.12
Humanized areas (ha)	3.32	0.00	70.00

2.4 Data analysis

We used R version 4.4.1 (R Core Team, 2022) and the R package spOccupancy (Doser *et al.*, 2022) that allows the creation of various types of occupancy models based on detection-nondetection data. We formatted our trail camera data into detection-nondetection data matrices that captured this information as “0” or “1” for the presence or absence of each species in three-day intervals for each location. Therefore, a species was recorded with as a “1”, independently of how many images we recorded in that three-days interval. The whole dataset was built from species-specific matrixes composed by 523 locations and 7 intervals (21 days divided in 3 days intervals). Species that appeared in less than 5% of our locations were excluded from the analysis (i.e., Iberian lynx, European wildcat and Eurasian otter). In these multispecies models, community parameters use as response variable the summatory of the individual species occurrence probability in each location. In particular, spOccupancy models use a Bayesian framework using Pólya-Gamma data augmentation that allows for faster convergence and the use of spatial explicit models in large datasets like ours.

To assess whether or not we needed to account for imperfect detection, spatial autocorrelation, residual species correlations, and/or spatially varying coefficients we fitted four alternative models; a non-spatial multi-species occupancy model (msPGOcc), a spatial, multi-species occupancy model (spMsPGOcc), a latent factor multi-species occupancy model (lfMsPGOcc), and a spatially varying coefficient multi-species occupancy model (svcMsPGOcc). We then used the function waicOcc from the spOccupancy package to assess model fit, which applies the Widely Applicable Information Criterion (WAIC; see table 2) (Gelman *et al.*, 2014). Then, we used the svcMsPGOcc function, that also allowed us to account for imperfect detection, spatial autocorrelation, residual species correlation, and assign rabbit abundance as a spatially varying factor (Doser *et al.*, 2024).

Table 5: Different spOccupancy models and their Widely Applicable Information Criterion values, that allowed us to select the Spatially varying coefficient multi-species occupancy model.

Model type	Expected log pointwise predictive density (elpd)	Effective number of parameters (pD)	Widely Applicable Information Criterion (WAIC)	Δ WAIC
Non-spatial multi-species occupancy model (msPGOcc)	-5745,8844	108,8991	11709,5670	
Spatial multi-species occupancy model (spMsPGOcc)	-5276,9349	520,7865	11595,4428	114
Latent factor multi-species occupancy model (lfMsPGOcc)	-5284,1610	475,2368	11518,7955	77
Spatially varying coefficient multi-species occupancy model (svcMsPGOcc)	-5146,4286	549,9217	11392,7006	126

From our initial variables we discarded length of railway and high voltage powerlines due to their low representativeness. We also excluded average daily traffic flow as it was highly correlated with length of both roads and motorways. Finally, we tried simplifying our saturated model comparing it with gradually less complex models using WAIC. However, none of the simpler models were better than the saturated one. In our final model we included rabbit abundance, length of paths, roads, motorways, permanent water courses, seasonal water courses, surface of crops, woody crops, coniferous forests, Mediterranean forests, and humanized areas of as factors that may modulate occupancy patterns for the whole community (Table 1). We included the abundance of rabbits as a possible spatially varying coefficient, as we hypothesized that its influence could spatially vary depending on land management practices (especially those related to hunting). To account for imperfect detection, we included relative vegetation cover around the cameras (as a factor with 4 levels) and the time between each contact and the day the lure was placed or replenished (Ferreras *et al.*, 2018; Tourani *et al.*, 2020). We tweaked both initial values and priors to achieve better convergence, however finally we used the default values besides the latent species-specific occurrence for which we included the presence/absence matrix for each location. Finally, we used the function pccOcc from the spOccupancy package to perform posterior predictive check an ensure good fit of our final model.

3. Results

3.1. Results overview

Our fieldwork resulted in 8,863 trap-days in which we recorded 46,055 carnivore pictures. Our survey detected foxes in 69% of our locations, Egyptian mongooses in 46% of our locations, domestic cats in 24% of our locations, genets in 18% of our locations, stone martens in 14% of our locations, badgers in 11% of our locations, polecats in 6% of our locations, Iberian lynxes in 3% of our locations, European wildcats in 3% of our locations and European otters in 2% of our locations. The best model for our analysis was the spatially varying coefficient multi-species occupancy model, which accounted for imperfect detection, spatial autocorrelation, residual species correlation and assigned rabbit abundance as a spatially varying factor.

3.2. Community level response

All this information allowed us to create a model that describes the variables explaining the occurrence of the carnivore community as a whole. The model showed how abundance of rabbits had a negative effect on the occupancy probability of the carnivore community (Figure 2). However, although mostly negative, rabbit abundance effect varied spatially, with some locations where the effect was positive (Figure 3). As our model is spatial explicit, it also describes a strong spatial effect of the overall response of the community, with clusters of increased occupancy probability around main rivers and in the West and Southwest of our study area (Figure 4).

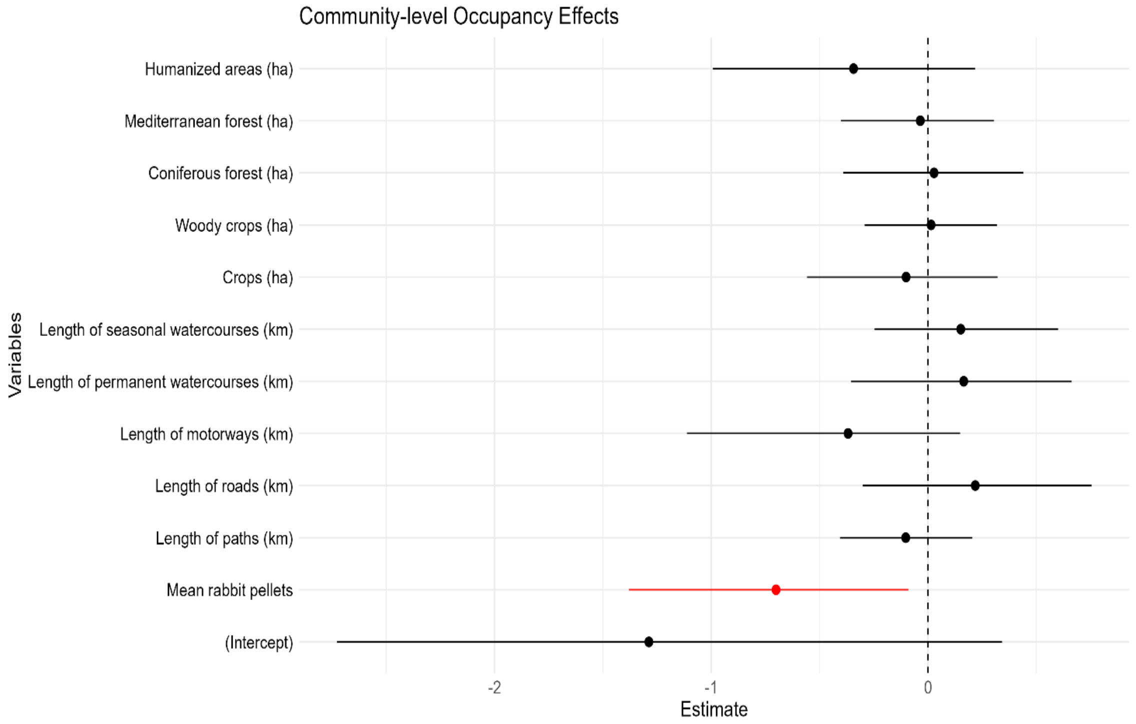


Figure 10: Community-level Occupancy Effects. Red lines show the significant variables (those which do not cross the 0 mark).

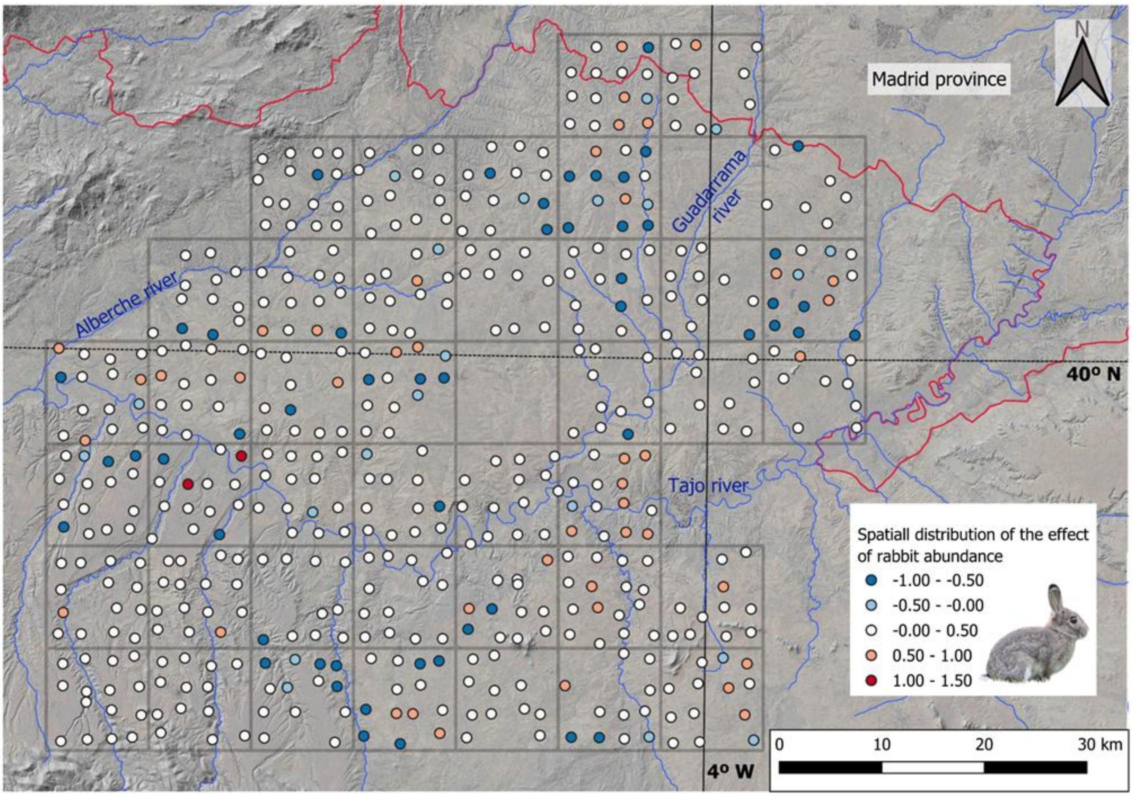


Figure 11: Distribution, size and direction of the effect relative rabbit abundance on carnivore community occupancy probability.

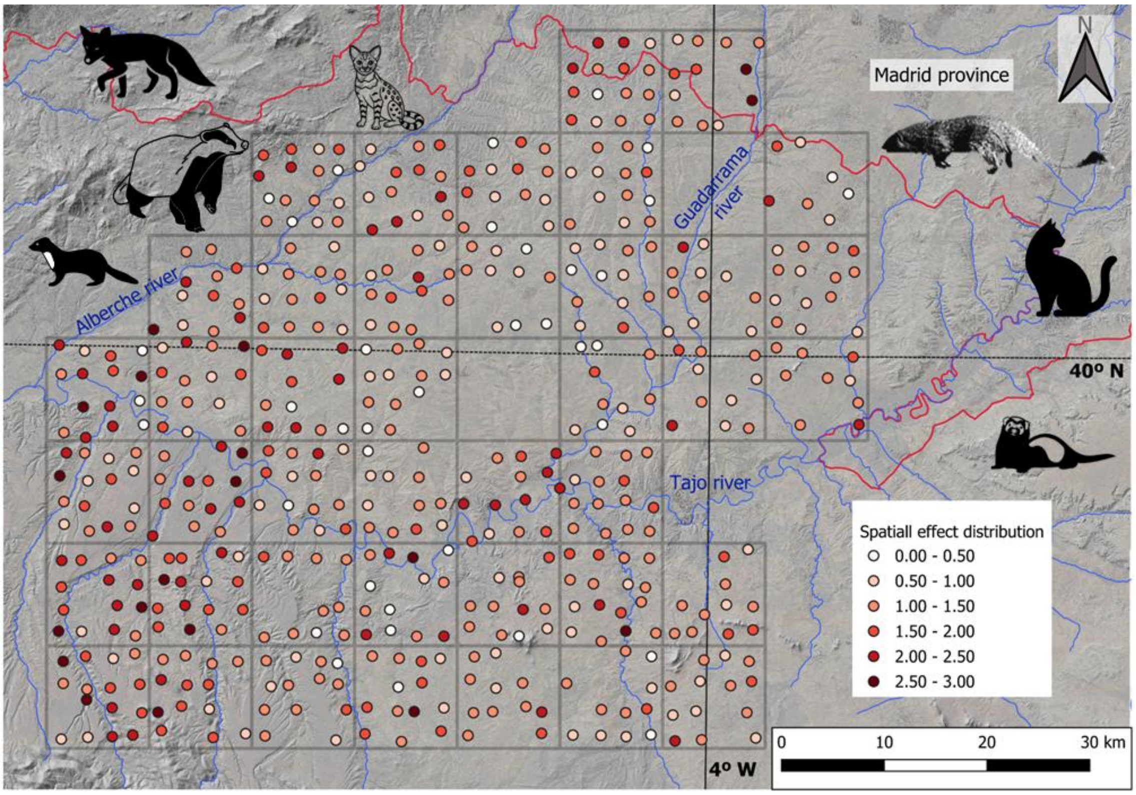


Figure 12: Spatial effect (i.e., carnivore community occupancy probability) distribution across our study area.

3.3. Species-specific patterns

The model also informed about the individual response of each species to the explanatory variables (Table 3). Only three of the species did not follow the community response and did not show a negative effect of rabbit abundance on their occupancy probability (i.e., red foxes, domestic cats and polecats). Humanized areas reduced occupancy probability for red foxes, Egyptian mongooses and badgers, but had positive effects on domestic cats. Length of permanent water courses (i.e., main rivers) was positively related to Egyptian mongooses, genets, and stone martens' occupancy probability, as well as the length of seasonal water courses for badgers. Road presence increased domestic cats and polecats' occupancy probability. Crops land cover and length of motorways diminished stone martens and genets' occupancy probability respectively.

Table 6: Summary of the effects of the significant variables in our model, for the community and for each species. Only significant effects (i.e., confident intervals do not cross the 0 mark) are shown. Estimate, and confident intervals are shown, but they are scaled and transformed: Log transformation for Mean rabbit pellets and Length of and arcsine transformation for ha of different land uses.

Variable	Community			*Vulpes vulpes*			*Herpestes ichneumon*			*Felis catus*		
	CI 2.5%	Estimate	CI 97.5%	CI 2.5%	Estimate	CI 97.5%	CI 2.5%	Estimate	CI 97.5%	CI 2.5%	Estimate	CI 97.5%
Mean rabbit pellets	-1,38	**-0,70**	-0,09				-1,11	**-0,76**	-0,43			
Lenght of paths (km)												
Lenght of road (km)										0,23	**0,60**	1,05
Lenght of motorways (km)												
Lenght of permanent watercourses (km)							0,09	**0,43**	0,81			
Lenght of seasonal watercourses (km)												
Crops (ha)												
Woody crops (ha)												
Coniferous forest (ha)												
Mediterranean forest (ha)												
Humanized areas (ha)				-0,66	**-0,37**	-0,09	-0,97	**-0,58**	-0,22	0,08	**0,47**	0,94

Variable	*Genetta genetta*			*Martes foina*			*Meles meles*			*Mustela putorius*		
	CI 2.5%	Estimate	CI 97.5%	CI 2.5%	Estimate	CI 97.5%	CI 2.5%	Estimate	CI 97.5%	CI 2.5%	Estimate	CI 97.5%
Mean rabbit pellets	-2,24	**-1,32**	-0,63	-2,74	**-1,62**	-0,78	-1,25	**-0,53**	-0,07			
Lenght of paths (km)												
Lenght of road (km)										0,34	**0,96**	1,74
Lenght of motorways (km)	-2,23	**-0,85**	-0,07									
Lenght of permanent watercourses (km)	0,30	**0,74**	1,23	0,30	**0,71**	1,21						
Lenght of seasonal watercourses (km)							0,01	**0,51**	1,10			
Crops (ha)				-1,28	**-0,74**	-0,26						
Woody crops (ha)												
Coniferous forest (ha)												
Mediterranean forest (ha)												
Humanized areas (ha)							-2,43	**-1,16**	-0,35			

3.4. Co-occurrence relationships

The model also described the co-occurrence relationships between species (Figure 5). In this sense, presence of badgers, red foxes, and stone martens was highly correlated, with genets also appearing with this group. Domestic cats and polecats formed the other group with matching occupancy probabilities between them and negative occupancy probabilities with members of the first group. Egyptian mongooses showed weak co-occurrence probabilities (both positive and negative).

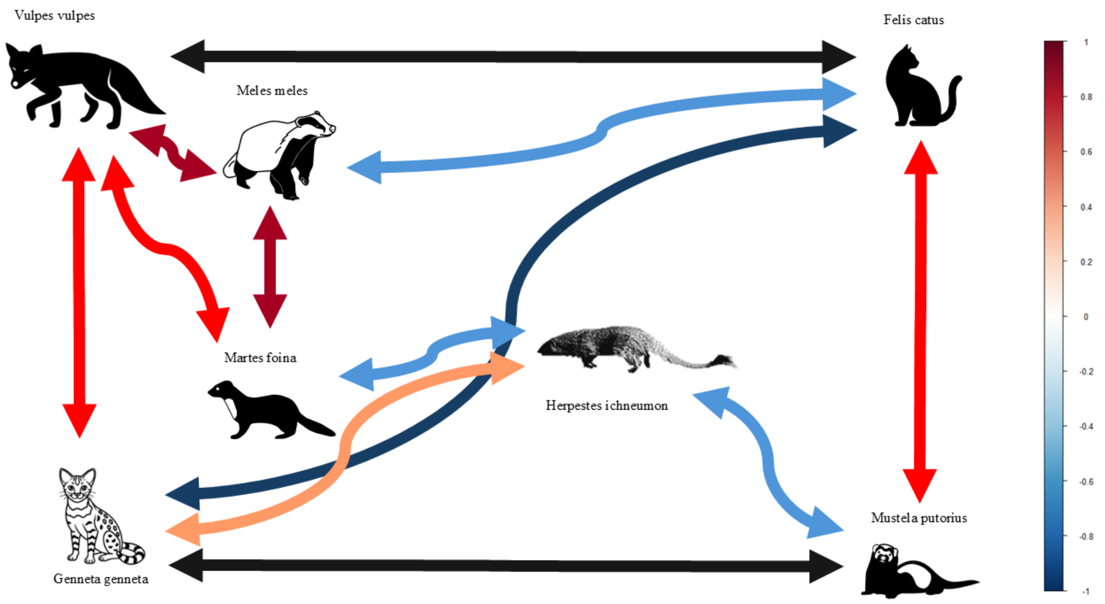


Figure 13: Co-occurrence probability based on residual co-occurrence patterns between pairs of species.

4. Discussion

Our study highlights how important -and complex- the relationship between mesocarnivores and their main prey is, a result that was possible due to the implementation of spatially varying coefficient occupancy model. The fact that this was the best type of model (Table 2), underlines that: (i) in order to correctly evaluate community and species level response to environmental factors, it is key to account for imperfect detection, spatial autocorrelation, and residual species correlation; (ii) how valuable modeling a factor as a spatially varying coefficient is, which allowed us to describe how the relationship between rabbit abundance and occurrence of Mediterranean carnivore species varies along our study area. We described how rabbit abundance had a mostly negative effect on this guild, but this effect turned positive in some particular locations of our study. Spatially, carnivore community occupancy probability increased around main rivers and in the West and Southwest regions of our study area, far away from the megacity of Madrid and inside the forested remnants riparian forest represent in mostly deforested agricultural landscapes. Our model described how each species had their own response to the model's explanatory variables, with humanized areas driving mostly negative probabilities for most of species while main rivers drove positive responses. Finally, based on positive and negative residual species correlations, two groups of species were identified, one formed by red foxes, stone martens, badgers and genets, and the second by domestic cats and polecats.

Rabbit abundance had a negative effect on the carnivore community, a pattern that might seem counterintuitive, as rabbits are a key component of Mediterranean carnivores diet (Delibes-Mateos *et al.*, 2007; Monterroso *et al.*, 2020), but that has been described before (Virgós and Travaini, 2005). Our study allowed us to model how the effects of rabbit abundance changed spatially and see how although the effect is mostly negative, it turned neutral to positive in some localities. We hypothesize that high rabbit abundance naturally increases occupancy probabilities for the whole carnivore community in some localities (Rabelo *et al.*, 2019), while in most of them, high rabbit abundance maybe be product of human wildlife management (Delibes-Mateos *et al.*, 2013). This later scenario may happen as a result of small-game hunting activities, in which landowners usually deploy non-selective techniques such as poisons and snare traps to reduce the carnivore community (Virgós and Travaini, 2005; Delibes-Mateos et al., 2013), and keep those small-game populations high. However, this hypothesis is difficult to test as those techniques are illegal and consequently data is not available. At the species level, and following the community response, our study described how rabbit abundance had a negative effect for all species except for red foxes, polecats, and domestic cats. If predator control is behind the negative effect of rabbit abundance, the neutral response for foxes, may be due to low effectiveness of those techniques on fox populations, as immigration processes rapidly replenish the lost individuals (Barrull *et al.*, 2014b; Porteus *et al.*, 2019). For the other coexisting carnivore species, the non-selective methods used for fox culling do hinder their populations (Fernández-López *et al.*, 2014). The lack of negative effect on polecats is likely due to polecat specialization in rabbit hunting in Mediterranean regions, where this lagomorph makes up to 87% of polecat consumed biomass (Santos *et al.*, 2009). Domestic cats were also not affected by rabbit abundance, which may be explained due to their ability to gather resources and refuge inside human settlements regardless of the characteristics of the habitat in the surroundings (Biró *et al.*, 2004; Germain *et al.*, 2008), something our own results support as domestic cat's occupancy probability increased with increased human areas.

Those human areas reduced occurrence probability for red foxes, Egyptian mongooses and badgers. This is a surprising result as red foxes, Egyptian mongooses are highly adaptable species (López-Martín, 2017; Mangas, 2017), with foxes usually described as common around urban areas (Recio *et al.*, 2015). Nonetheless, these are the most abundant species in our study, so the habitat loss produced by human areas may yield lower occurrence probabilities around our cameras. Badgers tend to select areas with some form of vegetation cover types, to stablish their setts (Virgós, 2017), which are reduced in human-dominated landscapes. Road density was positively related with the occurrence of both domestic cats and polecats. As we discussed before, domestic cat populations are tightly linked to human settlements (Biró *et al.*, 2004; Germain *et al.*, 2008), where road density tends to be higher. The positive effect on polecats is likely related to the overabundance of rabbit burrows on road embankments (Barrientos and Bolonio, 2009; Carmona *et al.*, 2024), as this lagomorph is its main prey (Santos *et al.*, 2009). Motorways only had negative effect on genet occurrence. This result contrasts with the ones obtained by Mata *et al.* (2017), and it could be related to the fact that these authors studied the use of motorway corridor on a low-traffic motorway, whereas traffic intensity in our study area (around a megacity like Madrid) could repel genets from using these corridors.

Presence of rivers was positively related to the occurrence of Egyptian mongooses, genets, and stone martens, while presence of seasonal streams was positive related to badgers' presence. Egyptian mongooses, genets, and stone martens have been described to frequent riparian forest looking for food, water and cooler temperatures during summer (Santos *et al.,* 2011b). As discussed before, badgers usually select other types of vegetation cover where stablishing their setts is easier, however intense agricultural areas leave them with no other choice than riparian forest (Virgós, 2001). Crop surface was negative related to occurrence of stone martens. In this sense, stone martens tend to select different types of forested areas (Mangas, 2017; Santos and Santos-Reis, 2010), although they also use small oak forest patches, scrublands (Sarmento *et al.*, 2011) or even open areas (Mangas, 2017).

Finally, or model allowed us to draw the co-occurrence probabilities between species trough residual co-occurrence patterns between pairs of species in the modeled community (Doser *et al.*, 2024). Although this could get us a picture of how these species may share the landscape, we need to be cautious in our interpretations, as these co-occurrences do not imply true biological interactions (Poggiato *et al.*, 2021). Nonetheless, there was a high co-occurrence probability between badgers, red foxes and stone martens as well as genets, which has been described already for the first three species in Mediterranean habitats (Barrull *et al.*, 2014a). Co-occurrence of domestic cats and polecats was also highly probable, due to both species selecting habitats with high road density. These sympatric medium-sized predators have similar habitat and food requirements but markedly differ on their trophic niche breadth and how that trophic niche changes over the seasons, ranging from rabbit or rodent hunters to scavengers and frugivorous (Clavero et al. 2003, Monterroso et al. 2020).

5. Conclusions

The use of these state-of-the-art Bayesian spatially explicit, multi-species varying coefficient occupancy models, allowed us to investigate the complex variables that modulate of mesocarnivores both at a species and community levels. Regarding the species specific response, we described how expansive humanized areas may reduce overall carnivore presence in the future and underlined the importance maintaining riparian forest in mostly deforested agrosystems. Critically, our study highlighted the relevance of rabbit abundance on mesocarnivore presence on agrosystems and how complex this relationship is. Particularly, high rabbit abundance naturally increased occupancy probabilities for the whole carnivore community in some localities, while in most of them, high rabbit abundance maybe be product of human wildlife management. So, in order to disentangle this complex relationship and provide better suggestions for mesocarnivore conservation, we need extensive quality data and continuous monitoring of this key prey species.

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7. Authors contributions.

PQ: conceptualisation, methodology, software, formal analysis, investigation, writing – original draft and visualisation. **JH:** fieldwork. **GF:** software, formal analysis, review and editing. **MR:** software, formal analysis. **RC:** software. **GC:** fieldwork. **RB:** conceptualisation, methodology, investigation, resources, review and editing, supervision, project administration and funding acquisition.

General discussion

General discussion

In this thesis we focused on the impact human activities, particularly roads, have on interspecific relationships, focusing our efforts on the negative effect they have on carnivore species. In particular we dug deeper into the study of roadkill patterns and the difficulties they present, from getting the correct data, to assessing the particular factors that could drive species-specific roadkill sensitivity.

To get a wider perspective on how human activities can modify interspecific relationships, in Chapter 1, we reviewed how the biggest human infrastructure, the road network, can alter these critical components of ecosystem processes. In our research, we described some broader knowledge gaps, such as the lack of studies on countries where most of the road network is predicted to grow, the lack of studies focused on parasitism, amensalism and commensalism relationships, or the lack of studies focused on taxa like amphibians. Regarding interspecific relationships we found a series of patterns worth highlighting: (i) prey species suffer from increased predation in roads used by predators and altered their anti-predator behaviours, while negative effects on predators are not so sound. (ii) Even though the prey trap hypothesis and predator release hypothesis are widely cited in road ecology literature, they have little empirical support. (iii) The habitat corridor created close to roads usually benefits more competitive species such as generalist, invasive and scavengers. (iv) Road barrier effect degrades both pollination and seed dispersal processes. (v) Parasitism rates are usually higher closer to the road and are exacerbated by road maintenance practices.

This overview allowed us to suggest a series of practises regarding road maintenance and use that could mitigate the negative effects that roads have in these interspecific relationships. Firstly, we suggest establishing common metrics for certain interactions, such as effective seed dispersal for mutualism, infection rates for parasitism or percentage of land use at different distances from the road for both prey and predators. This way we could assess better the effects newly constructed road have on this interactions. Secondly, we suggest keeping road margins as wide and heterogeneous as possible to allow for colonization of a diverse community of insects and plants that would maintain ecosystem processes such as seed dispersal and pollination. This heterogeneous margins could be achieved by changing the standard mowing practises for less frequent and intense ones. Thirdly, de-icing salt use should be put in check or eliminated as there are less damaging alternatives available. We suggest this change as using de-icing salt alters several species interactions (predation, competition, and parasitism), and negatively affects several freshwater taxa such as zooplankton, amphibians, and fishes living in nearby waterbodies. Moreover, the resulting cascade effects can alter food webs, leading to demographic changes. Fourthly, although useful, wildlife passages should not be constructed individually, as this could channel wildlife, increasing predation and parasitism rates. Fifthly, carcases on the road surface are used by scavengers and generalist species, giving them an unnatural advantage, but in turn, their roadkill probabilities increase greatly. In this scenario, native or less competitive species can be displaced, and more competitive species suffer increased mortality. So, intensive effort should be made to eliminate carcasses from the road. Finally, high traffic flow and vehicle speed hinder pollination and seed dispersal processes as well as antipredator behaviours, so traffic-calming schemes should be implemented in sensitive habitats.

We discussed in Chapter 1 how studies focused on how roads alter predator relationships are pretty common. We also found several studies focused on how roads can alter predator and prey behaviours, but there are fewer examples on how roads can alter predation relationships directly through roadkills. Roadkills have been much studied in road ecology literature, as their impact in wildlife is widely recognized, which has prompted researchers to find new ways to predict their patterns and to obtain the necessary data for these predictions. Some of those researchers have tried to use opportunistic data, such as those from wildlife Atlases, to investigate roadkill patterns (Battisti *et al.*, 2012; Visintin *et al.*, 2016). Although abundance has been described as positively related to roadkill probability (e.g., Canova and Balestrieri, 2019; D'Amico *et al.*, 2018; Gehrt, 2002; Visintin *et al.*, 2016), when abundance was based on atlas data, the relationship was blurred (Battisti *et al.*, 2012).

Although there is an increasing necessity for obtaining data related to road impacts, in Chapter 2 we aimed to describe how problematic the use of opportunistic data to infer roadkill patterns can be. To test it, we used data from the Spanish Atlas of Terrestrial Mammals to compare it with our own roadkill specific survey. We found that these data sources identified different patterns, mainly due to two factors: (i) the biases the atlas data has and (ii) the differences in roadkill sensitivity among species. In particular, opportunistic data such as the one that compiled in the Spanish Atlas of Terrestrial Mammals (last edition; Palomo *et al.*, 2007), then updated) has several biases. (i) uneven recording intensity over time, (ii) unequal spatial coverage, (iii) heterogeneous sampling effort in every visit, and (iv) different detectability of the sampled species. Moreover, typical Atlases scale could have a profound effect on model predictions based on them (Araújo *et al.*, 2005; Būhning-Gaese, 1997). Factors mismatching roadkill probability with species occurrence are likely influenced by species morphological, ecological, life-history or behavioural traits that make them to present different sensitivities to roadkills.

For instance, we found that the European polecat was roadkilled more than expected relative to its occurrence in the Atlas data. Polecats in the Mediterranean habitats are specialist in rabbit hunting, forming this lagomorph up to 87% of consumed biomass (Santos *et al.*, 2009). This makes polecat search for this prey in the road embankments where they build their burrows, highly increasing their chances of being roadkilled. On the other hand, otters were road-killed less than expected from Atlas data. Contrary to polecats, they are semi-aquatic carnivores that feed in and displace by water courses, only rarely leaving them (Quaglietta *et al.*, 2012, 2013, 2014). Also, in contrast with polecats, otter presence is easily detected by searching for their scats in protruding stones or in bridge foundations when infrastructures cross the rivers. Both factors together -roadkill sensitivity and detection-, drive to these differences between estimated abundance and roadkill records for both species, but in with opposing directions. Thus, to study road-kill rates and patterns, we suggest that classical surveys should be the primary choice. However, due to their time and budget constraints, alternative data sources can be utilized, but always with appropriate corrective measures for citizen-science and non-systematic datasets. When examining species-specific road-kill patterns, it is also crucial to consider the ecology and traits of the species involved.

This research prompted us to further investigate into the causes behind the high sensitivity to roadkills shown by polecats. Moreover, this mustelid species has proven to be cryptic and difficult to monitor, as most of its presence data comes from roadkilled individuals. Consequently, it is paramount for their conservation to understand the factors behind their roadkill sensitivity. Therefore, in Chapter 3 we used again our own roadkill survey, to get a detailed picture of the factors behind polecat roadkill patterns. Furthermore, we tested whether variables explaining roadkills were consistent over time and space.

We identified rabbit abundance in road embankments, speed limit, distance to irrigated crops, and scrubland as the factors behind polecat roadkill probability. Several of these variables can change over time in intensity and location. Particularly, we described how rabbit abundance was positively correlated with roadkill probability, but its effect changed over time. Additionally, we described how roadkill hotspots also spatially changed over time, which could be correlated with rabbit population fluctuations, that have been described as a consequence of disease cycles such as myxomatosis or haemorrhagic disease peaks, as well as changes in game management (Delibes-Mateos *et al.*, 2008; Delibes-Mateos *et al.*, 2009). As we expected from previous studies in road ecology, speed limit also positively correlated with polecat roadkill probability. Although this is a fairly "static" variable, road retrofitting can alter its effect and new roadkill probabilities could be overlooked. In summary, we provided evidence that in order to mitigate roadkills, static measures could be ineffective, and they will yield better results if we consistently monitor these factors over time. This is key to apply the correct mitigation measures and avoid wasting resources.

So far, this thesis showed us how sensitive carnivores and predator-prey relationships can be to human impact, and roads in particular. We also reviewed how carnivores as apex consumers hold important role in ecosystem processes. Therefore, continuing with this same carnivore guild embedded in the highly managed agricultural landscape of central Spain, in Chapter 4 we tested how human encroachment shapes the distribution and composition of the carnivore community as a whole. This chapter implied the biggest field work of the thesis, with almost 3 years of trial camera deployment and thousands of images to review. In order to accomplish this, we employed artificial intelligence to help us with image filtering (Beery *et al.*, 2019) and fitted the latest spatial multispecies occupancy models (Doser *et al.*, 2022).

Using those models, we were able to account for imperfect detection, spatial effects, and spatially varying factors. Our study highlighted how complex is the relationship between carnivore occurrence and rabbit abundance (the main prey for the community). In this relationship higher rabbit abundance is mainly related to lower occupancy probabilities for the carnivore guild, however the outcome of this relationship varies spatially. Depending on local management practices this relationship has two “faces”; a natural one (less prevalent), where prey abundance is positive correlated with predator presence, and an artificial one (more prevalent), where human wildlife management creates abundant rabbit populations while actively diminishing carnivore presence. The latter is the product of small-game hunting practices, one of the predominant economical activities in the area. With the aim of boosting small-game populations, gamekeepers deploy non-selective techniques, such as poisons and snare traps that target predators (Virgós and Travaini, 2005). However, this hypothesis is difficult to test as those techniques are illegal and consequently data is not available. At the species level, foxes, polecats, and domestic cats where the only species not negatively affected by high rabbit abundances. If predator control is behind the negative effect of rabbit abundance, the neutral response for foxes, may be due to low effectiveness of those techniques on fox populations, as immigration processes rapidly replenish the lost individuals (Barrull *et al.*, 2014b; Porteus *et al.*, 2019). For the other coexisting carnivore species, the non-selective methods used for fox culling do hinder their populations (Fernández-López *et al.*, 2014). Our study also delimitates species specific response to landscape features, with human areas having a negative effect for most of the species, while rivers and seasonal streams increasing occurrence probability for most of the carnivore community.

Conclusions

1. There is currently a knowledge gap on how roads may alter interspecific relationships on taxa and countries from the Global South, a region that will undergo large increases in its road network in the coming years.
2. Some species interactions (parasitism, amensalism and commensalism) have been little or no studied at all, and the same happens with taxa such as amphibians.
3. Road ecology literature shows that some changes in road management could mitigate the negative effects roads have on interspecific relationships. Those are: wider and structurally heterogeneous road verges through less intense mowing regimes, limitation on the use of de-icing salts, construction of wildlife passages in groups, elimination of carcases from roadkills and traffic-calming schemes in sensitive habitats.
4. Carnivore roadkill patterns do not mirror those from atlas data, probably due to survey biases in former data and to species-specific ecological or behavioural traits such as species morphology or species behaviour when facing the road.
5. Polecat roadkill hotspots are determined by rabbit abundance on road embankments, speed limit, distance to irrigated crops, and scrubland.
6. Roadkill patterns are dynamic both in space and time. So, to apply mitigation measures, we need to know both ecological and road-related factors behind roadkill patterns and implement continuous monitoring programs of these factors, especially those that fluctuate over time.
7. Carnivore presence is negatively influenced by the abundance of rabbits, a key prey but also a very important game species. However, this effect changes spatially due to wildlife management practices.

8. We suggest -although we could not test it- that the counterintuitive negative effect of prey abundance over predator presence, is due to the predator control applied in small hunting properties in order to boost small game populations.
9. If future human development demands further urban and agricultural expansion, we need to find ways to mitigate the negative effect this expansion has on carnivore populations, as their complete disappearing from our ecosystem would have major consequences.

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