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Tese de Doutorado

Abordagens analíticas para avaliar a alteração da cobertura vegetal nativa e mortalidade de fauna em rodovias

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Porto Alegre, abril de 2026

ABORDAGENS ANALÍTICAS PARA AVALIAR A ALTERAÇÃO DA COBERTURA VEGETAL NATIVA E MORTALIDADE DE FAUNA EM RODOVIAS

Ingridi Camboim Franceschi

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Motivação

Ao finalizar essa tese, realizo o sonho de uma guria de dez anos de idade. Uma criança que não sabia os desafios que iriam vir, mas também não sabia o quão feliz seria. Era apenas uma guriazinha sonhadora que queria salvar o mundo, salvar o meio ambiente e os animais. Era uma guriazinha que queria fazer a diferença e achava que o caminho era dentro da pesquisa científica e, para isso, tinha que cursar biologia, fazer mestrado e doutorado. Ainda na graduação, descobri a ecologia de estradas e que ali existia a possibilidade de contribuir e fazer algo importante cientificamente. Descobri um mundo imenso dentro de uma área tão pequena e recente que é a ecologia de estradas, e descobri que era isso que eu buscava: como avaliar os impactos antrópicos no meio ambiente e como mudar isso. Quem poderia imaginar que as estradas resultam em tantos impactos que vão para além das colisões com a fauna? E melhor, que é possível evitar os impactos, reduzir e minimizar. Muitas vezes não reconhecemos que fazemos parte do meio ambiente, mas sim, somos parte dele, da natureza, do ecossistema, logo, também cabe a nós preservarmos o nosso grande lar.

O sonho daquela guriazinha foi amadurecendo com o tempo, à medida que fui realizando as etapas e mergulhando na ecologia de estradas. Ainda há tanto para estudar e descobrir, as inúmeras possibilidades de fazer pesquisa aplicada, no sentido de dar retorno à sociedade, de melhorar a forma de fazer pesquisa ou parte do sistema, e tudo isso me fascina. Em setembro de 2021, iniciei a última etapa do sonho. Posso dizer com muito orgulho e alegria que hoje eu terminei de realizar os sonhos daquela guriazinha. Conclui a graduação em biologia, fiz mestrado e agora finalizo o doutorado. Acredito que, de alguma forma, mesmo que pequena, fiz alguma diferença. A guriazinha com certeza não esperava ter vivido tudo que foi vivido, ter conhecido tantas pessoas e ter viajado para fora do Brasil. Com certeza ela não esperava ter amizades leais e fiéis, nem que ter uma rede de apoio seria indispensável para sobreviver até o final desse sonho. Assim como não se faz pesquisa sozinha, essa tese também não foi feita sozinha, eu pude contar com as melhores pessoas para me ajudar e me dar força para continuar. Ao escrever isso, me sinto realizada; embora nem tudo tenha sido executado da forma planejada, me sinto feliz em terminar. Aprendi muito que o que planejamos quase nunca acontece, que a vida é cheia de surpresas, boas e nem tão boas. Com certeza tive mais momentos bons, de alegria, com risada, apoio e acolhimento. Não vou ignorar os momentos de ansiedades, desespero e frustração, mas também não vou dar destaque a esses sentimentos. Se esse caminho poderia ter sido mais fácil ou mais difícil, eu não sei; só sei que o meu foi assim. E tudo foi experiência, tudo que vivi molda a pessoa e a pesquisadora que sou.

Hoje terminam os sonhos da Ingridi de 20 anos atrás e se iniciam novos sonhos. Embora fazer pesquisa não seja fácil, e as dúvidas e as inseguranças existam, ainda, como a Ingridi criança, acredito que a pesquisa científica é o futuro e a salvação do mundo; ao menos é isso que faz os meus olhos brilharem.

Road ecology inverts our oldest joke about animals and transportation: *Why did the chicken cross the road*? Embedded in that chestnut is an assumption – that the road is inviolable and eternal, as fixed in its course as a river. The road is a given; it's the fowl whose actions demand explanation. But the riddle's logic is backward. It's the animals who have always moved; the road that's the upstart. A better question might be, *Why did the road cross the land*?

A ecologia de estradas inverte nossa piada mais antiga sobre animais e transporte: *Por que a galinha atravessou a estrada*? Embutida nessa charada está uma suposição – a de que a estrada é inviolável e eterna, tão fixada em seu curso quanto um rio. A estrada é um dado; é o comportamento da ave que exige explicação. Mas a lógica do enigma está invertida. São os animais que sempre se moveram; a estrada é que é a intrusa. Uma pergunta melhor seria, *Por que a estrada cruzou a terra*?

GOLDFARB, Ben. *Crossings: How Road Ecology Is Shaping the Future of Our Planet*. New York: W. W. Norton & Company, 2023, pp10.

Resumo

A maioria dos impactos humanos no meio ambiente está associada às estradas, que permitem o acesso aos ambientes e cujos impactos sobre a biodiversidade crescem junto com a expansão da infraestrutura viária. As estradas facilitam a conversão de vegetação nativa, alteram o uso do solo e causam impactos diretos e indiretos sobre a fauna silvestre, como mortalidade por colisões veículo-fauna e alterações na dinâmica populacional. O objetivo desta tese foi investigar os impactos das rodovias sobre a vegetação nativa e as populações de fauna silvestre, bem como identificar os métodos estatísticos utilizados na avaliação de padrões espaciais de colisões veículo-fauna. No Capítulo I, avaliei padrões de mudanças na vegetação nativa antes e depois da pavimentação de rodovias federais do Brasil por meio de um desenho amostral Antes-Depois-Gradiente. Em nível nacional, encontramos que, após a pavimentação, houve aumento ou desaceleração da perda de vegetação. Porém, as respostas dos biomas foram variadas, em que os biomas Amazônia, Cerrado e Pampa apresentaram perdas de vegetação nativa, e Mata Atlântica e Caatinga apresentaram ganhos. Apenas o bioma Cerrado apresentou diferença significativa na vegetação nativa ao longo do gradiente de distância à estrada. Esses resultados ressaltam que os impactos da pavimentação de estradas dependem de avaliações multiescalas, temporais e específicas para cada bioma. No Capítulo II, desenvolvi um modelo baseado em indivíduos para avaliar como o crescimento relativo de populações de espécies que variam em características populacionais, como o deslocamento diário, a estratégia reprodutiva e a probabilidade de travessia na estrada, responde a cenários com diferentes fluxos de veículos. Os impactos não foram lineares e dependeram da interação entre as características populacionais avaliadas. As populações com grande deslocamento diário e maturação tardia apresentaram crescimento negativo em todos os cenários, enquanto aquelas com baixo deslocamento e maturação precoce se mostraram resilientes mesmo sob alto tráfego. No Capítulo III, elaborei um mapeamento sistemático para identificar os métodos estatísticos utilizados para avaliar padrões espaciais de colisões veículo-fauna e os termos associados à definição de segmentos com maior concentração dessas colisões. Os resultados da síntese revelaram uma confusão terminológica e viés geográfico na escolha dos métodos, reforçando a necessidade de estudos que comparem o desempenho de métodos espaciais sob diferentes distribuições de dados. Por meio dessa tese, pude demonstrar como os impactos da pavimentação de rodovias variam entre biomas, como modelos preditivos podem auxiliar na percepção sobre respostas populacionais ao fluxo de veículos, e os padrões dos métodos estatísticos utilizados para identificar segmentos com maior concentração de colisões. Assim,

esses resultados demonstram que os impactos das rodovias são heterogêneos, sendo necessário adotar abordagens sensíveis ao contexto e às espécies, bem como maior clareza nas escolhas metodológicas frente à ampla diversidade de métodos existentes.

Palavras-chave: Análise espacial; Colisão veículo-fauna; Conversão de Vegetação Nativa; Ecologia de Estradas; Pavimentação de estrada; Persistência populacional; *Hotspots* de atropelamento.

Abstract

Most human impacts on the environment are associated with roads, which provide access to natural environments and whose impacts on biodiversity grow alongside the expansion of road infrastructure. Roads facilitate the conversion of native vegetation, alter land use, and cause direct and indirect impacts on wildlife, such as mortality from vehicle-wildlife collisions and changes in population dynamics. The aim of this thesis was to investigate the impacts of roads on native vegetation and wildlife populations, as well as to identify the statistical methods used to assess spatial patterns of vehicle-wildlife collisions. In Chapter I, I assessed patterns of native vegetation change before and after paving of federal highways in Brazil using a Before-After-Gradient sampling design. At the national level, we found that paving was followed by an increase in, or a deceleration of, vegetation loss. However, biome-level responses varied, with the Amazon, Cerrado, and Pampa biomes showing losses in native vegetation, while the Atlantic Forest and Caatinga showed gains. Only the Cerrado biome showed a significant difference in native vegetation along the distance gradient from the road. These results highlighted that the impacts of road paving depend on multiscale, temporal, and biome-specific assessments. In Chapter II, I developed an individual-based model to assess how the relative growth of populations with varying population traits — such as daily movement distance, reproductive strategy, and road-crossing probability — responds to scenarios with different traffic volumes. Impacts were nonlinear and depended on the interaction between the population traits evaluated. Populations combining large daily movement distances with late maturation showed negative growth across all traffic scenarios, whereas those with low movement distances and early maturation remained resilient even under high traffic volumes. In Chapter III, I conducted a systematic map to identify the statistical methods used to assess spatial patterns of vehicle-wildlife collisions, as well as the terms associated with defining road segments with higher collision concentration. The synthesis results revealed terminological confusion and geographic bias in method choice, reinforcing the need for studies comparing the performance of spatial methods under different data distributions. Through this thesis, I demonstrated how the impacts of road paving vary across biomes, how predictive models can help elucidate population responses to traffic volume, and the patterns in the statistical methods used to identify segments with higher collision concentration. Together, these results demonstrate that road impacts are heterogeneous, highlighting the need for context- and species-sensitive approaches, as well as greater clarity in methodological choices given the wide diversity of existing methods.

Keywords: Spatial analysis; Wildlife-vehicle collision; Native vegetation conversion; Road ecology; Road paving; Population persistence; Roadkill hotspots.

Introdução Geral

A maioria dos impactos humanos no meio ambiente está associada às estradas, pois sem elas o acesso aos ambientes é limitado. Os impactos das rodovias na biodiversidade são diversos, atuando de forma direta e indireta, desde a fase de planejamento até a operação da via (Trombulak; Frissell, 2000; van der Ree; Smith; Grilo, 2015). A presença dessas infraestruturas lineares remove vegetação nativa onde elas são construídas e facilita a conversão de vegetação nativa nos seus arredores, resulta em mortalidade da fauna por colisão com veículos e caça ilegal, bem como afugentamento da fauna por efeito barreira, contaminação do solo e da água, entre outros distúrbios (Forman; Alexander, 1998; Trombulak; Frissell, 2000). Como a expansão viária segue crescente em todo o mundo, tornam-se ainda mais necessárias pesquisas que busquem compreender os padrões desses impactos e, posteriormente, desenvolver alternativas para sua evitação, redução e mitigação (Laurence *et al*., 2014; van der Ree; Smith; Grilo, 2015; Abra *et al*., 2025).

A presença das estradas facilita a ocorrência de diversas atividades humanas, como o desmatamento, à caça ilegal, a presença de assentamentos e atividades agrícolas (Barber *et al*. 2014; Laurance *et al*., 2015; Engert *et al*., 2024). Na Amazônia brasileira, 94% do desmatamento ocorreu no entorno de estradas oficiais e não oficiais, evidenciando o papel das rodovias como vetor de acesso ao desmatamento (Barber *et al*., 2014). Esse processo se intensifica com a pavimentação, que pode ampliar os impactos já existentes em até 61% nas áreas de entorno em comparação com estradas não pavimentadas (Lupinetti-Cunha *et al*., 2022). Simulações para a BR-319, por exemplo, indicam que sua pavimentação poderia ampliar o desmatamento em 60% e estender seus efeitos até 40 km da estrada (Santos *et al*., 2023). A extensão dos impactos a partir da estrada é conhecida como "zona de efeito da estrada", referindo-se à distância a até a qual os efeitos ecológicos podem ser detectados (Forman & Deblinger, 2000). A zona de efeito varia de acordo com o objeto de estudo – por exemplo, fauna, flora, padrões de vegetação, serviços ecossistêmicos –, e o mecanismo de impacto – por exemplo, poluição sonora, química, colisões veículo-fauna –, além da escala espacial considerada – por exemplo, escala analítica, escala do processo ecológico. Mudanças no uso do solo, por exemplo, são impactos diretos que podem ocorrer em escalas de 1 a 10 km ou mais além da estrada (Lin *et al*., 2020; Zheng *et al*., 2021; Lisiak-Zielińska *et al*., 2022), assim como mudanças na composição e estrutura vegetal (Lisboa *et al*., 2022). Para a fauna, a zona de efeito é um impacto indireto pode variar na magnitude e extensão conforme o táxon e as características da estrada, como o fluxo de veículos, podendo diminuir a densidade

populacional a poucos metros até quilômetros de distância da estrada (Eigenbrod *et al*., 2009; Benítez-López *et al*., 2010; Belghali *et al*., 2025). Dependendo do organismo e do mecanismo estudado, as escalas espaciais e temporais precisam ser ajustadas de acordo.

O impacto direto das estradas nas populações de fauna silvestre mais evidente é as colisões veículo-fauna (Rytwinski; Fahrig, 2011; Grilo *et al*., 2020). Entretanto, as estradas também podem modificar o movimento e comportamento dos indivíduos na paisagem (Scrafford *et al*., 2018; Passoni *et al*., 2021), bem como representar uma barreira física pela própria presença ou devido ao volume de tráfego (Ascensão *et al*., 2016; Grilo *et al*., 2018). No entanto, a obtenção de dados empíricos para prever as respostas populacionais às estradas ainda é um desafio (Pinto *et al*., 2020; Barrientos *et al*., 2021). Modelos mecanísticos surgem como uma alternativa, pois permitem explorar os impactos das estradas integrando dinâmicas populacionais e processos ecológicos. Por exemplo, estudos de modelagem indicam que as colisões veículo-fauna podem ter um impacto maior no tamanho e na persistência populacional do que o efeito barreira isoladamente (Ceia-Hasse *et al*., 2018). Além disso, a variação no risco de colisões veículo-fauna é influenciada por características das espécies, particularmente aquelas relacionadas ao comportamento e ao movimento (Bénard *et al*., 2024). Essas abordagens podem ser aplicadas com espécies virtuais e validadas com dados empíricos de espécies reais, explorando respostas populacionais aos impactos causados pela estrada. Simulações utilizando dados de lobo-guará (*Chrysocyon brachyurus*) constaram que mesmo taxas moderadas de mortalidade levaram a declínios acentuados no tamanho da população (Barbosa *et al*., 2020), e modelos para tamanduás-bandeira (*Myrmecophaga tridactyla*) estimaram que uma perda de 18% da população adulta resultaria em uma probabilidade de extinção de 47% em 100 anos (Desbiez *et al*., 2020). O uso desses modelos pode ser uma alternativa para predizer impactos antes da construção, pavimentação ou duplicação de uma estrada e propor medidas de mitigação previamente. Da mesma forma, esses modelos também podem ser aplicados para avaliar a eficácia da implementação de medidas de mitigação com uma espécie-alvo (e.g., Ascensão *et al*., 2013; Wilansky; Jaeger, 2024). Posteriormente às avaliações por simulações, o desafio é identificar onde as medidas de mitigação devem ser implementadas.

A decisão sobre a implementação de medidas de mitigação envolve identificar onde os animais cruzam mais a estrada (Dasoler *et al*., 2026a) e/ou onde há maior concentração de registros de colisões veículo-fauna (Grilo *et al*., 2012; Neumann *et al*., 2012). Para identificar esses segmentos existem diversos métodos estatísticos espaciais que respondem a duas perguntas fundamentais: (1) se os dados de mortalidade são espacialmente concentrados e em

qual escala, e (2) qual a localização espacial da concentração de mortalidade (Coelho *et al*., 2012; Neumann *et al*., 2012; Ramp *et al*., 2005). Embora esses métodos sejam complementares, eles respondem perguntas diferentes, têm objetivos analíticos e resultados estatísticos distintos. Como consequência, a terminologia é aplicada a esses métodos espaciais sem uma distinção clara entre as perguntas e os objetivos que se almeja. As escolhas metodológicas e terminológicas na pesquisa científica podem ser influenciadas por múltiplos fatores (Culumber *et al*., 2019). Assim, as decisões analíticas podem influenciar os resultados da pesquisa, visto que diferentes métodos aplicados ao mesmo conjunto de dados podem levar a resultados distintos, o que ressalta a importância da transparência nas escolhas metodológicas (Sutherland, 2018; Sarstedt *et al*., 2024). Contudo, apesar da crescente literatura sobre colisões veículos-fauna (Pagany, 2020; Su *et al*., 2026), ainda não está claro se as escolhas metodológicas dos autores são baseadas nos dados ou refletem vieses de pesquisa. A escolha de métodos estatísticos adequados é essencial para identificar com precisão os segmentos prioritários nas rodovias, de forma a salvar ao máximo vidas humanas e dos animais, bem como economizar os recursos financeiros (Spanowicz *et al*., 2020; Karanasios *et al*., 2021). Embora alguns estudos tenham comparado métodos espaciais para mortalidade de fauna (Gomes *et al*., 2009; Borda-de-Água *et al*., 2019), ainda não foram avaliadas a acurácia e a precisão dos diferentes métodos considerando diferentes escalas, distribuição e quantidade de dados. Uma síntese global dos termos e métodos utilizados nessa temática poderia promover um uso mais consistente da terminologia e das questões analíticas, mas também identificar prioridades para o desenvolvimento metodológico futuro.

Nessa tese busquei contribuir ao investigar os impactos das rodovias sobre a vegetação nativa e as populações silvestres, bem como as escolhas metodológicas empregadas para identificar padrões espaciais de colisão veículo-fauna. Para isso, abordei múltiplas escalas espaciais, temporais e biológicas. Espacialmente, são realizadas análises em escala nacional, considerando os biomas brasileiros, e em escala local, simulando um trecho de rodovia. Temporalmente, são feitas comparações na taxa de mudança da vegetação antes e depois da pavimentação, além de simulações da persistência populacional ao longo do tempo sob efeito do tráfego. Em termos biológicos, a tese avalia os impactos das rodovias na vegetação e nas populações de fauna, além de investigar os padrões nas escolhas terminológicas e metodológicas para a avaliação espacial de colisões veículo-fauna. Para atingir tais objetivos, a tese foi dividida em três capítulos:

- Capítulo I: avaliação dos padrões de mudanças na vegetação nativa antes e depois da pavimentação em rodovias federais do Brasil por meio de um desenho amostral Antes-Depois-Gradiente.
- Capítulo II: execução de um modelo baseado em indivíduos (MBIs) com cenários variando fluxos de veículos, movimento diário, estratégia reprodutiva e probabilidade de travessia.
- Capítulo III: elaboração de um mapeamento sistemático para identificar os termos relacionados a definição de segmentos com maior concentração de colisões veículo-fauna e os métodos estatísticos usados para avaliar os padrões espaciais desses registros.

Os três capítulos desenvolvidos compartilham o objetivo comum de aprimorar a compreensão sobre como as rodovias afetam a biodiversidade e como avaliar esses impactos de forma metodologicamente robusta. Por fim, nessa tese demonstrei como os impactos da pavimentação são diferentes entre os biomas, destaca como modelos preditivos podem nos dar percepções importantes sobre como as populações silvestres respondem ao fluxo de veículos, e revela padrões nas escolhas dos termos e métodos para avaliar os padrões espaciais de colisão veículo-fauna. As abordagens desenvolvidas nesta tese têm potencial de aplicação para o planejamento de uso da terra e avaliações de impacto ambiental. No entanto, para que esses instrumentos sejam efetivos, é fundamental que partam da perspectiva das espécies — ou seja, que as perguntas sejam guiadas pelas características e requerimentos ecológicos da fauna e flora nativas, e não pelas características das infraestruturas.

Capítulo I

Native vegetation changes before and after road paving on landscape gradients

Esse capítulo será submetido na revista "*Global Change Biology*" e foi realizado em colaboração com Andreas Kindel, Carlos Augusto Peres, Cristian de Sales Dambros, Lucas Ferreira Colares e Juliano Sarmento Cabral.

Global Change Biology

Native vegetation changes before and after road paving on landscape spatial gradients

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ABSTRACT

Paving roads can intensify human activity, resulting in increased changes in land use and native vegetation in surrounding areas. Here, we aimed to understand the effects of road paving on native vegetation over time and space, using Brazil as case study to take advantage of its continental size and diverse biomes. We applied a Before-After-Gradient (BAG) sampling design to compare rates of change of native vegetation before and after paving along a distance gradient from the road at both national and Brazilian biome scales. Our analysis used two time-frame datasets (5-year vs. 10-year periods) and seven distance zones (1 to 15 km) to examine whether patterns of change depend on the temporal scale and to compare road-affect zones on native vegetation change rates over time. Generalized additive mixed models were applied to explore the relationship between native vegetation change rates and the periods before and after paving in the zones. The effects of road paving in Brazil were dependent on the time frame analysed: while no significant differences between periods were found in the 5-year dataset, the 10-year dataset revealed significant changes. Contrary to our expectations, the national-scale analysis showed a general net gains or deceleration in loss rates after paving, particularly in the zones closest to the road (up to 3 km). However, these findings masked high spatial variation in responses across biomes. Native vegetation loss continued in the Amazon, Cerrado, and Pampa, whereas the Atlantic Forest and Caatinga exhibited net gains. Significant distance-dependent interactions were not found, occurring only in the Cerrado 10-year dataset. These results emphasize that road paving impacts are context-dependent, and that multi-scale temporal and biome-specific assessments are essential for informing public policies and environmental licensing.

KEYWORDS: Before-after gradient (BAG); Land-use change; Road ecology; Road-effect zone; Road networks; Temporal-Spatial heterogeneity.

RESUMO

A pavimentação de estradas pode intensificar a atividade humana, resultando em maiores mudanças na vegetação nativa em áreas ao entorno. Neste estudo, buscamos compreender os efeitos da pavimentação na vegetação nativa ao longo do tempo e do espaço, utilizando o Brasil como estudo de caso devido à sua dimensão continental e diversidade de biomas. Aplicamos um delineamento de amostragem Antes-Depois-Gradiente (BAG) para comparar as taxas de mudança da vegetação nativa antes e depois da pavimentação ao longo de um gradiente de distância da estrada, tanto em escala nacional em escala nacional e por biomas brasileiros. Nossa análise utilizou dois conjuntos de dados temporais (períodos de 5 vs. 10 anos) e sete zonas de distância (1 a 15 km) para avaliar se os padrões de mudança dependem da escala temporal e para comparar as zonas de efeito da estrada nas taxas de mudança da vegetação nativa ao longo do tempo. Utilizamos modelos aditivos mistos generalizados para explorar a relação entre as taxas de mudança da vegetação nativa e os períodos antes e depois da pavimentação nas zonas. Os efeitos da pavimentação de estradas no Brasil foram dependentes da escala temporal analisada, no qual apenas o conjunto de dados de 10 anos revelou mudanças significativas. Contrariamente ao esperado, a análise nacional indicou um aumento geral ou desaceleração na perda de vegetação após a pavimentação, especialmente em zonas de até 3 km. Contudo, esses resultados mascararam a heterogeneidade espacial entre os biomas. A perda de vegetação nativa continuou na Amazônia, Cerrado e Pampa, enquanto a Mata Atlântica e a Caatinga exibiram ganhos. Interações significativas entre período e distância foram detectadas apenas no Cerrado no período de 10 anos. Estes resultados enfatizam que os impactos da pavimentação de estradas são dependentes do contexto e que avaliações temporais multiescala e específicas por bioma são essenciais para informar políticas públicas e o licenciamento ambiental.

1. INTRODUCTION

Deforestation and native vegetation fragmentation disrupt ecosystem structure, stability, and functionality (Newbold et al., 2015). These disruptions can lead to the loss of native biodiversity and key ecosystem services, such as natural resource availability (Nahuelhual et al., 2014), and biodiversity shortfalls (Thompson et al., 2011; Oguh et al., 2021; Sharma & Birman, 2024). Among the anthropogenic drivers of land use and land cover change, the construction of roads is particularly disruptive, affecting ecosystem structure and resilience (Forman & Alexander, 1998, Forman et al., 2003). There has been a rapid worldwide expansion of road networks in recent decades, and several studies focus on the impacts of road construction on native vegetation cover (e.g., Bürgi et al., 2005; Verburg & Veldkamp, 2004; Fiedeń, 2019; Zheng et al., 2025). However, it remains unclear how road paving affects native vegetation cover (Nepstad et al., 2001; Soares-Filho et al., 2004; Fearnside, 2007).

Land-use patterns and human activities play a key role in determining road networks, directly influencing the planning of roads (Forman et al., 2003). Initial opening of roads and infrastructure improvement, such as paving, are the main driver for deforestation of primary vegetation (Nepstad et al., 2001; Laurance et al., 2002; 2015; Marsik et al., 2011). Otherwise, in tropical countries like Brazil, the main impact of new major roads is the increase of indirect deforestation by secondary road encroachment (Fearnside, 2007; Perz et al., 2008). Road construction and paving are often economically justified by expected increase in commodities production transport, particularly in remote hinterlands under active expansion of economic frontiers (World Bank, 2021). After the paving intervention, the human presence and activity tend to increase and can exacerbate resource exploitation, as well as lead to additional changes in native vegetation (National Research Council, 2005; Seiler, 2003; Laurance et al., 2009; Xiaofeng et al., 2021). As an example, paved roads increased environmental degradation in surrounding areas by up to 61% compared to dirt roads in Brazil (Lupinetti-Cunha et al., 2022). Projections for the proposed pavement of BR 319, a major highway that will cross the centre of the Brazilian Amazonia, estimate an increase of 60% of the deforestation by the year 2100, when compared with a scenario of no road improvement (Santos et al., 2023).

One approach to assess the impacts of road construction or improvement on the areas surroundings from a road is known as the 'road-effect zone' (Forman & Alexander, 1998, Forman & Deblinger, 2000). The road-effect zone includes the area on both sides of a road that is affected by its presence and operation, and it often extends asymmetrically from road margins

due to spatial factors such as topography and vegetation, resulting in boundary variation (Forman & Deblinger, 2000). Identifying land-use changes and their effect-zone is essential for informed transportation policy and planning (Forman, 2000). This knowledge also supports decision making during the environmental permitting process, which is required in most countries (Abaza et al., 2004). Nevertheless, the spatial extent (effect zone) and magnitude of vegetation conversion after road paving remain poorly understood.

Our goal was to understand the effects of road paving on native vegetation change across distance from the road. We took advantage of Brazil's continental size – the world's largest tropical country – to explore temporal (before-after) and spatial (distance from road) dimensions – assessing native vegetation change rates across both national and biome scales. We applied a Before-After-Gradient (BAG) sampling design on Brazilian federal roads to answer the question: Does the native vegetation change rate differ before and after paving, and across road distance zones? Our hypothesis was that native vegetation change rates would be higher near the road before paving, due to limited access surrounding and less human presence, and would extend over larger distances after paving as improved access promotes the expansion of human activities. In addition, we expected that biomes with longer histories of human occupation would exhibit lower conversion rates than more recently explored biomes.

2. METHODS

2.1 Study area

Brazil is the largest tropical country (~8.5 million km^2) and is also one of the most biodiverse (Nash, 2022). It has developed an extensive road network under the federal and state administrations. Only for federal roads, almost 66,000 km are paved from a total of approximately 76,000 km (Ministério dos Transportes, 2023). We examine the whole forest and non-forest native vegetation cover change rates surrounding paved federal roads throughout Brazil and across the six major terrestrial biomes: Amazon Forest, Atlantic Forest, Caatinga Dry Forest, Cerrado Savannah, Pampa Grassland, and Pantanal Wetlands (**Figure 1**). We considered the definitions and boundaries of Brazilian biomes to explore the heterogeneity in vegetation and human occupation history, as well as to assess the trends within each biome. The expansion in the use and land cover conversion of Brazil's territory since European exploitation has been highly heterogeneous in space, with most economic activity concentrated in the Atlantic Forest domain (Bogoni et al., 2023), which still comprises approximately 70% of the Brazilian population (Metzger, 2009). The road network has since the half of 20^{th} century

progressively expanded inland into more remote hinterlands, paving the way to more recent mining, logging, and agricultural conversion (Douglas & Julien, 2023). Amazon and Cerrado are under the highest rates of contemporary conversion pressure (Souza et al., 2020). Furthermore, both biomes have the largest territorial extent (ICMBio, 2024) and the highest native vegetation cover, respectively 84% and 55% (Alencar et al., 2020; INPE, 2024). In contrast, the Atlantic Forest and the Caatinga succumbed to extensive loss since the 16th century, retaining respectively 28% and 11% of native vegetation (Araujo et al., 2023; Rezende et al., 2018). The Pampa and Pantanal are the smallest biomes in Brazil, both with ~2% of Brazil's territory (Ministério do Meio Ambiente, 2024) and are covered by approximately 40% and 80% of the original vegetation, respectively (Ribeiro et al., 2021; Azevedo et al., 2024).

2.2 Survey design and data collection

We applied a Before-After-Gradient (BAG) design to evaluate temporal and spatial variation and compare native vegetation change rates before and after road paving in different distance zones on both sides of road segments. Unlike the traditional Before-After-Control-Impact (BACI) approach, which requires a control area, the BAG design does not (Ellis & Schneider, 1997). Although control and impact sites can provide information on how the system changes over time after the intervention, defining these sites is a challenge mainly when effects are expected to have limited spatial and temporal extent (Methratta, 2020). In contrast, BAG design is particularly useful in contexts where spatial impact gradients are expected, quantifying effects when a response is anticipated to decrease as distance from the intervention increases (Morrison et al., 2008). The BAG approach has been used in wind farm impact studies (Methratta, 2020, 2021). Here, we adapt it to road ecology, as we were interested in assessing gradient effects before and after the paving intervention.

Paving year for each road and road segment were obtained from the open access online platform of the Annual Mapping Project for Land Use and Land Cover in Brazil (MapBiomas, 2023), which compiled road data from the National Department of Transport Infrastructure (DNIT; https://www.gov.br/dnit). These data include information such as the year of project implementation (e.g., road opening, road paving, and road duplication). However, as this information was unevenly available across roads, we restricted our study to major paved roads, or highways – with clear information on the year of paving. We used landscape images from the same platform to obtain annual landscape images, which were limited between 1985 and 2022 (MapBiomas, 2023). Based on image availability, we selected roads paved between 1990

and 2017 for 5-year dataset and 1995 and 2012 for 10-year dataset. This selection allowed us to analyse two-time frame datasets, 5-year and 10-year periods, which represent 5 or 10 years before and 5 or 10 years after paving for each road segment. We sought to assess short- and intermediate-time changes and examine whether native vegetation rates depend on the time frame chosen for analysis. The selected roads were then split into segments of 5 km, which we considered as our spatial sampling unit. All roads with the same official identification code were segmented to this length for assessment purposes and segments shorter than 5 km were excluded. For the 5-year dataset, the road splitting resulted in 2,143 road segments of 5 km assessed across 25 Brazilian states (from a total of 26 states and one federal district), whereas the 10-year dataset resulted in a total of 1,666 segments across 24 states (**Figure 1**; **Table 1**). Note, Pantanal biome had few roads and segments, thus the results for this biome should be interpreted with caution. The selected federal road segments represent 16.23% of the total federal road network in Brazil.

For each segment, we determined seven distance zones to evaluate the effect of the road paving zone on both roadsides (**Figure 2**). Our sampling design considered two sizes of buffer areas, similar to the description of Zheng et al. (2021). The first five neighbouring zones were narrower, increasing by 1 km each. These distances are commonly used to assess roadside changes (e.g., Su et al., 2014; Igondova et al., 2016; Fiedeń, 2019). The last two outer zones were 5-km wide to assess broader landscape trends and provide insight into native vegetation changes further from the intervention area (e.g., Tisler et al., 2022). We assumed that buffer width would not significantly influence native vegetation changes across distances and that native vegetation was homogeneous between different classes, despite the presence of different classes of native vegetation classes. Within each of these seven distance zones, we extracted the proportion of native vegetation cover (range 0.0 to 1.0) and calculated the rates of native vegetation change. These data were obtained for the 5-year and 10-year datasets before and after the year of paving (but not including the year of intervention). Information about land cover classes about landscape was obtained through the most the MapBiomas Collection 8 (MapBiomas, 2023). Our classification of native vegetation considered all classes and subclasses of natural vegetation types available on the MapBiomas platform. We aggregated all the following vegetation classes as native vegetation: forest formation, savanna formation, mangrove, seasonally flooded forest, wooded sandbank vegetation, wetland, grassland, hypersaline tidal flat, rocky outcrop, herbaceous sandbank vegetation, other non-forest formations. The MapBiomas vegetation classification was based on Landsat images, with a 30

m resolution and a vegetation classification accuracy of 90% (see MapBiomas 2023 for complete documentation on classification procedures).

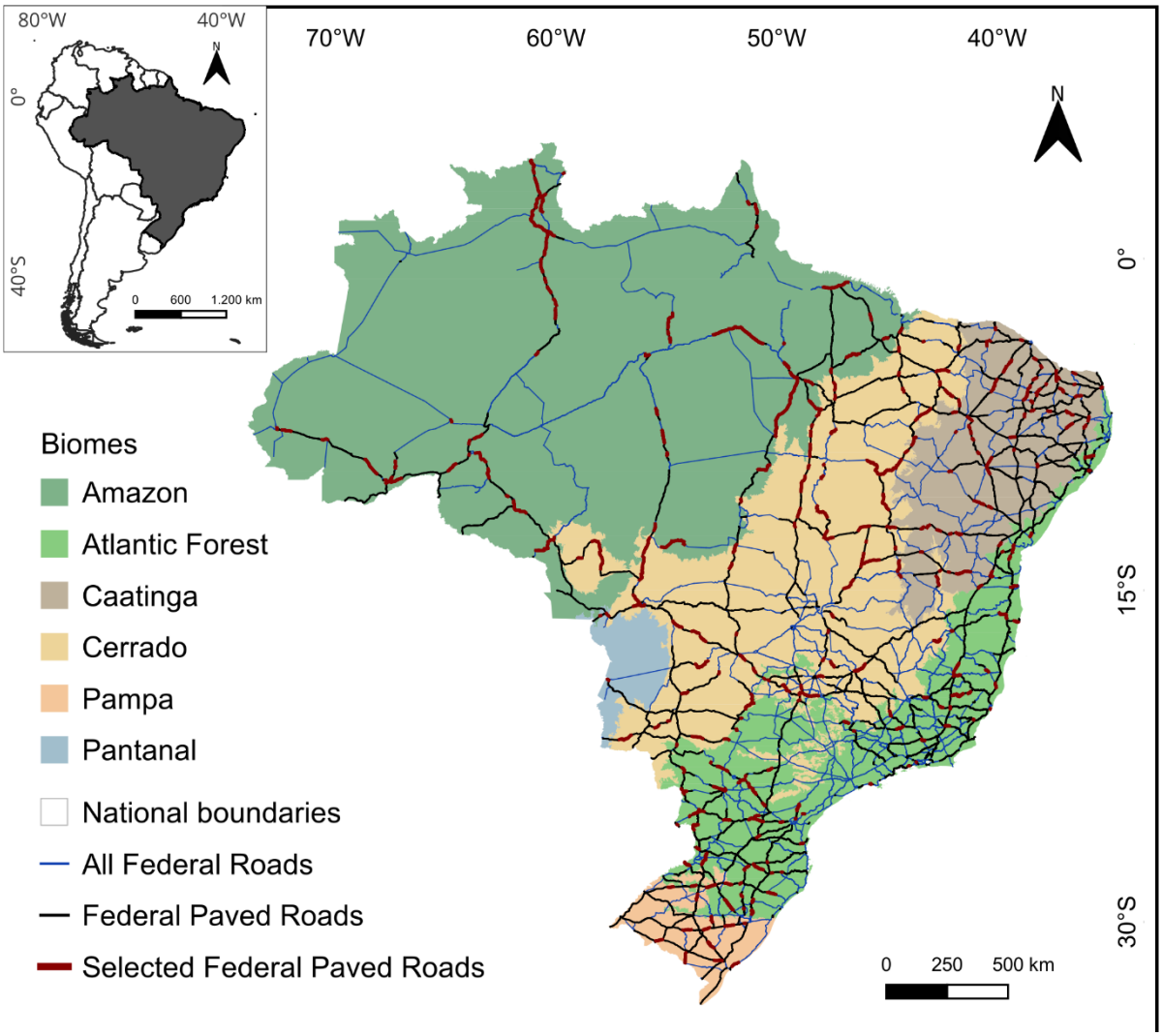


Figure 1. Location of the study area and distribution of analysed road segments across Brazilian biomes. The inset map displays Brazil's position within South America (grey). The main map illustrates the six terrestrial biomes of Brazil, overlaid with the federal road network: blue lines represent major federal highways, black lines indicate paved federal roads, and dark red lines highlight the specific paved segments selected for this study.

Table 1. Number of highways and 5-km segments selected for each Brazilian biome for both time frame datasets (5-year and 10-year) considered in this study.

	5-year dataset		10-year dataset	
biomes	**No. of roads**	**No. of segments**	**No. of roads**	**No. of segments**
Amazon	26	673	24	480
Atlantic Forest	55	416	45	327
Caatinga	31	265	25	184
Cerrado	36	685	31	591
Pampa	7	100	7	80
Pantanal	2	4	2	4
Total	137	2,143	116	1,666

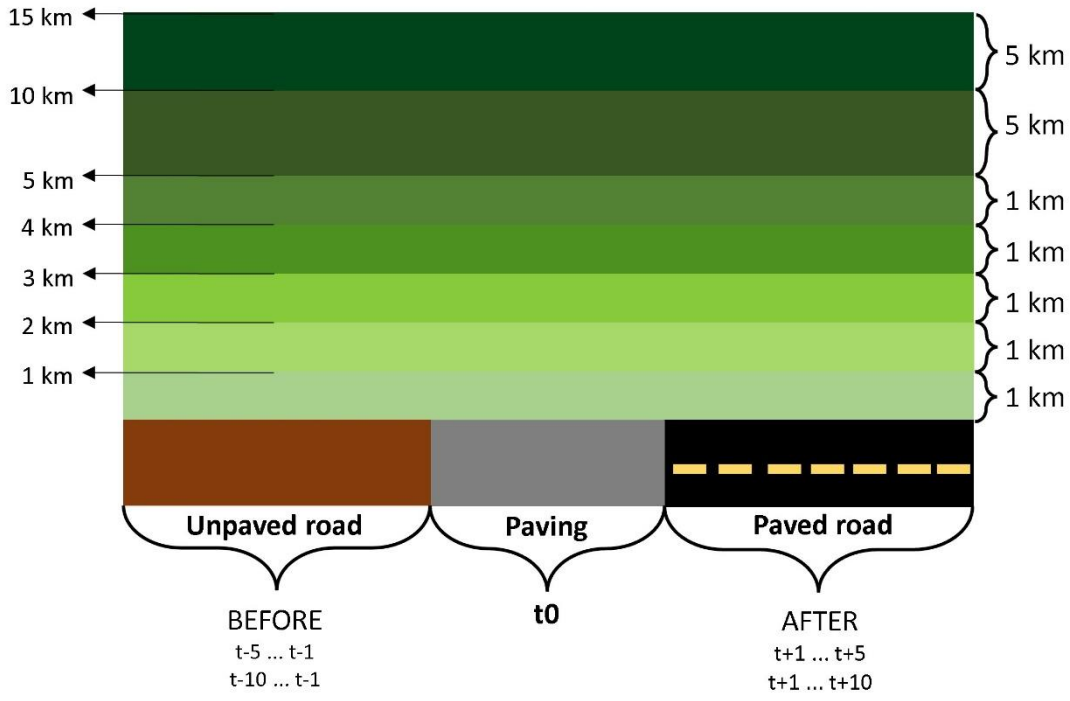


Figure 2. Before-After-Gradient (BAG) sampling design for extracting roadside land cover data. Euclidean distances from the road (km) are indicated on the left, with corresponding road-effect zone intervals on the right. Native vegetation change rates were calculated for each zone across 5-year and 10-year time frame datasets.

2.3 Data analysis

To assess the native vegetation changes over time and spatially, we calculated the native vegetation change rate before and after road paving (e.g., Silveira et al., 2022) for each distance zone separately. Native vegetation change rates were calculated as proportional changes relative to the initial vegetation cover, allowing comparisons among distance zones with

different baseline vegetation levels. The following equations were used to compute the native vegetation change rates:

Equation (1):

$$\text{Change rate before paving} = \frac{\text{one year before} - \text{five or ten years before}}{\text{five or ten years before}}$$

Equation (2):

$$\text{Change rate after paving} = \frac{\text{five or ten years after} - \text{one year after}}{\text{one year after}}$$

When the results from these equations were negative values, it indicates a decrease in native vegetation cover in that zone. On the contrary, a positive value suggests an increase in native vegetation cover. Note that although negative values indicate a decrease of native vegetation, when comparing the periods, it can indicate a deacceleration in the rate of vegetation loss. Outliers exhibiting high rates of change were visually inspected using high-resolution Google Earth historical satellite imagery. In cases where land cover misclassifications were identified, data were corrected to reflect zero native vegetation change.

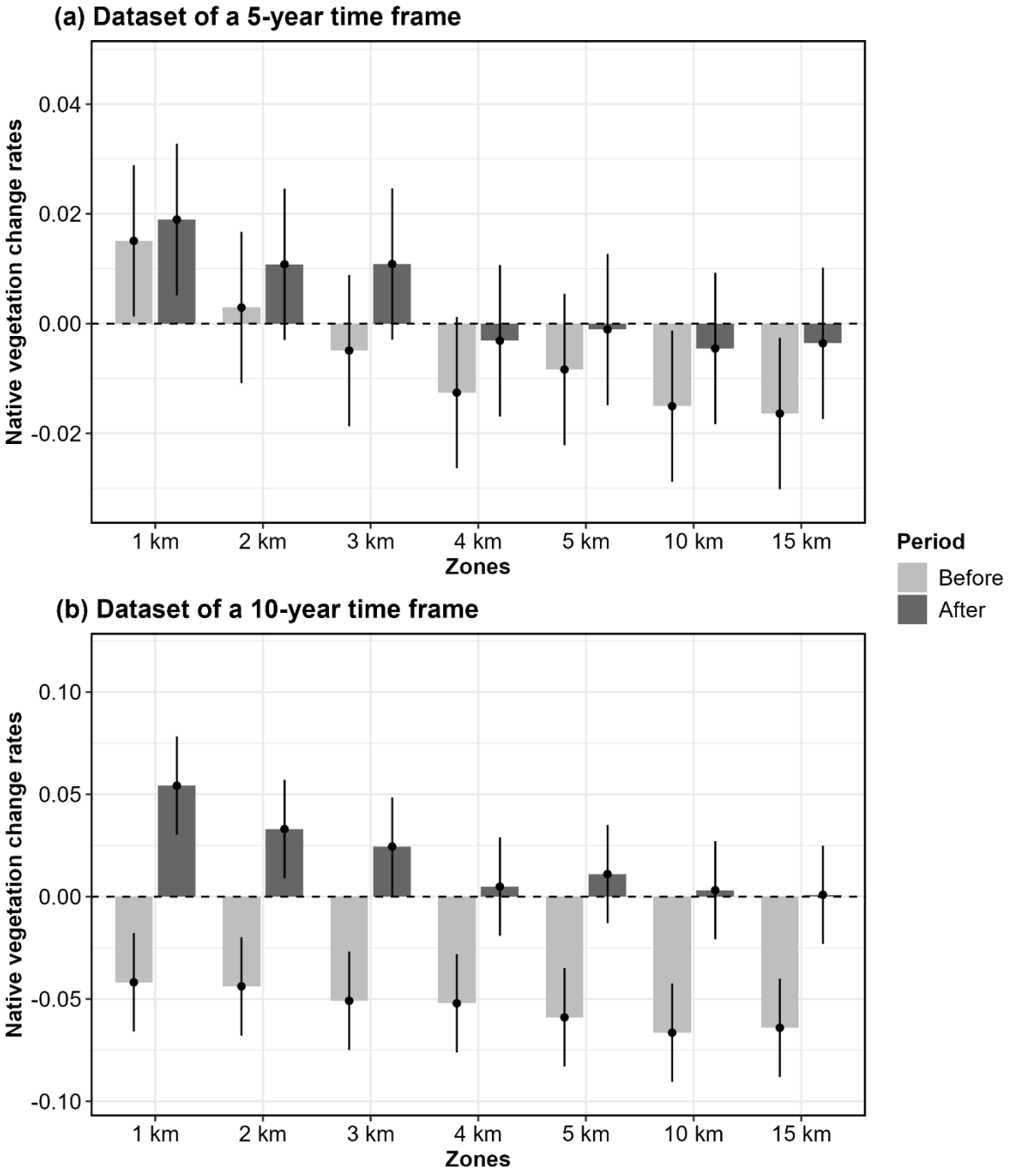
We used Generalized Additive Mixed Models (GAMM; Pedersen et al., 2019), an analytical method suitable when observations are not independent (e.g., segments of a road). GAMM also explores non-linear functional relationships between predictor variables and outcomes through a random effect in the models (Kim, 2015). We used a GAMM to evaluate how the native vegetation changes rates (response variable) differ between periods (before vs. after) and distance zones from the road. The same model structure was used to explore the overall response on a national scale, and across biomes separately.

The structure of the model was $y \sim x_1 * x_2 + s(x_3)$, where x_1 represents the period, x_2 corresponds to the zone and x_3 is the road identification in a smooth term with a random wiggly curve to account for the variability among roads. For this model, we used REML (restricted maximum likelihood) parameter estimates, which means that smooth terms were penalised through maximum likelihood (Wood, 2011). We used the *Gaussian* family with an *identity* link, which is appropriate for values ranging from negative to positive. GAMM analyses were performed using the '*gam*' function in "*mgcv*" package (Wood, 2017; 2023). Interpretation of results was made through *post hoc* analysis using '*emmeans*' and '*contrast'* functions in "*emmeans*" package (Lenth, 2023). For the '*contrast'* functions, we tested whether the native

vegetation change rates between periods differed between adjacent zones, and we applied a multivariate adjustment. All required datasets and analyses were developed using R software (R Core Team, 2023).

3. RESULTS

In Brazil, the effects of road paving on native vegetation changes depended on the time frame adopted for the analysis (**Figure 3**). For the 5-year dataset, we did not observe significant differences between periods (before-after paving) between the road-distance zones ($R^2 = 0.082$; EDF = 119.7; F-value = 19.18; **Figure 3a**; **Table S1**). We also did not find significant differences in native vegetation change rates across periods between adjacent zones (**Table S2**). Although there were no differences when comparing periods, up to the 3 km zone we observed increased gains in native vegetation after paving whereas on more distant zones the rate of vegetation losses decreased (**Figure 3a**; **Table S2**). In contrast, the 10-year dataset revealed significant differences between the before and after periods across distance zones ($R^2 = 0.14$; EDF = 104.67; F-value = 30.29; **Figure 3b**; **Table S3**), but without statistical differences between adjacent zones (**Table S4**). Before paving, native vegetation was consistently lost across all zones whereas after paving there was a gain of native vegetation in the nearest zones, up to 3 km (**Figure 3b**; **Table S4**). The impact of road paving on native vegetation change rates varied with road distance across Brazilian biomes. We observed native vegetation loss in the Amazon, Cerrado, and Pampa, and native vegetation gain in the Atlantic Forest and Caatinga in both time periods; however, the magnitude of these changes increased after road paving. These general trends were consistent across all buffer distances regardless of the time frame analysed (**Figures 3**, **4**; **Tables S5–S8**). The Pantanal biome had few road segments evaluated thus we observed no consistent responses of gains and losses (**Figure 4**). Cerrado was the only biome with a significant value for the interaction of the period and distance zone to road with a smaller decrease of vegetation loss after paving in the 2km zone when compared to the 1km zone, and this was observed only in the 10-year dataset (**Figure 4b**; **Table S8**).



254

255 **Figure 3.** Estimated Marginal Means of native vegetation change rates for each period – before
256 and after paving – across the seven distance zones from federal roads for a) 5-year time frame
257 dataset and b) 10-year dataset. Solid dots indicate estimated marginal mean values, vertical
258 lines represent 95% confidence intervals, and the dashed black line highlights the zero point.

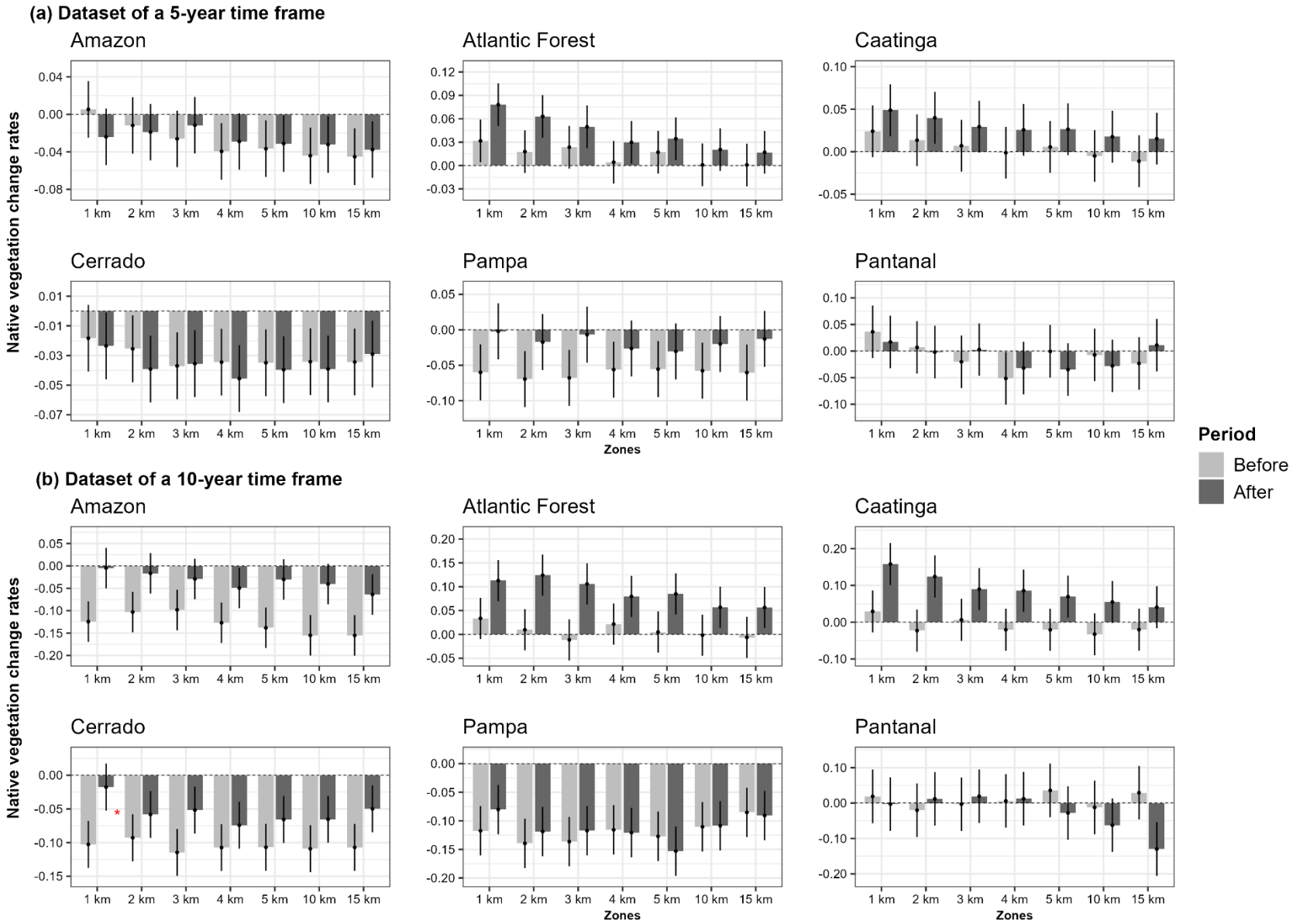

(a) Dataset of a 5-year time frame
Amazon
Atlantic Forest
Caatinga
Cerrado
Pampa
Pantanal
Native vegetation change rates
1 km
2 km
3 km
4 km
5 km
10 km
15 km
Zones
(b) Dataset of a 10-year time frame
Amazon
Atlantic Forest
Caatinga
Cerrado
Pampa
Pantanal
Native vegetation change rates
Zones
Period
Before
After

Figure 4. Estimated Marginal Means of native vegetation change rates for each period – before and after paving – across the seven distance zones from federal roads for both time frame datasets, separately for each major terrestrial biome of Brazil. The red asterisk highlights significant differences ($p<0.05$) in native vegetation change rates between periods and adjacent zones. Solid dots indicate estimated marginal means values, vertical lines represent 95% confidence intervals, and the dashed black line highlights the zero point.

4. DISCUSSION

Our results highlighted that native vegetation cover changes after road paving depended on the temporal scale of analysis. Selecting different time frames can substantially change the estimated magnitude, timing, and even direction of road-related vegetation effects. Significant differences in vegetation change rates between before and after paving periods were only detectable in the 10-year dataset. As expected, the negative change rates before paving likely reflect land-use changes-initiated years prior to paving, where road opening represents the primary impact. However, contrary to literature expectations, our national-scale analysis revealed net gains in native vegetation cover at all distances from roads after paving in the 10-year dataset. This finding aligns with evidence of non-linear temporal trajectories in vegetation response to road interventions. Time lags in deforestation have been documented for Brazil's Atlantic Forest (Freitas et al., 2010), while studies in the Asia-Pacific region show that deforestation peaks soon after road opening and then declines as accessible forest becomes exhausted (Engert et al., 2024). Similarly, shifts in deforestation rates over time have been observed after road paving in the Brazilian Amazon, with increases shortly after paving (Southworth et al., 2011). Measuring only early years may therefore overestimate long-term average impacts, whereas focusing only on later years may suggest weak or absent road effects. Adopting a multi-scale temporal approach is essential to capture the pre-road baseline, post-opening peak, and saturation phases of road effects on vegetation change (e.g., Newman et al., 2014). However, current road-related databases require improvement, particularly regarding the timing of construction (e.g., Valle et al., 2023), paving, and lane expansion, to allow evaluation of vegetation change dynamics at finer resolutions and broader temporal scales. This would allow explicit modelling of time since road paving while controlling for time since construction, rather than relying on arbitrary time frames (e.g., Engert et al., 2025).

Beyond temporal scale, native vegetation responses to road paving also depended on distance from the road. While our national-scale analysis revealed net vegetation gains after paving in the 10-year dataset, biome-scale analyses showed contrasting responses across biomes in both time frames. These biome-specific patterns responses are consistent with Souza et al. (2020), who demonstrated that road paving effects on native vegetation are not uniform across Brazilian biomes. Contrary to expectations of increased native vegetation loss following road paving (Southworth et al., 2011; Sánchez-Cuervo et al., 2020), we observed net gains or deceleration in loss rates after paving, though the magnitude and direction varied regionally. MapBiomas (2024) data shows an increase in secondary vegetation over recent years in most

Brazilian biomes, which may reduce the net impact of primary forest loss and help explain our findings. The distinct biome-level responses likely reflect different land-use histories and current development pressures. In the Amazon and Cerrado, the most deforested regions over the past four decades (Souza et al., 2020), recent years have been characterized by expanding logging and agricultural frontiers (Barbosa et al., 2023; DeArmond et al., 2023), where road opening and paved road density are well-known drivers of vegetation conversion (Espírito-Santo et al., 2016). These findings are particularly important given that public policies driving economic development directly influence land-use changes in these biomes (Funderburg et al., 2010; Patarasuk & Binford, 2012; Espírito-Santo et al., 2016). The deceleration in native vegetation loss we observed may reflect multiple concurrent processes, such as depletion of remaining exploitable vegetation (Rudel et al., 2005; Fearnside, 2017), expansion of protected areas and Indigenous territories, and conservation policies such as the soybean moratorium (Kastens et al., 2017; Gonçalves-Souza et al., 2021). However, this deceleration represents slower loss compared to the pre-paving period, not net gains; paving may still enable a "second cycle" of exploitation in areas previously unfeasible due to access costs, meaning losses likely remain higher than in a no-paving scenario. In contrast, the Atlantic Forest and Caatinga have experienced centuries of land-use pressure (Silva et al., 2017; Solórzano et al., 2021), and vegetation gains in these biomes may be partly attributable to farmland abandonment in rural areas (Castro et al., 2020; da Silva et al., 2017). Although initially unexpected, the gain of native vegetation on these biomes has also been observed in previous studies (Araujo et al., 2023; Bicudo da Silva et al., 2023; Jardim et al., 2022; Piffer et al., 2022; da Silva et al., 2020). The observed variations in road effect magnitude among biomes can be attributed to factors we did not explicitly model, such as regional topography (Lin et al., 2020; Seiler, 2003), vegetation type (Lisiak-Zielińska et al., 2022), and urban activities (Hu & Lo 2007; Mothorpe et al., 2013). Moreover, substantial intra-biome variability exists at the scale of individual projects, demonstrating that road paving effects are also dependent on local landscape contexts. To exemplify, the projections of vegetation change for the BR-319 highway reinforce that environmental planning and licensing processes should prioritize localized, project-specific assessments rather than relying solely on generalized biome-scale trends.

Regardless of the time frame or biome considered, we detected no significant differences in vegetation change rates among distance zones, up to 15 km from roads, between pre- and post-paving periods. This response contrasts with most studies of road opening, which report strongest vegetation losses within 1–5 km of roads and decreasing impacts with distance

(Zhang et al., 2002; Gao et al., 2011; Long & Li, 2001; Zhu et al., 2001). However, growing evidence demonstrates that land-use impacts can extend well beyond 5 km, reaching 10–15 km or more (Zhang et al., 2002; Yan et al., 2003; Zheng et al., 2021; Lisiak-Zielińska et al., 2022), suggesting that distance alone may not fully capture road impact gradients. Lisiak-Zielińska et al. (2022) showed that landscape structure and land cover types respond differently across road-effect zones, while Zheng et al. (2021) found heterogeneous responses even within the same distance zone, indicating that local landscape characteristics may override simple distance-decay patterns. However, our results revealed one exception to the general pattern, in the Cerrado biome's 10-year dataset, we observed a significant period-by-distance interaction, with smaller decreases in vegetation loss after paving at 2 km compared to 1 km zones. This suggests that some localized distance-dependent effects may exist but require longer observation periods and biome-specific analyses to be detected. One future improvement in modelling studies should be the inclusion of variables that likely modulate road effects across space, such as elevation, protected area and urban cover, concurrent new road openings or improvements, and the influence of government policies. These variables could provide deeper understanding of vegetation change drivers across Brazil, identify the most important factors at different spatial scales, and support decision-making for individual road projects. Our findings demonstrate that broader generalizations should be used with cautions and local assessments are needed.

Our analysis was restricted to approximately 16% of Brazil's federal paved road network due to limited data on the precise timing of road paving interventions, thus before use our findings to support any decision we recommend further investigation of larger time series, controlling for other variables than distance and biome and if data allow, explore BACI designs. However, our results demonstrated, for the spatial and temporal extends considered, that paving has context dependent effects on native vegetation cover.

AUTHOR CONTRIBUTIONS

Ingridi Camboim Franceschi: Conceptualization; Methodology; Data Curation; Formal analysis; Visualization, Writing – original draft (lead); Writing – review and editing. **Andreas Kindel**: Conceptualization; Methodology; Supervision, Writing – review and editing. **Cristian de Sales Dambros**: Conceptualization; Methodology; Funding acquisition; Writing – review and editing. **Carlos A. Peres**: Conceptualization; Methodology; Funding acquisition; Writing – review and editing. **Lucas Ferreira Colares**: Formal analysis; Validation, Writing – review

and editing. **Juliano Sarmento Cabral**: Conceptualization; Methodology; Formal analysis; Resources, Funding acquisition; Supervision, Writing – review and editing.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Global Change Biology

SUPPORTING INFORMATION

Native vegetation changes before and after road paving on landscape spatial gradients

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SUPPORTING INFORMATION

Table S1: Statistical results of GAMM comparing the 5-year before and after paving across Brazil.

Table S2: Statistical results of *post-hoc* analysis on native vegetation change rates across periods and distance zones in the 5-year dataset across Brazil.

Table S3: Statistical results of GAMM comparing the 10-year before and after paving across Brazil.

Table S4: Statistical results of *post-hoc* analysis on native vegetation change rates across periods and distance zones in the 10-year dataset.

Table S5: Statistical results of GAMM comparing the 5-year before and after paving for each Brazilian biome.

Table S6: Statistical results of *post-hoc* analysis on native vegetation change rates across periods and distance zones across six Brazilian biomes over the 5-year dataset.

Table S7: Statistical results of GAMM comparing the 10-year before and after paving for each Brazilian biome.

Table S8: Statistical results of *post-hoc* analysis on native vegetation change rates across periods and distance zones across six Brazilian biomes over the 10-year dataset.

Table S1. Predictors of native vegetation change rate across Brazil. We fitted a Generalized Additive Mixed Model to assess the effects of time (five years before vs. five years after federal roads paving), distance zones from the road (zone 0: 1 km; zone 1: 2 km; zone 2: 3 km; zone 3: 4 km; zone 4: 5 km; zone 5: 10 km; zone 6: 15 km), and road identity as a random effect. The values shown represent the estimates of the regression coefficients, the standard error (SE) and the *p*-value of significance ($p<0.05$). For the random smooth term has the Effective Degrees of Freedom value (EDF) that quantifies the flexibility of the smooth term, the F-value that determines the ratio of explained variance to unexplained variance and the *p*-value. Model fit is indicated by the coefficient of determination (R^2).

Parametric	**Coefficients**			
Predictors	**Estimate**	**SE**	**t Value**	**p-value**
Intercept	0.015	0.007	2.143	0.032
After	0.004	0.006	0.653	0.514
zone 1	-0.012	0.006	-2.036	0.042
zone 2	-0.020	0.006	-3.351	0.001
zone 3	-0.028	0.006	-4.637	<0.001
zone 4	-0.023	0.006	-3.930	<0.001
zone 5	-0.030	0.006	-5.050	<0.001
zone 6	-0.031	0.006	-5.275	<0.001
After: zone 1	0.004	0.008	0.472	0.637
After: zone 2	0.012	0.008	1.408	0.159
After: zone 3	0.006	0.008	0.659	0.510
After: zone 4	0.003	0.008	0.404	0.687
After: zone 5	0.007	0.008	0.785	0.433
After: zone 6	0.009	0.008	1.056	0.291
Smooth term				
Predictors	**Edf**	**Ref.df**	**F**	**p-value**
s(codRoad)	119.7	136	19.18	<0.001
NcodRoad	137			
Observations	30002			
Conditional R^2	0.082			

Table S2. *Post hoc* pairwise comparisons based on the GAMM results for the 5-year dataset across Brazil. The first section presents the Estimated Marginal Means (EMMs) of native vegetation change rate for each combination of time periods – Before and After the paving of federal roads in Brazil – and the seven distance zones from the roads (zone 0: 1 km; zone 1: 2 km; zone 2: 3 km; zone 3: 4 km; zone 4: 5 km; zone 5: 10 km; zone 6: 15 km). The second section presents the interaction contrasts of native vegetation change rates between periods varies between pairs of adjacent zones. The reported values include the EMMs (emmean), estimated difference (Estimate), standard error (SE), degrees of freedom (df), the lower and upper bounds of the 95% confidence interval (lower.CL and upper.CL), t-statistic (t.ratio), and the *p-value* of significance (p<0.05).

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	0.015	0.007	29868	0.001	0.029
After	0	0.019	0.007	29868	0.005	0.033
Before	1	0.003	0.007	29868	-0.011	0.017
After	1	0.011	0.007	29868	-0.003	0.025
Before	2	-0.005	0.007	29868	-0.019	0.009
After	2	0.011	0.007	29868	-0.003	0.025
Before	3	-0.013	0.007	29868	-0.026	0.001
After	3	-0.003	0.007	29868	-0.017	0.011
Before	4	-0.008	0.007	29868	-0.022	0.005
After	4	-0.001	0.007	29868	-0.015	0.013
Before	5	-0.015	0.007	29868	-0.029	-0.001
After	5	-0.005	0.007	29868	-0.018	0.009
Before	6	-0.016	0.007	29868	-0.030	-0.003
After	6	-0.004	0.007	29868	-0.017	0.010
Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	0.004	0.008	29868	0.472	0.637
Before - After	1 - 2	0.008	0.008	29868	0.936	0.349
Before - After	2 - 3	-0.006	0.008	29868	-0.749	0.454
Before - After	3 - 4	-0.002	0.008	29868	-0.255	0.799
Before - After	4 - 5	0.003	0.008	29868	0.381	0.703
Before - After	5 - 6	0.002	0.008	29868	0.271	0.786

Table S3. Predictors of native vegetation change rate across Brazil. We fitted a Generalized Additive Mixed Model to assess the effects of time (10 years before vs. 10 years after federal roads paving), distance zones from the road (zone 0: 1 km; zone 1: 2 km; zone 2: 3 km; zone 3: 4 km; zone 4: 5 km; zone 5: 10 km; zone 6: 15 km), and road identity as a random effect. The values shown represent the estimates of the regression coefficients, the standard error (SE) and the *p*-value of significance ($p<0.05$). For the random smooth term has the Effective Degrees of Freedom value (EDF) that quantifies the flexibility of the smooth term, the F-value that determines the ratio of explained variance to unexplained variance and the *p*-value. Model fit is indicated by the coefficient of determination (R^2).

Parametric	**Coefficients**			
Predictors	**Estimate**	**SE**	**t Value**	***p*-value**
Intercept	-0.042	0.012	-3.416	0.001
After	0.096	0.009	10.243	<0.001
zone 1	-0.002	0.009	-0.209	0.835
zone 2	-0.009	0.009	-0.960	0.337
zone 3	-0.010	0.009	-1.092	0.275
zone 4	-0.017	0.009	-1.823	0.068
zone 5	-0.025	0.009	-2.621	0.009
zone 6	-0.022	0.009	-2.366	0.018
After: zone 1	-0.019	0.013	-1.449	0.147
After: zone 2	-0.021	0.013	-1.565	0.118
After: zone 3	-0.039	0.013	-2.946	0.003
After: zone 4	-0.026	0.013	-1.967	0.049
After: zone 5	-0.026	0.013	-1.996	0.046
After: zone 6	-0.031	0.013	-2.344	0.019
Smooth term				
Predictors	**Edf**	**Ref.df**	**F**	***p*-value**
s(codRoad)	104.67	115	30.29	<0.001
NcodRoad	116			
Observations	23324			
Conditional R^2	0.145			

Table S4. *Post hoc* pairwise comparisons based on the GAMM results for the 10-year dataset across Brazil. The first section presents the Estimated Marginal Means (EMMs) of native vegetation change rate for each combination of time periods – Before and After the paving of federal roads in Brazil – and the seven distance zones from the roads (zone 0: 1 km; zone 1: 2 km; zone 2: 3 km; zone 3: 4 km; zone 4: 5 km; zone 5: 10 km; zone 6: 15 km). The second section presents the interaction contrasts of native vegetation change rates between periods varies between pairs of adjacent zones. The reported values include the EMMs (emmean), estimated difference (Estimate), standard error (SE), degrees of freedom (df), the lower and upper bounds of the 95% confidence interval (lower.CL and upper.CL), t-statistic (t.ratio), and the *p-value* of significance (p<0.05).

Estimated Marginal Means						
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	-0.042	0.012	23205	-0.066	-0.018
After	0	0.054	0.012	23205	0.030	0.078
Before	1	-0.044	0.012	23205	-0.068	-0.020
After	1	0.033	0.012	23205	0.009	0.057
Before	2	-0.051	0.012	23205	-0.075	-0.027
After	2	0.024	0.012	23205	0.000	0.048
Before	3	-0.052	0.012	23205	-0.076	-0.028
After	3	0.005	0.012	23205	-0.019	0.029
Before	4	-0.059	0.012	23205	-0.083	-0.035
After	4	0.011	0.012	23205	-0.013	0.035
Before	5	-0.066	0.012	23205	-0.091	-0.042
After	5	0.003	0.012	23205	-0.021	0.027
Before	6	-0.064	0.012	23205	-0.088	-0.040
After	6	0.001	0.012	23205	-0.023	0.025
Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	-0.019	0.013	23205	-1.449	0.147
Before - After	1 - 2	-0.002	0.013	23205	-0.116	0.908
Before - After	2 - 3	-0.018	0.013	23205	-1.381	0.167
Before - After	3 - 4	0.013	0.013	23205	0.979	0.327
Before - After	4 - 5	0.000	0.013	23205	-0.029	0.977
Before - After	5 - 6	-0.005	0.013	23205	-0.348	0.728

Table S5. Predictors of the accumulative rate of native vegetation across all six biomes of Brazil. We performed a Generalized Additive Mixed Model, to assess the effects of time (five years before vs. five years after Federal roads paving), the six Brazilian biomes, seven zones of distance from the road (zone 0: 1 km, zone 1: 2 km; zone 2: 3 km, zone 3: 4 km, zone 4: 5 km, zone 5: 10 km, zone 6: 15 km), and road identity as a random effect. The values shown represent the estimates of the regression coefficients, the standard error (SE), and the *p*-value of significance ($p<0.05$). For the random smooth term has the Effective Degrees of Freedom value (EDF) that quantifies the flexibility of the smooth term, the F-value that determines the ratio of explained variance to unexplained variance and the *p*-value. Model fit is indicated by the coefficient of determination (R^2).

	Amazon			**Atlantic Forest**			**Caatinga**			**Cerrado**			**Pampa**			**Pantanal**		
Parametrics	**Coefficients**																	
Predictors	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**
Intercept	0.01	0.02	0.729	0.03	0.01	0.024	0.02	0.02	0.121	-0.02	0.01	0.110	-0.06	0.02	0.003	0.04	0.02	0.146
After	-0.03	0.01	0.005	0.05	0.02	0.003	0.02	0.02	0.118	-0.01	0.01	0.623	0.06	0.01	<0.001	-0.02	0.03	0.579
zone 1	-0.02	0.01	0.100	-0.01	0.02	0.372	-0.01	0.02	0.503	-0.01	0.01	0.498	-0.01	0.01	0.515	-0.03	0.03	0.395
zone 2	-0.03	0.01	0.003	-0.01	0.02	0.599	-0.02	0.02	0.279	-0.02	0.01	0.077	-0.01	0.01	0.592	-0.06	0.03	0.107
zone 3	-0.04	0.01	<0.001	-0.03	0.02	0.076	-0.03	0.02	0.109	-0.02	0.01	0.126	0.00	0.01	0.789	-0.09	0.03	0.014
zone 4	-0.04	0.01	<0.001	-0.01	0.02	0.346	-0.02	0.02	0.242	-0.02	0.01	0.116	0.00	0.01	0.758	-0.04	0.03	0.289
zone 5	-0.05	0.01	<0.001	-0.03	0.02	0.046	-0.03	0.02	0.065	-0.02	0.01	0.134	0.00	0.01	0.877	-0.04	0.03	0.211
zone 6	-0.05	0.01	<0.001	-0.03	0.02	0.045	-0.04	0.02	0.026	-0.02	0.01	0.129	-0.00	0.01	0.985	-0.06	0.03	0.089
After: zone 1	0.02	0.01	0.133	-0.00	0.02	0.953	0.00	0.02	0.937	-0.01	0.01	0.571	-0.01	0.02	0.779	0.01	0.05	0.832
After: zone 2	0.04	0.01	0.003	-0.02	0.02	0.349	-0.00	0.02	0.918	0.01	0.01	0.654	0.00	0.02	0.883	0.04	0.05	0.389
After: zone 3	0.04	0.01	0.007	-0.02	0.02	0.331	0.00	0.02	0.917	-0.01	0.01	0.693	-0.03	0.02	0.170	0.04	0.05	0.430

After: zone 4	0.03	0.01	0.018	-0.03	0.02	0.181	-0.00	0.02	0.861	0.00	0.01	0.971	-0.03	0.02	0.110	-0.02	0.05	0.755
After: zone 5	0.04	0.01	0.005	-0.03	0.02	0.216	-0.00	0.02	0.927	0.00	0.01	0.984	-0.02	0.02	0.325	-0.00	0.05	0.976
After: zone 6	0.04	0.01	0.012	-0.03	0.02	0.163	0.00	0.02	0.931	0.01	0.01	0.480	-0.01	0.02	0.608	0.05	0.05	0.274
Smooth term																		
Predictors	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**
s(codRoad)	22.97	27.56	<0.001	41.74	7.74	<0.001	25.93	11.08	<0.001	29.84	15.45	<0.001	5.83	30.13	<0.001	0.24	0.31	0.26
$N_{codRoad}$	26			55			31			36			7			2		
Observations	9422			5824			3710			9590			1400			56		
R^2	0.07			0.07			0.09			0.05			0.15			-0.003		

Table S6. *Post hoc* pairwise comparisons based on the GAMM results for the 5-year dataset across the six biomes in Brazil. For each biome individually, two results are presented: The first section presents the Estimated Marginal Means (EMMs) of native vegetation change rate for each combination of time periods – Before and After the paving of federal roads in Brazil – and the seven distance zones from the roads (zone 0: 1 km; zone 1: 2 km; zone 2: 3 km; zone 3: 4 km; zone 4: 5 km; zone 5: 10 km; zone 6: 15 km). The second section presents the interaction contrasts of native vegetation change rates between periods varies between pairs of adjacent zones. The reported values include the EMMs (emmean), estimated difference (Estimate), standard error (SE), degrees of freedom (df), the lower and upper bounds of the 95% confidence interval (lower.CL and upper.CL), t-statistic (t.ratio), and the *p-value* of significance (p<0.05).

Amazon						
Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	0.005	0.015	9385	-0.025	0.035
After	0	-0.024	0.015	9385	-0.054	0.006
Before	1	-0.012	0.015	9385	-0.042	0.018
After	1	-0.019	0.015	9385	-0.049	0.011
Before	2	-0.026	0.015	9385	-0.056	0.004
After	2	-0.012	0.015	9385	-0.042	0.019
Before	3	-0.040	0.015	9385	-0.070	-0.009
After	3	-0.029	0.015	9385	-0.059	0.001
Before	4	-0.037	0.015	9385	-0.067	-0.007
After	4	-0.031	0.015	9385	-0.061	-0.001
Before	5	-0.044	0.015	9385	-0.074	-0.014
After	5	-0.032	0.015	9385	-0.062	-0.002
Before	6	-0.045	0.015	9385	-0.075	-0.015
After	6	-0.038	0.015	9385	-0.068	-0.007
Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	0.022	0.015	9385	1.503	0.133
Before - After	1 - 2	0.022	0.015	9385	1.466	0.143
Before - After	2 - 3	-0.004	0.015	9385	-0.269	0.788
Before - After	3 - 4	-0.005	0.015	9385	-0.340	0.734
Before - After	4 - 5	0.006	0.015	9385	0.437	0.662

Before - After	5 - 6	-0.004	0.015	9385	-0.297	0.766

Atlantic Forest

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	0.032	0.014	5768	0.004	0.059
After	0	0.078	0.014	5768	0.051	0.106
Before	1	0.018	0.014	5768	-0.010	0.045
After	1	0.063	0.014	5768	0.036	0.090
Before	2	0.023	0.014	5768	-0.004	0.051
After	2	0.050	0.014	5768	0.022	0.077
Before	3	0.004	0.014	5768	-0.023	0.032
After	3	0.030	0.014	5768	0.002	0.057
Before	4	0.017	0.014	5768	-0.010	0.044
After	4	0.034	0.014	5768	0.007	0.062
Before	5	0.001	0.014	5768	-0.026	0.028
After	5	0.021	0.014	5768	-0.007	0.048
Before	6	0.001	0.014	5768	-0.027	0.028
After	6	0.017	0.014	5768	-0.010	0.044

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	-0.001	0.022	5768	-0.059	0.953
Before - After	1 - 2	-0.019	0.022	5768	-0.877	0.380
Before - After	2 - 3	-0.001	0.022	5768	-0.037	0.971
Before - After	3 - 4	-0.008	0.022	5768	-0.366	0.714
Before - After	4 - 5	0.002	0.022	5768	0.101	0.919
Before - After	5 - 6	-0.003	0.022	5768	-0.156	0.876

Caatinga

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	0.024	0.016	3670	-0.006	0.055
After	0	0.049	0.016	3670	0.018	0.079
Before	1	0.014	0.016	3670	-0.017	0.044
After	1	0.040	0.016	3670	0.009	0.070
Before	2	0.007	0.016	3670	-0.023	0.037
After	2	0.029	0.016	3670	-0.001	0.060
Before	3	-0.001	0.016	3670	-0.032	0.029

After	3	0.026	0.016	3670	-0.005	0.056
Before	4	0.006	0.016	3670	-0.025	0.036
After	4	0.026	0.016	3670	-0.004	0.057
Before	5	-0.005	0.016	3670	-0.035	0.025
After	5	0.018	0.016	3670	-0.013	0.048
Before	6	-0.011	0.016	3670	-0.042	0.019
After	6	0.015	0.016	3670	-0.015	0.046

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	0.002	0.022	3670	0.079	0.937
Before - After	1 - 2	-0.004	0.022	3670	-0.181	0.856
Before - After	2 - 3	0.005	0.022	3670	0.207	0.836
Before - After	3 - 4	-0.006	0.022	3670	-0.279	0.780
Before - After	4 - 5	0.002	0.022	3670	0.083	0.934
Before - After	5 - 6	0.004	0.022	3670	0.178	0.859

Cerrado

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	-0.018	0.011	9546	-0.041	0.004
After	0	-0.024	0.011	9546	-0.046	-0.001
Before	1	-0.025	0.011	9546	-0.048	-0.003
After	1	-0.039	0.011	9546	-0.062	-0.017
Before	2	-0.037	0.011	9546	-0.059	-0.014
After	2	-0.035	0.011	9546	-0.058	-0.013
Before	3	-0.034	0.011	9546	-0.057	-0.012
After	3	-0.046	0.011	9546	-0.068	-0.023
Before	4	-0.035	0.011	9546	-0.057	-0.012
After	4	-0.040	0.011	9546	-0.062	-0.017
Before	5	-0.034	0.011	9546	-0.057	-0.012
After	5	-0.039	0.011	9546	-0.062	-0.017
Before	6	-0.034	0.011	9546	-0.057	-0.012
After	6	-0.029	0.011	9546	-0.052	-0.007

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	-0.008	0.015	9546	-0.566	0.571
Before - After	1 - 2	0.015	0.015	9546	1.014	0.310

Before - After	2 - 3	-0.013	0.015	9546	-0.843	0.399
Before - After	3 - 4	0.006	0.015	9546	0.431	0.667
Before - After	4 - 5	0.000	0.015	9546	-0.017	0.987
Before - After	5 - 6	0.010	0.015	9546	0.687	0.492

Pampa

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	-0.060	0.020	1380	-0.100	-0.021
After	0	-0.002	0.020	1380	-0.042	0.037
Before	1	-0.069	0.020	1380	-0.109	-0.030
After	1	-0.017	0.020	1380	-0.057	0.022
Before	2	-0.068	0.020	1380	-0.107	-0.028
After	2	-0.007	0.020	1380	-0.046	0.033
Before	3	-0.056	0.020	1380	-0.096	-0.017
After	3	-0.026	0.020	1380	-0.066	0.013
Before	4	-0.056	0.020	1380	-0.095	-0.016
After	4	-0.030	0.020	1380	-0.070	0.009
Before	5	-0.058	0.020	1380	-0.097	-0.018
After	5	-0.020	0.020	1380	-0.060	0.019
Before	6	-0.060	0.020	1380	-0.100	-0.021
After	6	-0.013	0.020	1380	-0.052	0.027

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	-0.006	0.021	1380	-0.280	0.779
Before - After	1 - 2	0.009	0.021	1380	0.428	0.669
Before - After	2 - 3	-0.031	0.021	1380	-1.521	0.129
Before - After	3 - 4	-0.005	0.021	1380	-0.225	0.822
Before - After	4 - 5	0.013	0.021	1380	0.615	0.539
Before - After	5 - 6	0.010	0.021	1380	0.470	0.638

Pantanal

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	0.036	0.024	42	-0.013	0.086
After	0	0.017	0.024	42	-0.032	0.067
Before	1	0.007	0.024	42	-0.043	0.056
After	1	-0.002	0.024	42	-0.051	0.047

Before	2	-0.020	0.024	42	-0.070	0.029
After	2	0.003	0.024	42	-0.047	0.052
Before	3	-0.051	0.024	42	-0.101	-0.002
After	3	-0.032	0.024	42	-0.081	0.017
Before	4	-0.001	0.024	42	-0.050	0.049
After	4	-0.035	0.024	42	-0.084	0.015
Before	5	-0.007	0.024	42	-0.057	0.042
After	5	-0.028	0.024	42	-0.077	0.022
Before	6	-0.023	0.024	42	-0.073	0.026
After	6	0.011	0.024	42	-0.038	0.061

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	0.010	0.048	42	0.214	0.832
Before - After	1 - 2	0.032	0.048	42	0.656	0.515
Before - After	2 - 3	-0.004	0.048	42	-0.074	0.942
Before - After	3 - 4	-0.054	0.048	42	-1.110	0.273
Before - After	4 - 5	0.014	0.048	42	0.283	0.779
Before - After	5 - 6	0.055	0.048	42	1.138	0.261

Table S7. Predictors of the accumulative rate of native vegetation across all six biomes of Brazil. We performed a Generalized Additive Mixed Model, to assess the effects of time (10 years before vs. five years after Federal roads paving), the six Brazilian biomes, seven zones of distance from the road (zone 0: 1 km, zone 1: 2 km; zone 2: 3 km, zone 3: 4 km, zone 4: 5 km, zone 5: 10 km, zone 6: 15 km), and road identity as a random effect. The values shown represent the estimates of the regression coefficients, the standard error (SE), and the *p*-value of significance ($p<0.05$). For the random smooth term has the Effective Degrees of Freedom value (EDF) that quantifies the flexibility of the smooth term, the F-value that determines the ratio of explained variance to unexplained variance and the *p*-value. Model fit is indicated by the coefficient of determination (R^2).

	Amazon			**Atlantic Forest**			**Caatinga**			**Cerrado**			**Pampa**			**Pantanal**		
Parametrics	**Coefficients**																	
Predictors	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**	**Estimate**	**SE**	***p*-value**
Intercept	-0.12	0.02	<0.001	0.03	0.02	0.127	0.03	0.03	0.316	-0.10	0.02	<0.001	-0.12	0.02	<0.001	0.02	0.04	0.621
After	0.12	0.02	<0.001	0.08	0.02	<0.001	0.13	0.04	<0.001	0.09	0.02	<0.001	0.04	0.02	0.087	-0.02	0.05	0.643
zone 1	0.02	0.02	0.247	-0.02	0.02	0.206	-0.05	0.04	0.145	0.01	0.02	0.514	-0.02	0.02	0.311	-0.04	0.05	0.404
zone 2	0.03	0.02	0.155	-0.05	0.02	0.017	-0.02	0.04	0.522	-0.01	0.02	0.429	-0.02	0.02	0.382	-0.02	0.05	0.639
zone 3	-0.00	0.02	0.886	-0.01	0.02	0.522	-0.05	0.04	0.165	-0.00	0.02	0.753	0.00	0.02	0.937	-0.01	0.05	0.786
zone 4	-0.01	0.02	0.451	-0.03	0.02	0.128	-0.05	0.04	0.164	-0.00	0.02	0.776	-0.01	0.02	0.654	0.02	0.05	0.715
zone 5	-0.03	0.02	0.097	-0.04	0.02	0.062	-0.06	0.04	0.084	-0.01	0.02	0.672	0.01	0.02	0.750	-0.03	0.05	0.506
zone 6	-0.03	0.02	0.095	-0.04	0.02	0.034	-0.05	0.04	0.167	-0.00	0.02	0.767	0.03	0.02	0.139	0.01	0.05	0.822
After: zone 1	-0.03	0.03	0.204	0.04	0.03	0.188	0.02	0.05	0.719	-0.05	0.02	0.018	-0.02	0.03	0.588	0.05	0.07	0.416
After: zone 2	-0.05	0.03	0.052	0.04	0.03	0.153	-0.05	0.05	0.371	-0.02	0.02	0.295	-0.02	0.03	0.557	0.04	0.07	0.505
After: zone 3	-0.04	0.03	0.107	-0.02	0.03	0.430	-0.02	0.05	0.654	-0.05	0.02	0.015	-0.04	0.03	0.170	0.03	0.07	0.672
After: zone 4	-0.01	0.03	0.656	0.00	0.03	0.970	-0.04	0.05	0.445	-0.04	0.02	0.040	-0.06	0.03	0.040	-0.04	0.07	0.522
After: zone 5	-0.01	0.03	0.846	-0.02	0.03	0.441	-0.04	0.05	0.416	-0.04	0.02	0.052	-0.04	0.03	0.250	-0.03	0.07	0.662
After: zone 6	-0.03	0.03	0.279	-0.02	0.03	0.540	-0.07	0.05	0.180	-0.03	0.02	0.191	-0.04	0.03	0.164	-0.14	0.07	0.041
Smooth term																		
Predictors	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**	**EDF**	**F-value**	***p*-value**
s(codRoad)	20.8	32.99	<0.001	39.11	17.64	<0.001	16.36	3.90	<0.001	27.21	25.11	<0.001	4.66	11.74	<0.001	0.81	4.40	0.025

NcodRoad	24	45	25	31	6	2
Observations	6720	4578	2576	8274	1120	56
R^2	0.126	0.168	0.057	0.092	0.058	0.204

Table S8. *Post hoc* pairwise comparisons based on the GAMM results for the 10-year dataset across the six biomes in Brazil. For each biome individually, two results are presented: The first section presents the Estimated Marginal Means (EMMs) of native vegetation change rate for each combination of time periods – Before and After the paving of federal roads in Brazil – and the seven distance zones from the roads (zone 0: 1 km; zone 1: 2 km; zone 2: 3 km; zone 3: 4 km; zone 4: 5 km; zone 5: 10 km; zone 6: 15 km). The second section presents the interaction contrasts of native vegetation change rates between periods varies between pairs of adjacent zones. The reported values include the EMMs (emmean), estimated difference (Estimate), standard error (SE), degrees of freedom (df), the lower and upper bounds of the 95% confidence interval (lower.CL and upper.CL), t-statistic (t.ratio), and the *p-value* of significance (p<0.05).

Amazon						
Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	-0.124	0.023	6685	-0.170	-0.079
After	0	-0.005	0.023	6685	-0.050	0.040
Before	1	-0.103	0.023	6685	-0.148	-0.058
After	1	-0.017	0.023	6685	-0.062	0.029
Before	2	-0.098	0.023	6685	-0.143	-0.053
After	2	-0.029	0.023	6685	-0.074	0.016
Before	3	-0.127	0.023	6685	-0.172	-0.082
After	3	-0.049	0.023	6685	-0.095	-0.004
Before	4	-0.138	0.023	6685	-0.183	-0.093
After	4	-0.030	0.023	6685	-0.075	0.015
Before	5	-0.155	0.023	6685	-0.200	-0.110
After	5	-0.040	0.023	6685	-0.086	0.005
Before	6	-0.155	0.023	6685	-0.200	-0.110
After	6	-0.064	0.023	6685	-0.109	-0.019
Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	-0.033	0.026	6685	-1.270	0.204
Before - After	1 - 2	-0.018	0.026	6685	-0.672	0.501
Before - After	2 - 3	0.009	0.026	6685	0.332	0.740
Before - After	3 - 4	0.030	0.026	6685	1.165	0.244

Before - After	4 - 5	0.007	0.026	6685	0.251	0.802
Before - After	5 - 6	-0.023	0.026	6685	-0.888	0.375

Atlantic Forest

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	0.034	0.022	4525	-0.010	0.077
After	0	0.113	0.022	4525	0.070	0.156
Before	1	0.010	0.022	4525	-0.033	0.053
After	1	0.124	0.022	4525	0.081	0.167
Before	2	-0.011	0.022	4525	-0.055	0.032
After	2	0.106	0.022	4525	0.063	0.149
Before	3	0.022	0.022	4525	-0.022	0.065
After	3	0.080	0.022	4525	0.036	0.123
Before	4	0.005	0.022	4525	-0.038	0.048
After	4	0.085	0.022	4525	0.042	0.128
Before	5	-0.002	0.022	4525	-0.045	0.042
After	5	0.057	0.022	4525	0.014	0.100
Before	6	-0.006	0.022	4525	-0.050	0.037
After	6	0.056	0.022	4525	0.013	0.100

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	0.035	0.027	4525	1.317	0.188
Before - After	1 - 2	0.003	0.027	4525	0.114	0.909
Before - After	2 - 3	-0.059	0.027	4525	-2.220	0.026
Before - After	3 - 4	0.022	0.027	4525	0.826	0.409
Before - After	4 - 5	-0.022	0.027	4525	-0.807	0.419
Before - After	5 - 6	0.004	0.027	4525	0.157	0.875

Caatinga

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	0.029	0.029	2546	-0.028	0.086
After	0	0.158	0.029	2546	0.101	0.215
Before	1	-0.023	0.029	2546	-0.080	0.034
After	1	0.124	0.029	2546	0.067	0.181
Before	2	0.006	0.029	2546	-0.051	0.064
After	2	0.090	0.029	2546	0.033	0.147

Before	3	-0.020	0.029	2546	-0.078	0.037
After	3	0.086	0.029	2546	0.028	0.143
Before	4	-0.021	0.029	2546	-0.078	0.037
After	4	0.069	0.029	2546	0.012	0.127
Before	5	-0.033	0.029	2546	-0.090	0.024
After	5	0.055	0.029	2546	-0.002	0.112
Before	6	-0.020	0.029	2546	-0.077	0.037
After	6	0.041	0.029	2546	-0.017	0.098

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	0.018	0.051	2546	0.360	0.719
Before - After	1 - 2	-0.064	0.051	2546	-1.255	0.210
Before - After	2 - 3	0.023	0.051	2546	0.446	0.656
Before - After	3 - 4	-0.016	0.051	2546	-0.316	0.752
Before - After	4 - 5	-0.002	0.051	2546	-0.049	0.961
Before - After	5 - 6	-0.027	0.051	2546	-0.529	0.597

Cerrado

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	-0.103	0.018	8233	-0.137	-0.068
After	0	-0.018	0.018	8233	-0.052	0.017
Before	1	-0.093	0.018	8233	-0.128	-0.058
After	1	-0.058	0.018	8233	-0.093	-0.024
Before	2	-0.115	0.018	8233	-0.149	-0.080
After	2	-0.052	0.018	8233	-0.087	-0.017
Before	3	-0.107	0.018	8233	-0.142	-0.073
After	3	-0.074	0.018	8233	-0.109	-0.039
Before	4	-0.107	0.018	8233	-0.142	-0.072
After	4	-0.066	0.018	8233	-0.100	-0.031
Before	5	-0.109	0.018	8233	-0.144	-0.074
After	5	-0.065	0.018	8233	-0.100	-0.031
Before	6	-0.107	0.018	8233	-0.142	-0.072
After	6	-0.050	0.018	8233	-0.085	-0.015

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	-0.051	0.021	8233	-2.376	0.018

Before - After	1 - 2	0.028	0.021	8233	1.328	0.184
Before - After	2 - 3	-0.030	0.021	8233	-1.388	0.165
Before - After	3 - 4	0.008	0.021	8233	0.378	0.706
Before - After	4 - 5	0.002	0.021	8233	0.115	0.909
Before - After	5 - 6	0.014	0.021	8233	0.636	0.525

Pampa

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	-0.117	0.022	1101	-0.161	-0.074
After	0	-0.080	0.022	1101	-0.123	-0.037
Before	1	-0.139	0.022	1101	-0.183	-0.096
After	1	-0.119	0.022	1101	-0.162	-0.076
Before	2	-0.136	0.022	1101	-0.180	-0.093
After	2	-0.117	0.022	1101	-0.160	-0.074
Before	3	-0.116	0.022	1101	-0.159	-0.073
After	3	-0.121	0.022	1101	-0.164	-0.077
Before	4	-0.127	0.022	1101	-0.170	-0.084
After	4	-0.153	0.022	1101	-0.196	-0.110
Before	5	-0.111	0.022	1101	-0.154	-0.067
After	5	-0.109	0.022	1101	-0.152	-0.065
Before	6	-0.085	0.022	1101	-0.128	-0.042
After	6	-0.091	0.022	1101	-0.134	-0.048

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	-0.017	0.031	1101	-0.542	0.588
Before - After	1 - 2	-0.001	0.031	1101	-0.046	0.963
Before - After	2 - 3	-0.024	0.031	1101	-0.785	0.433
Before - After	3 - 4	-0.021	0.031	1101	-0.686	0.493
Before - After	4 - 5	0.028	0.031	1101	0.907	0.365
Before - After	5 - 6	-0.007	0.031	1101	-0.242	0.809

Pantanal

Estimated Marginal Means		**Coefficients**				
Period	**Zone**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
Before	0	0.019	0.037	41	-0.057	0.094
After	0	-0.003	0.037	41	-0.079	0.073
Before	1	-0.020	0.037	41	-0.096	0.055

After	1	0.012	0.037	41	-0.064	0.088
Before	2	-0.003	0.037	41	-0.079	0.072
After	2	0.019	0.037	41	-0.056	0.095
Before	3	0.006	0.037	41	-0.070	0.082
After	3	0.012	0.037	41	-0.063	0.088
Before	4	0.036	0.037	41	-0.040	0.111
After	4	-0.028	0.037	41	-0.104	0.048
Before	5	-0.012	0.037	41	-0.088	0.063
After	5	-0.063	0.037	41	-0.138	0.013
Before	6	0.029	0.037	41	-0.046	0.105
After	6	-0.130	0.037	41	-0.206	-0.054

Interaction Contrasts		**Coefficients**				
Period	**Zone**	**Estimate**	**SE**	**df**	**t.ratio**	***p*-value**
Before - After	0 - 1	0.054	0.065	41	0.822	0.416
Before - After	1 - 2	-0.010	0.065	41	-0.149	0.882
Before - After	2 - 3	-0.016	0.065	41	-0.247	0.806
Before - After	3 - 4	-0.070	0.065	41	-1.071	0.290
Before - After	4 - 5	0.013	0.065	41	0.205	0.838
Before - After	5 - 6	-0.109	0.065	41	-1.666	0.103

Capítulo II

Behavioural and life-history traits and road traffic drive population persistence: a mechanistic modelling framework

Esse capítulo será submetido na revista "*Ecological Modelling*" e foi realizado em colaboração com Larissa Oliveira Goncalves, Andreas Kindel, Vinicius A. G. Bastazini e Érika da Rocha Garcez.

Ecological Modelling

Behavioural and life-history traits and road traffic drive population persistence: a mechanistic modelling framework

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Abstract

Road networks and traffic flow are expanding globally, increasing impacts on wildlife populations. Wildlife-vehicle collision represents a major source of direct wildlife mortality and can lead to population decline. Although the impact of traffic flow on populations is often assumed to be linear, evidence suggests non-linear responses dependent on species' behavioural and life-history traits. Here, we developed a mechanistic theoretical model to explore how traffic flow influences population persistence across different combinations of behavioural and life-history traits – daily movement distance, reproductive strategy, and road-crossing probability – using terrestrial medium-to-large mammals as model. Traffic flow impacts on population growth were non-linear and trait-dependent ($R^2 = 0.84$), with response shapes varying across trait combinations. Behavioural and life-history traits did not act independently but interacted to shape population responses to traffic scenarios. Populations which travel large daily movement and late maturation showed consistently negative relative growth across all traffic scenarios, representing the most vulnerable trait combination. In contrast, populations with low daily movement and early maturation, maintained positive growth even under high traffic flow. Daily movement influence individual exposure to roads, whereas reproductive strategy mediated the population's capacity to offset losses from wildlife-vehicle collisions. Sensitivity analysis revealed that model outputs were driven by parameter interactions ($T_i \approx 0.76–1.06$) with a significant interaction between minimum step length and traffic flow ($S_{ij} = 0.438$). These findings provide a theoretical basis for predicting population vulnerability to traffic flow and how population relative growth response to different scenarios.

Keywords

Agent-based model; daily movement; population dynamics; relative growth; reproduction strategy; road ecology; wildlife-vehicle collision.

Highlights

- Traffic flow impacts on population persistence are non-linear and trait dependent.
- Behavioural and life-history traits interacted to shape population responses.
- Daily movement influenced wildlife–vehicle collision rates.
- Reproductive strategy mediated population capacity to offset collision losses.
- High mobility and late maturation represent the most vulnerable trait combination.

1. Introduction

Road network and traffic flow continue to expand worldwide due to human development (van der Ree et al., 2015; van Strien and Grêt-Regamey, 2025), intensifying pressures on natural landscapes and wildlife populations. Roads affect wildlife through multiple mechanisms, including habitat loss, barrier effects, behavioural changes, and direct mortality caused by wildlife-vehicle collisions (van der Ree et al., 2015; Bennett, 2017). Wildlife-vehicle collisions represent one of the primary drivers of direct wildlife mortality globally (Hill et al., 2019; Barrientos et al., 2021; Grilo et al., 2025) and are influenced by road-related attributes such as traffic volume, road density, and sinuosity (Bénard et al., 2024).

Traffic flow is assumed to have a linear impact on roadkill (Sadleir and Linklater, 2016); however, there is evidence that responses may be non-linear, with critical thresholds that may depend on species' behavioural and life-history traits (Denneboom et al., 2024; González-Suárez et al., 2018). Traits related to daily movement patterns, behavioural road responses, and reproductive strategies are essential to define population vulnerability to road impacts (Rytwinski and Fahrig, 2012). Despite growing efforts to synthesize species traits associated with road vulnerability, there is still no clear consensus on which traits most strongly determine population-level impacts (Rytwinski and Fahrig, 2012; González-Suárez et al., 2018). For instance, animals with large home range and low number of offspring per litter are more susceptible to population decline (Grilo et al., 2021; Patterson et al., 2025). In other cases, populations with early maturation and high fecundity (many offspring per event) may also have their population affected by wildlife-vehicle collision (Grilo et al., 2020; Medrano-Vizcaíno et al., 2022). Beyond intrinsic species traits, behavioural responses to road presence and traffic directly influence road-crossing probability and, consequently, exposure to collision risk. Avoidance behaviour varies across species and contexts, with some large mammals avoiding traffic, while others avoid roads more generally regardless of the surface or traffic volume (Jacobson et al., 2016; D'Amico et al., 2016). Based on population life-history traits and responses to roads, we can identify patterns that indicate which populations are more vulnerable to road mortality driven by traffic flow.

Population vulnerability emerges from interactions among multiple behavioural and life-history traits, such as daily movement distance, reproductive strategy, and species-specific responses to road impacts, such as wildlife-vehicle collision, barrier effect, and habitat loss due to road avoidance (Ceia-Hasse et al., 2017, 2018; Patterson et al., 2025). Nevertheless,

collecting empirical data to predict population-level responses to roads remain challenging (Pinto et al., 2020; Barrientos et al., 2021). Hence, theoretical models can provide important insights by exploring potential outcomes under different ecological scenarios. Mechanistic modelling approaches exploring road impacts have increased in recent years, as they allow the integration of multiple interacting traits and processes. For instance, modelling studies indicate that wildlife-vehicle collisions can have a stronger impact on population size and persistence than barrier effects, highlighting the central role of road mortality in shaping population dynamics (Ceia-Hasse et al., 2018). In addition, variation in wildlife–vehicle collision risk is strongly influenced by species traits, particularly those related to behaviour and movement (Bénard et al., 2024; Dasoler et al., 2026). These approaches can be applied both to focal species and to virtual species, exploring how different trait combinations influence population responses to road disturbance (e.g., Desbiez et al., 2020; Ascensão and Desbiez, 2022; Barbosa et al., 2020). Despite these advances, there is still a limited theoretical framework explaining how combinations of species' behavioural and life-history traits respond to traffic flow (but see Jaeger et al., 2005).

Our aim was to develop a mechanistic theoretical framework to explore how traffic flows influence population persistence across different behavioural and life-history traits. We focus on two goals: (1) to evaluate how populations respond to increasing traffic flows, and (2) to determine which combinations of daily movement distance, reproductive strategy, and road-crossing probability make populations more vulnerable to traffic impacts. For the first goal, we expected traffic impacts on population would be non-linear, and each population would decline at different traffic levels depending on their trait combinations. For the second, we expected species with large daily movement distance, late maturation, and small offsprings would be more vulnerable to population decline as traffic flow increases, whereas species with shorter daily movements, early reproductive, and higher number of offspring would be less likely to be affected. For road-crossing probability, we expected population vulnerability to increase with increasing crossing probability, such that populations with low crossing probability would be less impacted by traffic, regardless of variation in daily movement and reproductive strategy. By identifying these patterns, our study provides a theoretical basis for predicting population vulnerability to traffic flow and for guiding the prioritization of populations for mitigation.

2. Methods

We developed an theoretical agent-based model to evaluate the impact of different levels of traffic flow on road mortality and population persistence of virtual species with different combinations of behaviour and life history traits, such as daily movement distance, reproductive strategy, and crossing-behaviour responses to traffic flow. Population persistence was defined as positive relative population growth, whereas negative relative growth indicated population decline. The model parametrization was based on ecological information from medium-large mammals worldwide (**Appendix B**). Our model provides mechanistic insights into potentially vulnerable populations, allowing us to associate with real mammal populations and to identify early which wildlife populations are most likely to decline due to traffic flow.

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing agent-based models (Grimm et al., 2006), as updated by Grimm et al. (2020), and is available in **Appendix A**. We implemented the model using R programming environment (R Core Team, 2026). The codes developed can be accessed through: https://github.com/ingridi-franceschi/IBM-road. Here we present a brief overview of the model's structure and processes. The model includes two entities: the landscape and species individuals, all comprising a single population. The landscape and the temporal scale were fixed for all simulated populations.

2.1. Landscape description

The virtual landscape is a toroidal space represented by a two-dimensional grid of 2,000 x 2,000 square cells. Each cell represents a 50 x 50 m square (2,500 m^2), resulting in a total landscape area of 10,000 km^2, with roads of 5 meters width. This environment is composed of three types of cells: habitat cells, risk areas, which are cells adjacent to the road, and the road itself, represented by a single horizontal line of cells.

2.2. Temporal scale

Each simulation has the same temporal scale, represented by the model's simulation step. The parameters that control these simulations steps in the model are days and years. For each simulation scenario, we performed simulations lasting 20 years with 365 days per year, and 144 simulation steps per day, which represents the locations of individuals movement every 10 minutes per day. It is important to highlight that the simulation step does not represent explicitly an individual's steps. At every simulation, we extracted the following metrics: number of wildlife-vehicle collisions and crossings per day and year, annual population size, total

numbers of stochastic deaths and births, and net and relative population growth. This information allows us to understand how the wildlife-vehicle collisions affect population persistence.

2.3. Population data and simulated scenarios

Both individual and population attributes are briefly presented in **Table 1** (more details in **Appendix A**). The individual attributes are unique identification of each individual, information about whether the individual is alive or dead, individual age, angle for movement direction, current individual location, and the full trajectory. Initially, all individuals are placed randomly within habitat cells, have a unique ID, start alive, their age is sampled between one to three, and the initial movement angle is defined following a Normal distribution. The population attributes are parameters are: number of simulation steps, step length parameters (minimum step length, maximum step length, shape distribution parameter), turn angle parameters (mean and standard deviation of movement angle), reproduction parameters (mature age, reproduction period, reproduction frequency, number of offspring, carrying capacity), and roads crossing parameters (mean and standard deviation of the crossing speed, minimum and maximum crossing probability).

We created four categories of mammal populations by combining behavioural and life-history traits, such as daily movement distance, maturity age, maximum number of offspring per reproduction event, and road-crossing behaviour (**Table 2**). We define potential species examples in **Appendix B**. We classified Categories 1 and 4 as those with low daily movement and Categories 2 and 3 as the ones with large daily movement. Categories 1 and 2 were defined as early-maturing, while Categories 3 and 4 were defined as late-maturing.

Table 1. List of the parameters at population level and individuals state variables. For each one is informed of the type, unit, and descriptions.

Population parameters		
Variable	**Type and units**	**Meaning**
steps	Discrete value; steps	The steps in the model that tracks the individual movement.
mu	Discrete value; null	Shape parameter of the truncated Pareto distribution.
lmin	Continuous value; meter	The minimum individual's step length in a simulation step.

lmax	Continuous value; meter	The maximum individual's step length in a simulation step.
angle_mean	Continuous value; degree	This value defines the *angle_abs* in the starts and after it is used to calculate the new angle.
angle_sd	Continuous value; degree	This value defines *angle_sd* in the starts and after it is used to calculate the new angle.
mature	Discrete value; years	The maturity age to reproduce.
reprod_period	Discrete value; years	The number of years between reproductive events.
reprod_freq	Discrete value; events/year	The frequency of reproduction within a year.
num_offspring	Discrete value; number of individuals	The maximum number of offspring per reproductive event.
speed_mean	Discrete value; meters/minute	This value defines individual speed.
speed_sd	Discrete value; meters/minute	This value defines individual speed.
min_prob_cross	Continuous value; probability	The minimum probability used in the Uniform distribution.
max_prob_cross	Continuous value; probability	The maximum probability used in the Uniform distribution.
K	Discrete value; null	The carrying capacity of the population.
Individual's state variables		
Variable	**Type and units**	**Meaning**
ID	Discrete value; null	Unique identification.
alive	Logical number; null	Alive = 1, dead = 0.
age	Discrete value; years	Individual age. Value = 0 is juvenile, value >= 1 is adult.
angle_abs	Continuous value; degree	This value is initialized randomly through the parameters *angle_mean* and *angle_sd.*
x	Integer; cell index	The x-coordinate of the individual's current position.
y	Integer; cell index	The y-coordinate of the individual's current position.
track	Integer; cell index pairs	A sequence list recording the individual's movement history with x and y coordinates.

149 **Table 2.** Population categories used in the simulation scenarios. The range of daily movement
150 distance (meters) was used to calculate the minimum (*lmin*) and maximum (*lmax*) step lengths
151 into 144 simulation steps. For each category, we defined the age at maturity (*mature*) at which

individuals can begin to reproduce and the maximum number of offspring (*num_offspring*) that each individual can have per reproduction event. Each population category has its own carrying capacity, which was previously calibrated.

Category	Range of daily movement (m)	*lmin* (m)	*lmax* (m)	*mature* (age)	*num_offspring* (individuals)	Carrying capacity
1	1000-5000	6.94	34.72	1	8	58
2	5000-10000	34.72	69.44	1	3	55
3	5000-10000	34.72	69.44	2	3	60
4	1000-5000	6.94	34.72	3	2	95

To define the step lengths for each category, we used existing knowledge of daily movement distance for some species (**Appendix B**). We divided the minimum daily movement distance by the number of simulation steps (total of 144 steps daily as each step represent 10 minutes) to obtain the minimum step length, and the maximum daily movement by the simulation step to obtain the maximum step length. For instance, a population with a daily movement range of 1000-5000 m, would have a minimum step length of 6.94 m and the maximum of 34.72 m, considering 144 simulation steps. Age at maturity ranged from one to three years ranged from one to three years, and the maximum number of offspring per reproduction event varied from one to eight. These two reproduction parameters were also defined based on potential real species (**Appendix B**). For example, *Myrmecophaga tridactyla*, reaches maturity at around three years of age, gives birth one or two offspring (Gaudin et al., 2018), and has daily movement range of 1000 to 5000 m (Bertassoni et al., 2017). Each population category was simulated with three levels of road-crossing behaviour: low (0–0.33), medium (0.33–0.66), and high (0.66–1), using a Uniform distribution. Although all individuals within a population category shared the same minimum and maximum probability of crossing the road, this probability was calculated individually for each one in a risk area to determine whether it would attempt to cross it. It is important to highlight that the crossing-behaviour should not be interpreted as analogous to behavioural responses to traffic flow, such as speeders or freezers, which change movement speed in direct responses to approaching vehicles (Jacobson et al., 2016; D'Amico et al., 2016). To avoid misinterpretation, we hereafter refer as crossing probability, defined exclusively as the intrinsic behavioural probability of an individual to cross or not a road. In total, we modelled 12 populations, varying in daily

movement distance, age at maturity, maximum number of offspring, and crossing probability (**Appendix C**).

Due to the different reproduction strategy, each population category would have its own carrying capacity to stabilize the population. For each category, we tested several carrying capacity values with 100 replicates over 100 years for each population category, without considering traffic flow, to find the carrying capacity that resulted in a stable population. Further, we used this result as a "baseline" population for comparations with the outcomes emerging from traffic flow scenarios. We selected the carrying capacity value at which population size fluctuated less than 15% around its temporal mean across replicates. More details and explanations are provided in **Appendix D**.

Considering the evidence of female-biased collision rates may be critical factor in population persistence as population growth is determined by female reproductive output (Moore et al., 2023; Desbiez et al., 2020), all individuals in the simulated populations were females that gave birth to other females. Some population parameters were fixed across all populations simulated, such as step length distribution parameter (*mu* = 0), movement angle mean (*angle_mean* = 0), angle standard deviation (*angle_sd* = π / 2), reproduction period (*reprod_period* = 1 per year), reproduction frequency (*reprod_freq* = 1 event per year), speed mean (*speed_mean* = 84 meters/min), and speed standard deviation (*speed_sd* = 100 meters/min). The parameters related to movement, such as distribution parameter, movement angle mean and angle standard deviation, followed the pattern described in other studies to represent a routine movement within a home range (Börger et al., 2008; Getz et al., 2024). The reproduction period and reproduction frequency parameters were fixed to simplify our model. Animal speed is rarely available information; due to this fact, we fixed the mean, standard deviation, minimum, and maximum in plausible values to represent medium-large mammals (e.g., Blanco and Gambini, 2007; Dyer et al., 2023). The minimum and maximum values of truncated Normal distribution were fixed in the equation within the model with values of 50 and 700 meters/minute, respectively. Therefore, the initial population dynamic parameters were also fixed for all population simulated: birth rate (b = 0.5), stochastic death rate (d = 0.2), and population size (N_0 = 50 individuals).

Each of the 12 populations was submitted to four levels of traffic flow (vehicle per minute: zero, one, five, and ten), resulting in a structured set of 48 simulations scenarios. We ran 100 replicates for each of the 48 population scenarios, resulting in 4800 observations. With this,

our set explored the effects of population traits (daily movement distance and reproduction strategy), road-crossing probability, and traffic intensity.

2.4. Mechanism process description

The model operates based on the consequences of decision events (**Figure 1)**. For each simulation step it is verified which cell type the individuals are in (**Figure 1a**). If the individual is in a habitat cell, it keeps moving following the correlated Lévy walk based on truncated Pareto distribution (details below), and its location is updated at each simulation step. When the individual reaches a risk area, the probability of crossing is calculated following a Uniform distribution. In the case of an individual decides not to cross the road, it returns to a habitat cell. However, if it decides to cross the road, it enters the road and the probability of death from a vehicle collision is then calculated (described below). If the individual dies, it is removed from the population. However, if the individual survives, it crosses the road to a habitat cell. This cycle is repeated until completing all simulation steps in a day, representing the daily temporal scale, and it repeats for all days (**Figure 1a**).

At the end of each simulation year (all days were completed), stochastic mortality and reproduction occur (**Figure 1b**). First, individuals that still alive (*i.e.,* those that did not die due to vehicle collision) may randomly die following a Binomial distribution and are removed from the population. Posteriorly, individuals that remain alive and are in reproductive conditions may give birth to new individuals based on Poisson distribution following the logistic population growth (Sibly et al. 2005). This final part represents the annual temporal scale. This schedule was chosen to reflect the biological processes under study: daily movement and collision risk, followed by annual demographic events such as aging and reproduction.

The individual movement follows the correlated Lévy walk based on truncated Pareto distribution (Ríos-Uzeda et al., 2019). The parameters used are minimum step length, maximum step length, distribution parameter, mean movement angle, and standard deviation of the angle. For each movement step calculated the step length from the truncated Pareto distribution, the new turning angle is sampled from a Normal distribution with predefined mean and standard deviation, and the final turning angle is calculated as the sum of the current angle and the new sampled angle. The x and y coordinates are always adjusted to ensure the toroidal space. This process is repeated for each simulation step and for each individual that is alive during the simulation.

Wildlife-vehicle collision starts in the sixth year to allow population stability. The probability of wildlife-vehicle collision follows the equation described by Litvaitis and Tash (2008):

$$P_{killed} = \frac{N * a}{v}$$

where the probability of collision (P_{killed}) is based on number of vehicles per minute (N), the width of kill zone in meters (a) and the velocity of the animal moving through kill zone in meters/minute (v). The N (vehicle/minute) is defined by the user. We considered the width of kill zone as the road width, which is also fixed for the landscape. Animal speed was calculated based on truncated Normal distribution with values of mean, standard deviation, minimum and maximum limits.

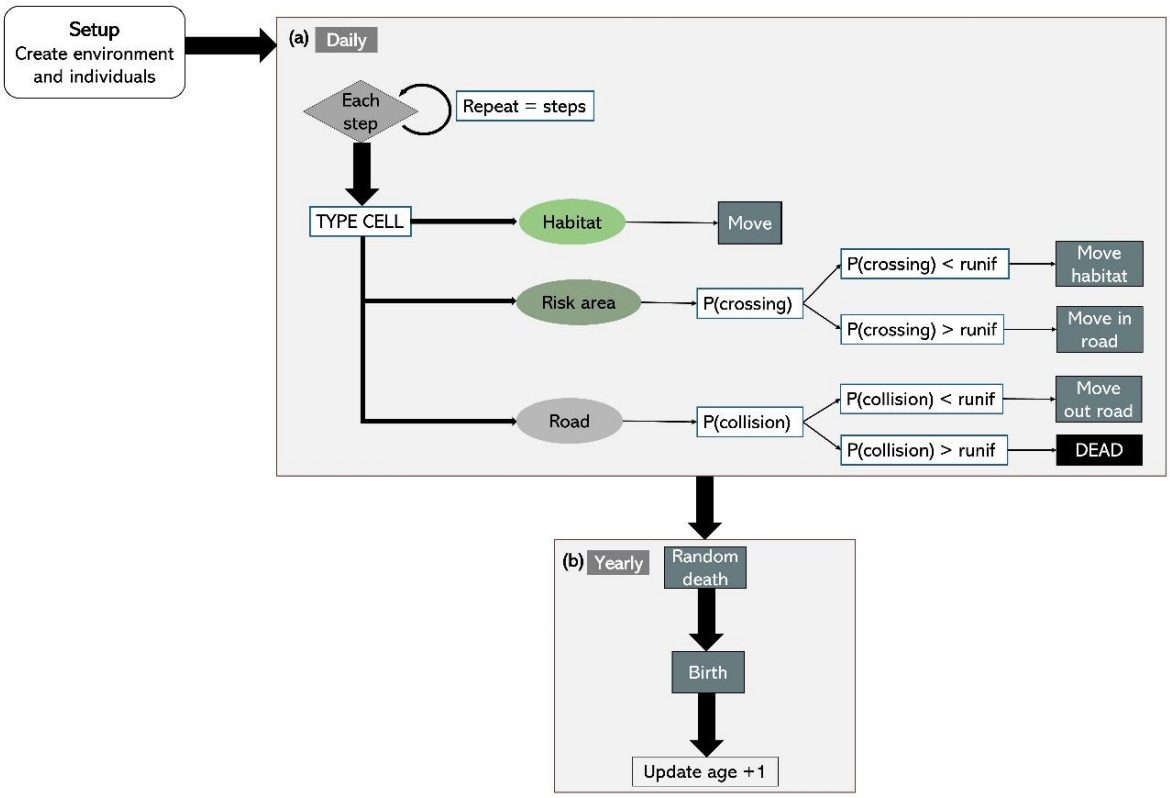


Figure 1. The flowchart represents the events that are applied for all individuals in each population scenarios simulated. (a) Schematic representation of simulation step decision events, the steps repeat until all simulation steps are complete for all individuals in the population, across all days. (b) Schematic representation of the yearly events, they happen after all days are completed.

2.5. Model analysis

To evaluate how populations respond to increasing traffic flow, we tested for linear and non-linear trends in mean relative growth using polynomial contrasts. Traffic flow was treated as an ordered categorical variable with levels: 0, 1, 5, and 10 vehicles/min. Mean relative growth was calculated for each simulation replicate by averaging across the 20 simulated years, resulting in 4800 independent observations. Orthogonal polynomial contrasts were weighted according to the actual numeric values of each traffic level, using the '*contr.poly'* function (Chambers and Hastie, 1992). We tested two models: first an overall effect of traffic flow; and the second including the categories and crossing probability as interacting factors; using the analysis of variance models fitted with the '*aov'* function. Both analyses were performed using the base *stats* package in R (R Core Team, 2025). This approach decomposes the effect of traffic flow into linear, quadratic, and cubic components, allowing formal tests of different categories responses shapes. Significant linear terms indicate monotonic trends, whereas significant higher-order terms indicate non-linear responses of population growth to traffic intensity.

We conducted a global sensitivity analysis to quantify the relative contribution of each parameter and their interactions to model output variability, using the '*sensobol'* package in R (Puy et al., 2022; R Core Team, 2025). Eight parameters were varied: daily movement distance (minimum and maximum steps length), reproductive strategy (age at sexual maturity, carrying capacity, and number of offspring per reproductive event), crossing probability (minimum and maximum probability), and traffic flow (vehicles/min). These parameter values were sampled within the global ranges defined by the minimum and maximum values across all four population categories. All remaining parameters were constant across simulations. We constructed the sampling matrix using a quasi-random number design (QRN) using matrices A, B, and AB with N = 100 samples per matrix, resulting in 3,800 simulations. This matrix design allows estimation of both individual and interaction effects by contrasting model outputs across matrix pairs (Saltelli et al., 2010). First-order indices (S_i) were estimated using the Saltelli estimator, measuring the individual contribution of each parameter to output variance independently of interactions. Total-order indices (T_i) were estimated using the Sobol estimator, quantifying each parameter's total contribution including all higher-order interactions. Second-order indices (S_{ij}) were also computed to capture pairwise interactions between parameters. Bootstrap confidence intervals (95%) were derived from R = 10^5

resamples using the normal method (Puy et al., 2022). The model output used as the sensitivity metric was the relative population growth, averaged over a 5-year simulation period (365 days per year), under the same landscape and population dynamics settings used in the main model.

3. Results

We found that traffic flow influenced population persistence, with relative population growth declining as traffic flow increased (**Figure 2**). Across most scenarios, the impact was non-linear and unpredictable (linear: $p < 0.001$; quadratic: $p = 0.003$; cubic: $p = 0.004$; **Table E1**; **Figure 2**). This response varied considerably across behavioural and life-history traits combinations, indicating that population vulnerability to traffic is trait-dependent ($R^2 = 0.84$, $F = 535.1$, $p < 0.001$; **Table E2**). Large daily movement populations were more sensitive to traffic increases regardless of age at maturity, showing non-linear responses (Categories 2 and 3;). Although populations combining large daily movement with early maturation (Category 2) showed a significant non-linear response to traffic ($p = 0.003$; **Table E2**), their responses differed from populations combining large daily movement with late maturation (Category 3) response (quadratic: $p < 0.001$; cubic: $p < 0.001$; **Table E2**). Category 3 showed consistently negative growth across all traffic flows, representing the most vulnerable trait combination identified. When low daily movement was associated with late maturation (Category 4), populations showed a declining trend, with significant non-linear responses to traffic (quadratic: $p = 0.003$; cubic: $p < 0.001$; **Table E2**). The combination of low daily movement and early maturation (Category 1) was the only trait combination that maintained positive relative growth across all traffic levels and crossing probability classes, showing no significant response to increasing traffic intensity (linear: $p = 0.37$; quadratic: $p = 0.52$; cubic: $p = 0.10$; **Table E2**).

When considering temporal dynamics, relative growth recovered after the initial roadkill-induced decline (by year 6) and remained consistent over time, with late maturation populations demonstrating greater instability compared to early maturation ones (**Figure 3**). Collision rates were linked to daily movement and road crossing probability, mediating the relationship between traffic flow and population growth. Large daily movement populations experienced the highest collision rates as traffic flow increased and the crossing probability on collision rate was most evident at low traffic flow (Categories 2 and 3; **Figure 4**). Low crossing probability (Categories 1 and 4) combined with low traffic flow (1 vehicle/min) resulted in lower daily collision rates compared to medium and high crossing probability and higher traffic volumes

(5 and 10 vehicles/min; **Figure 4**). Collision rates showed no difference between medium and high crossing probabilities, nor between traffic flows of 5 and 10 vehicles/min (**Figure 4**).

The sensitivity analysis revealed that no parameter had a significant independent effect on mean relative population growth, as first-order indices (S_i) were close to zero and associated confidence intervals largely overlapped zero (**Figure 5**; **Table E3**). In contrast, total-order indices (T_i) were consistently high for all parameters (T_i = 0.76-1.06), indicating that each parameter contributed significantly to output variability when interactions were considered (**Figure 5**; **Table E3**). Traffic flow showed the highest total effect (T_i = 1.06), followed by minimum and maximum step length (T_i = 1.00-1.01), age at maturity (T_i = 0.97), minimum and maximum crossing probability (T_i = 0.90-0.96), carrying capacity (T_i = 0.85), and number of offspring (T_i = 0.76). The large difference between S_i and T_i indices across all parameters indicates that model output variability is primarily driven by interactions rather than independent parameter effects. Second-order indices (S_{ij}) were generally associated with wide confidence intervals overlapping zero, suggesting low precision in the estimation of pairwise interactions (**Figure 6**; **Table E3**). This is likely due to the relatively small sample size (N = 100), which limits the identification of specific pairwise interactions. The only exception was the interaction between minimum step length and traffic flow (S_{ij} = 0.44; 95% CI: 0.05–0.82; **Figure 6**; **Table E3**).

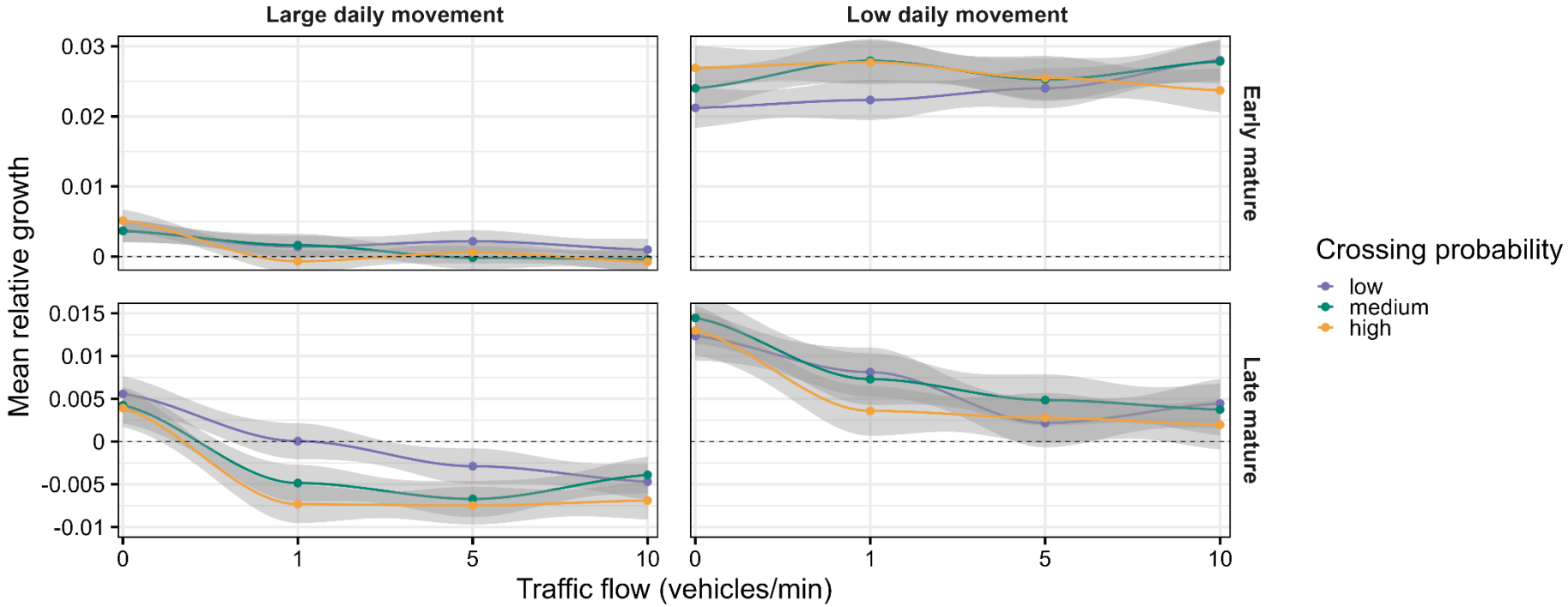
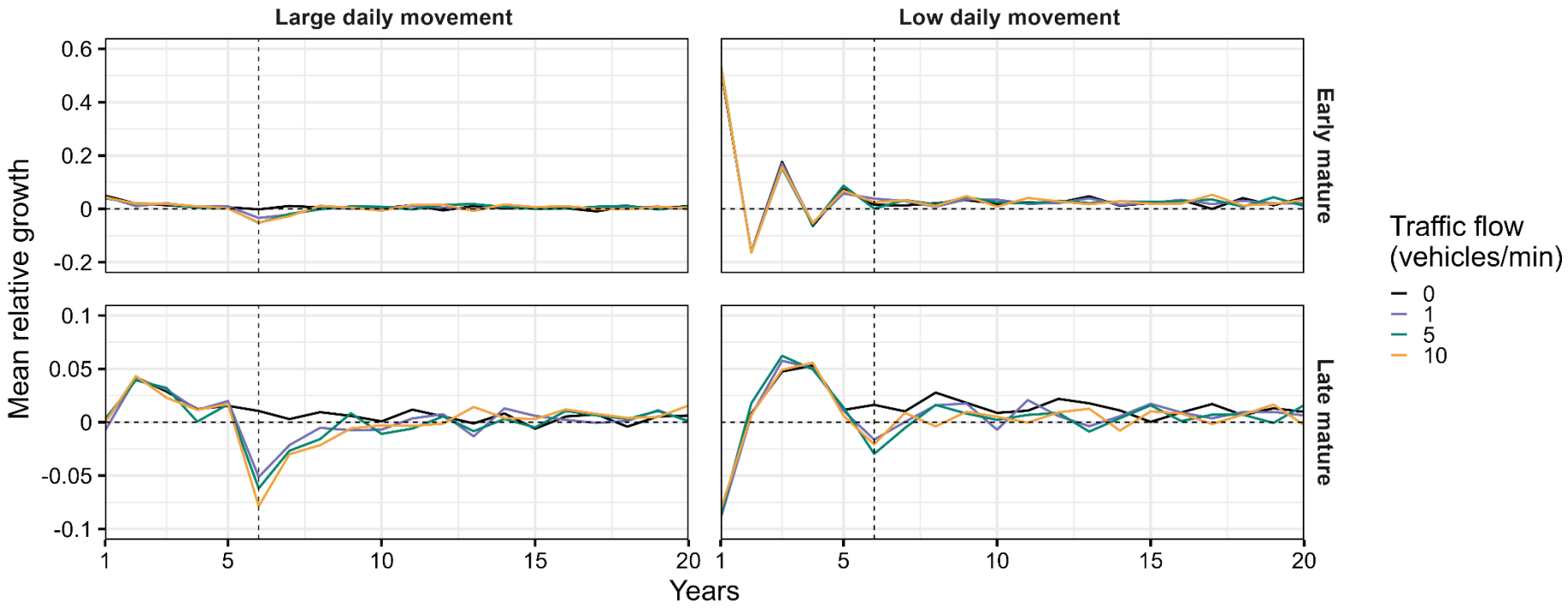


Figure 2. Effects of traffic flow on population persistence across behavioural and life-history traits scenarios. Points represent the mean relative population growth over 20 years for each combination of traffic flow and crossing probability, and shaded areas indicate 95% confidence intervals. Crossing probability was classified as low (0–0.33), medium (0.33–0.66), and high (0.66–1). Large daily movement populations (Categories 2 and 3) had daily movement distances between 5000 and 10000 m, whereas low daily movement populations (Categories 1 and 4) ranged from 1000 to 5000 m. Early-maturing populations (Categories 1 and 2) reproduced after one year, whereas late-maturing populations (Categories 3 and 4) reproduced after two to three years.



345

346 **Figure 3.** Temporal dynamics of relative population growth over the 20-year simulation period across traffic flow and behavioural and life-history
347 traits scenarios. Crossing probabilities were grouped to represent the mean relative growth over time. Crossing probability was classified as low
348 (0–0.33), medium (0.33–0.66), and high (0.66–1). Large daily movement populations (Categories 2 and 3) had daily movement distances between
349 5000 and 10000 m, whereas low daily movement populations (Categories 1 and 4) ranged from 1000 to 5000 m. Early-maturing populations
350 (Categories 1 and 2) reproduced after one year, while late-maturing populations (Categories 3 and 4) reproduced after two to three years. The
351 vertical dotted indicate the begin of wildlife-vehicle collisions.

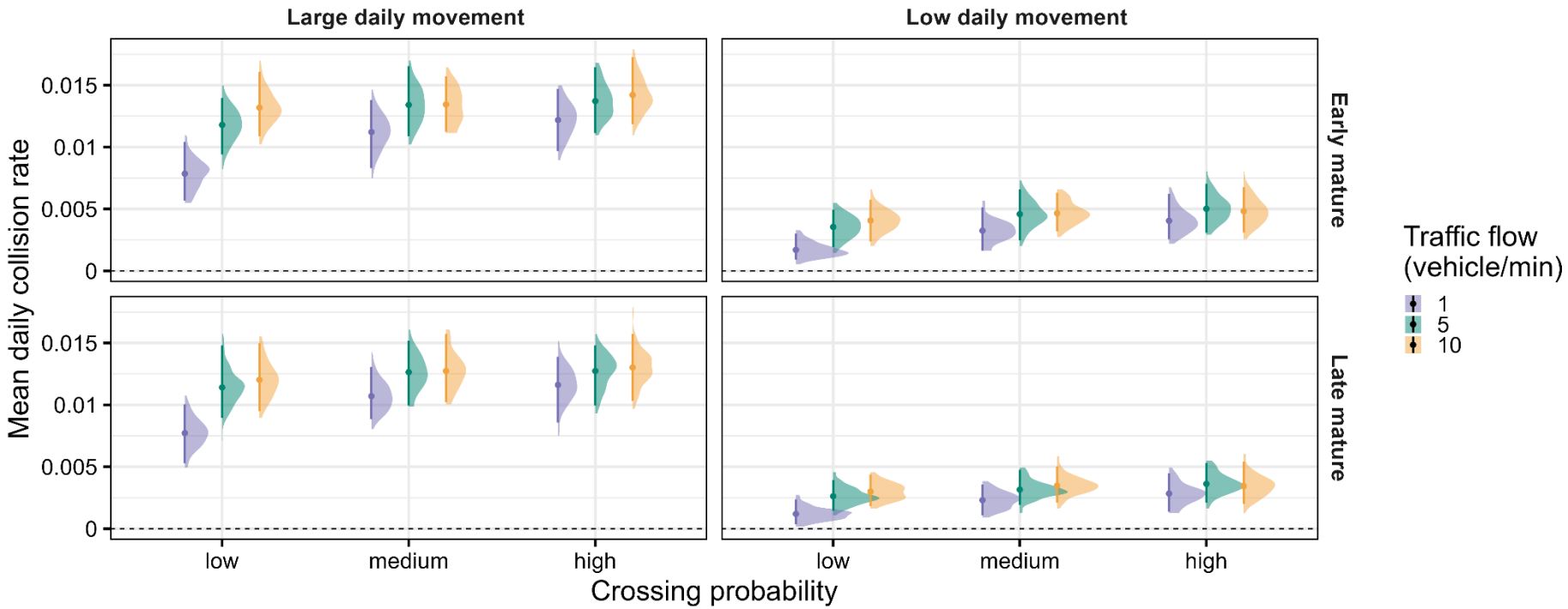


Figure 4. Differences in daily collision rates across behavioural and life-history traits and traffic flow scenarios. Crossing probability was classified as low (0–0.33), medium (0.33–0.66), and high (0.66–1). Large daily movement populations (Categories 2 and 3) had daily movement distances between 5000 and 10000 m, whereas low daily movement populations (Categories 1 and 4) ranged from 1000 to 5000 m. Early-maturing populations (Categories 1 and 2) reproduced after one year, whereas late-maturing populations (Categories 3 and 4) reproduced after two to three years.

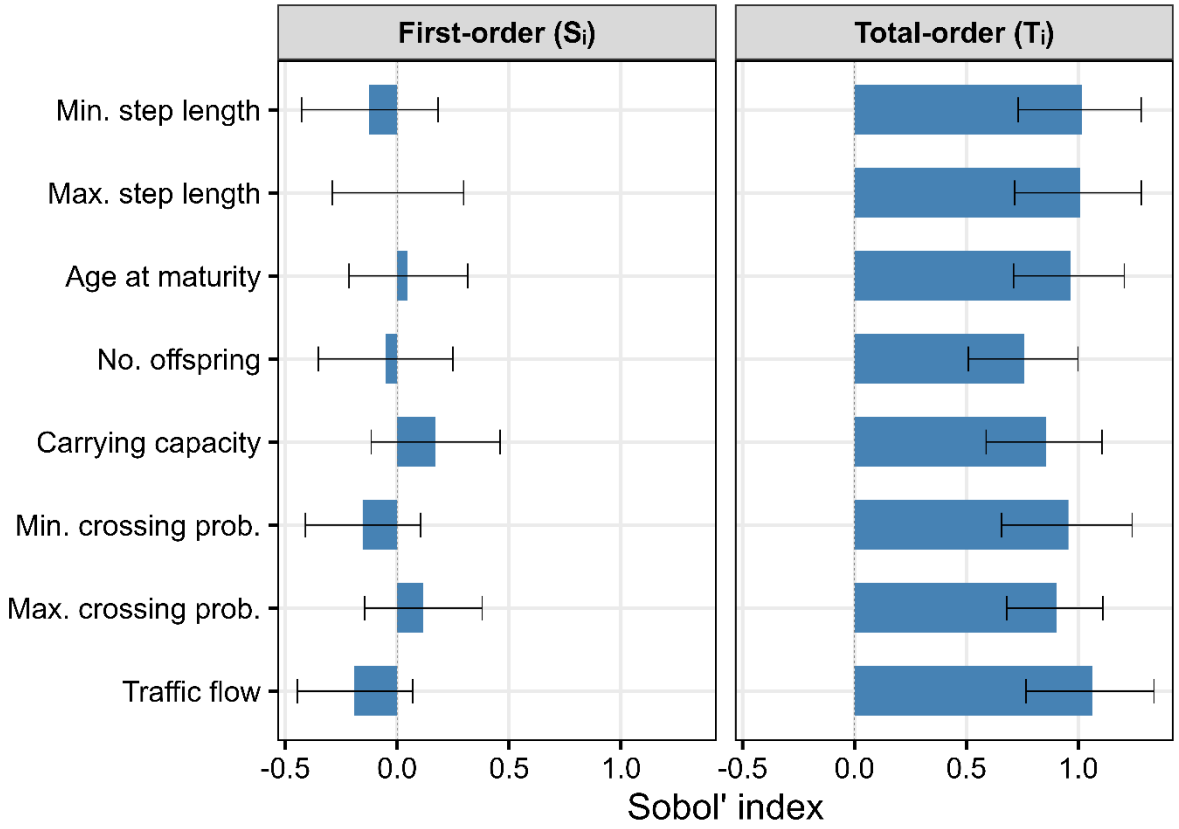


Figure 5. Sobol' sensitivity analysis to evaluate the contribution of each parameter to relative growth variability. The first-order index (S_i) quantifies the individual contribution of each parameter, and the total-order index (T_i) quantifies the total contribution of each parameter considering interactions with all other parameters. Bars represent estimate values and error bars indicate 95% bootstrap confidence intervals (R = 10^5 resamples). Parameter abbreviations: Min./Max. step length = minimum and maximum steps length (m); Age at maturity = age at first reproduction (years); No. offspring = number of offspring per reproductive event; Carrying capacity (K); Min./Max. crossing prob. = minimum and maximum road-crossing probability; Traffic flow (vehicles/min).

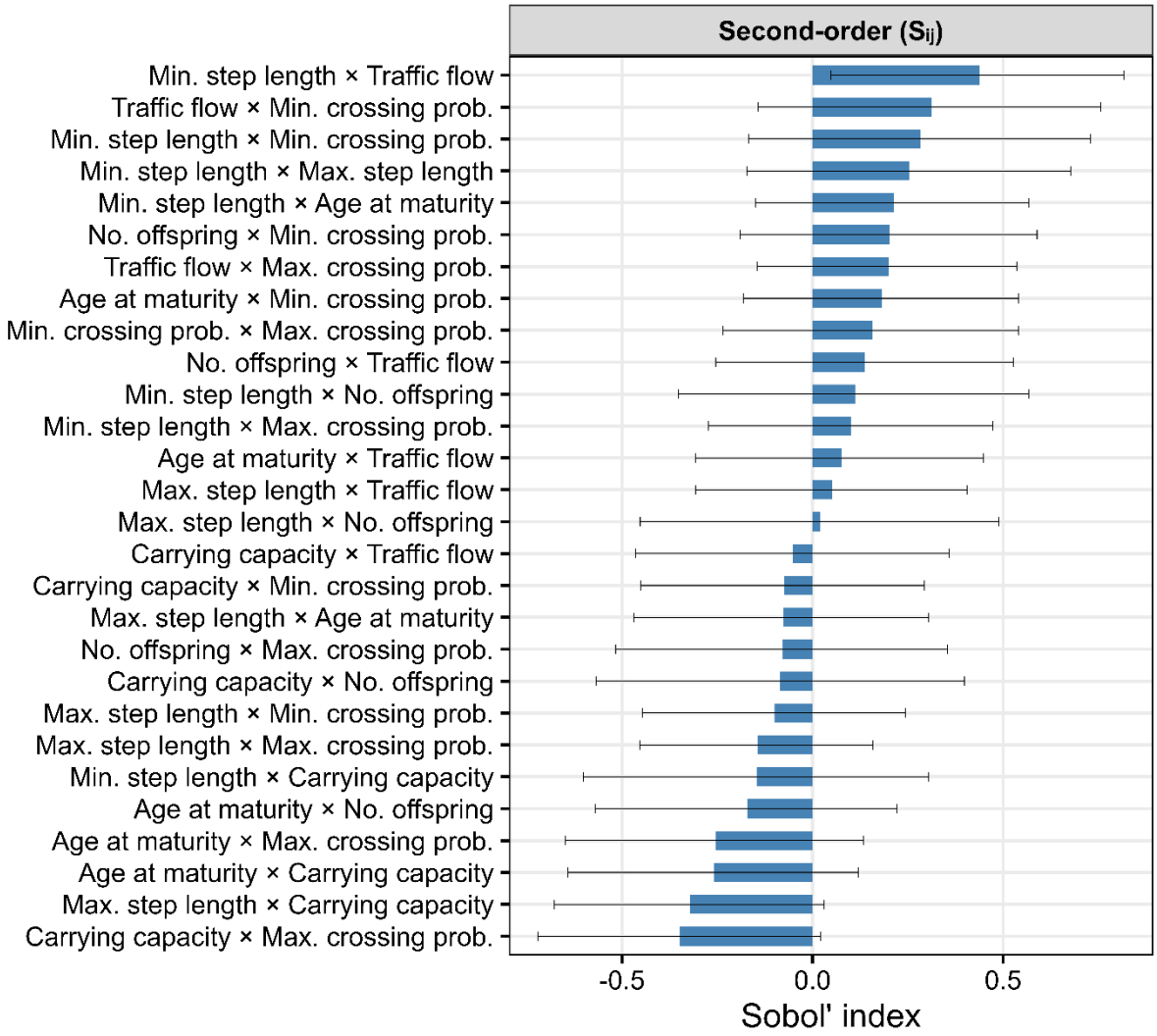


Figure 6. Second-order Sobol' sensitivity indices (S_{ij}) representing the contribution of pairwise parameter interactions to relative growth variability. Bars represent estimate values and error bars indicate 95% bootstrap confidence intervals (R = 10^5 resamples). Positive values indicate synergistic interactions, and negative values indicate antagonistic interactions between parameter pairs. Parameter abbreviations: Min./Max. step length = minimum and maximum steps length (m); Age at maturity = age at first reproduction (years); No. offspring = number of offspring per reproductive event; Carrying capacity (K); Min./Max. crossing prob. = minimum and maximum road-crossing probability; Traffic flow (vehicles/min).

4. Discussion

Our mechanistic model allowed us to make inferences about population vulnerability under different traffic scenarios, showing that behavioural and life-history traits did not act independently but interacted to shape population responses. Our results showed that daily movement influence individual exposure to roads and, consequently, collision rates, while reproductive strategy mediated the population's capacity to offset losses from wildlife-vehicle collisions. Different traits are complementary and play an important role in wildlife-vehicle collision (González-Suárez et al. 2018; Grilo et al., 2021).

Wildlife–vehicle collision impacts driven by traffic flow do not follow a simple linear relationship, a pattern previously attributed to road avoidance behaviour (Denneboom et al., 2024; Jaarsma et al., 2006) but also observed independently of it (Bénard et al., 2024). Responses to traffic are not uniform across populations and depend on population traits (González-Suárez et al., 2018; Pagany, 2020). Most trait combinations showed decline relative growth even at low traffic flow, however, populations with low daily movement and early maturation (Category 1) showed no response to traffic flow. Overall, even low traffic flow can represent a threat to most populations, and its impact depend on trait combinations to determine both the magnitude and the shape of population responses to traffic flow (van Langevelde and Jaarsma, 2004; Bénard et al., 2024; Denneboom et al., 2024).

Daily movement influenced how often individuals were exposed to roads. Large daily movement increased the probability of individuals encountering roads and, consequently, collision rates (Categories 2 and 3). This pattern is consistent with empirical evidence from large carnivores and ungulates, as they typically combine large home ranges with late maturation and few offspring per reproductive event – the trait combination considered most vulnerable to road impacts (Ceia-Hasse et al., 2017; Grilo et al., 2025; Patterson et al., 2025). Even when reproductive strategy was early maturation, large daily movement continued to drive population decline through collision rates (Category 2; Sidorovich et al., 2020). In contrast, populations with low daily movement encountered roads less frequently, reducing short-term collision rates. However, when combined with late maturation, this reduced exposure may only postpone population decline (Category 4; Rytwinski and Fahrig, 2011, 2012). Populations with early maturation, high litter sizes, and multiple reproductive events per year, were better able to compensate for collision losses and, maintain positive relative growth across all traffic scenarios (Category 1; Sidorovich et al., 2020; Rytwinski and Fahrig,

2012). However, early maturation combined with small home ranges can also be associated with higher collision rates (Grilo et al., 2020; Medrano-Vizcaíno et al., 2022), possibly because faster reproductive strategies support higher local abundance and more frequent road crossing attempts (D'Amico et al., 2015; González-Suárez et al., 2018).

Wildlife-vehicle collisions can be represented as the outcome of several combined processes, including individual daily movement, probability of encountering a road, crossing probability once the road is reached, and traffic flow (Litvaitis and Tash, 2008; Visintin et al., 2016; Bénard et al., 2024). Our findings demonstrated that crossing probability modulated collision rates, particularly under low traffic flow, with higher crossing probability increasing daily collision rates mainly in populations with large daily movement. Road encounters driven by daily movement and crossing probability influence collision rates, depending on traffic flow (Bénard et al., 2024). Thus, for populations with large daily movement, even low crossing probability may be insufficient to prevent high collision rates, because individuals encounter roads frequently. Conversely, populations with low daily movement encounter roads less often, making crossing probability a less influential trait.

Our results provide a theoretical basis for understanding how traffic flow impacts populations with different behavioural and life-history traits, revealing that vulnerability to road impacts is dependent on combinations of interacting traits. Although our model was parameterized for terrestrial medium-to-large mammals, the framework can be applied to other taxa by adjusting relevant trait parameters, expanding its utility for conservation planning. Future studies could explore additional trait combinations, such as different movement distances, reproductive frequencies, and periods, as well as validate these patterns with empirical data. Other factors known to influence wildlife–vehicle collisions also deserve further investigation, including road density, road width and vehicle speed (Jaeger et al., 2005; Jaarsma et al., 2006; Visintin et al., 2016), dynamic behavioural responses upon vehicle detection, such as speeder and pausers behaviours (Jaeger et al., 2005; D'Amico et al., 2016; Jacobson et al., 2016), interactions among individuals (Bernardi and Scianna, 2020), and landscape matrix effects (Smith et al., 2025; Rogers et al., 2025; Dasoler et al., 2026). We encourage future studies to investigate how these factors modulate individual movement and, consequently, collision rates and population persistence. Theoretical models are a valuable tool for exploring how behavioural and life-history traits interact with road-related mechanisms and can contribute to qualitative assessments of potential road impacts on wildlife populations.

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CRediT authorship contribution statement

Ingridi Camboim Franceschi: Writing – review & editing, Writing – original draft, Methodology, Software, Validation, Formal analysis, Visualization, Data curation, Conceptualization. **Larissa Oliveira Gonçalves:** Writing – review & editing, Methodology, Conceptualization. **Vinicius Augusto Galvão Bastazini:** Writing – review & editing, Methodology, Conceptualization. **Andreas Kindel:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Érika Garcez da Rocha:** Writing – review & editing, Supervision, Methodology, Software, Validation, Formal analysis, Data curation, Conceptualization.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Ecological Modelling

Appendix Information

Behavioural and life-history traits and road traffic drive population persistence: a mechanistic modelling framework

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Appendix summary

Appendix A. ODD protocol

Appendix B. Potential species example

Appendix C. Population categories

Appendix D. Carrying capacity definition

Appendix E. Analyses results

Appendix A. Objectives, Design concepts, and Details (ODD protocol)

Overview

1. Purpose and patterns

1.1. Purpose

The purpose of our model is to understand how wildlife-vehicle collision affects populations with distinct daily movement distance, reproductive strategy, and crossing probability, identifying which traits increase population persistence under different traffic flows. The main question is: How do these traits determine population persistence across different traffic flows? The model provides theoretical insights for potential vulnerable populations that can require some mitigation strategies to avoid the decline of population due to wildlife-vehicle collision.

1.2. Patterns

This model aims to explore theoretical patterns emerging from the interaction between species' behavioural and life-history traits and wildlife-vehicle collision under varying traffic flow. It aims to evaluate whether and how the effect of traffic flow on population persistence changes for populations with different daily movement distance, reproductive strategy, and crossing behavior. A general pattern expected that species with longer daily movement distance, which also can indicate large home ranges, would often cross a road (Rytwinski and Fahrig, 2012; Patterson et al., 2025). While species with short daily movement distance, small home range, would not reach the road frequently. Another expected pattern is that populations with early maturation age and high fecundity (many offspring per reproductive event) would be able to compensate for the loss with new individuals, thus postponing their vulnerability (Rytwinski and Fahrig, 2012; Patterson et al., 2025). Otherwise, population with late maturation age and low fecundity would not be able to reproduce new individuals as they lose, then this population would decline to extinction (Rytwinski and Fahrig, 2012; Patterson et al., 2025). The crossing probability pattern can determine how vulnerable a population would be, low crossing probability would be less exposed to wildlife-vehicle collisions, whereas higher crossing probability increases the crossings frequency and would be the population more susceptible to wildlife-vehicle collisions and population decline (Jacobson et al., 2016).

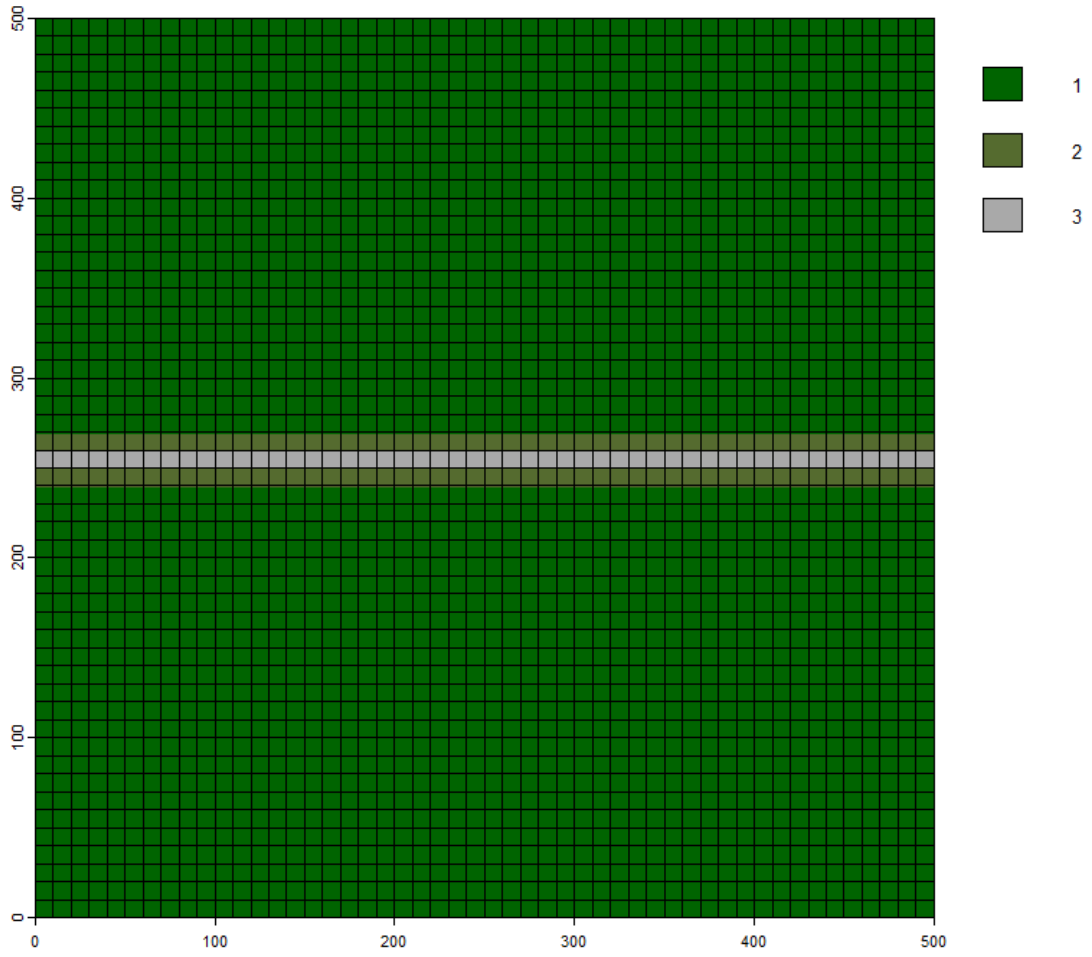
2. Entities, state variables, and scales

2.1 The landscape

The environment is composed of three types of cells: habitat cells (green cells with value = 1), risk area (dark green cells with value = 2), which are cells adjacent to the road, and the road itself

represented by a fixed single horizontal line of cells across the landscape (grey cells with value = 3) (see an example in **Figure A1**). The width of the risk area is defined based on the maximum step length of each population; therefore, populations with large daily movement distances have larger risk areas than populations with shorter daily movements.

The spatial element represents a landscape without a specific Coordinate Reference System (CRS) thus, the implicit unit is meters. The landscape is toroidal space represented by a grid with 2,000 rows and 2,000 columns, where each cell has a resolution of 50 meters (50 x 50 m), totalizing an area of 10,000 km². The landscape area was defined based on the maximum home range explored, and it is also a suitable size area for the smaller home range tested. The temporal scale is represented by the simulation step of the model, which represents the locations of individual movement per day. The parameters that control the simulation steps in the model are days and years. For instance, we can simulate 20 years, each year has 365 days, and we can use simulation step as the individual movement each 10 minutes, that results in 144 locations of individual movement per day. Alternatively, setting the simulation step for every 30 minutes results in 48 locations of individual movement per day. While using simulation step for every one hour represents 24 locations movement per day. Note that the simulation step is not how many steps the individual gives per day, one simulation step can represent a set of individual steps. This temporal definition was chosen to calculate daily and annual information. The model calculates how many individuals die and cross the road every day. Posteriorly, it calculates annual information, such as the initial and final population size, total numbers of stochastic deaths and births, total number of roadkill and crossings, roadkill and crossing rate, and net and relative growth, for each population evaluated. This information allows us to understand how wildlife-vehicle collisions influence population persistence.



2.2 *The individuals*

Each individual represents a wild animal within the population, which is characterized by the following independent state variables: *ID*, *alive*, *age*, *angle_abs*, *coordinates x* and *y*, and *track*. These variables are described below in **Table A1**. Additionally, each population is characterized by specific parameters that distinguish it from the others, such as: *lmin*, *lmax*, *angle_mean*, *angle_sd*, *mature*, *reprod_period*, *reprod_freq*, *num_offspring*, *K*, *speed_mean*, *speed_sd*, *min_prob_cross,* and *max_prob_cross*. These population parameters are described in detail in Section 5 in **Table A2**.

Table A1. Individuals' state variables. Each variable has a description of the type, unit, and the meaning for the model.

Variable name	Variable type and units	Meaning
ID	Discrete value; null	Identification of each individual.
alive	Logical number; null	Individual is alive = 1 or individual is dead = 0.

age	Discrete value; years	Time since the individual was created or born, influencing the processes of reproduction. Value = 0 is juvenile, value >= 1 is adult.
angle_abs	Continuous value; degree	This value is initialized by random sampling from a Normal distribution with parameters *angle_mean* and *angle_sd* (see details Section 7.2). Afterwards, it refers to the absolute angle realized on the previous movement step, representing the movement direction.
x	Integer; cell index	The x-coordinate of the individual's current position in the landscape.
y	Integer; cell index	The y-coordinate of the individual's current position in the landscape.
track	Integer; cell index pairs	A sequence list of the individual's previous positions in the landscape. It recorded the movement history as ordered pairs of x and y coordinates.

3. Process overview and scheduling

The flow diagram in **Figure A2** details the model processes and their schedule:

1. The 'setup' initializes the environment and creates the individuals.

2. The simulation starts with year = 1 and day = 1.

3. Each individual performs a simulation step, so that the model checks the cell type the individual is located in.

4. If the individual is in a habitat cell, it continues moving through the landscape.

5. If the individual is in a risk area, the model calculates whether the individual will attempt to cross the road; if not, it moves back to a habitat cell; if yes, it moves to the road.

6. If the individual is in a road cell, the model calculates the probability of this individual dying by collision with a vehicle. If the probability is higher than the random threshold, the individual dies; otherwise, it successfully crosses the road to the other side.

4. This process is repeated until all individuals complete their defined simulation steps, which also represents the end of the day.

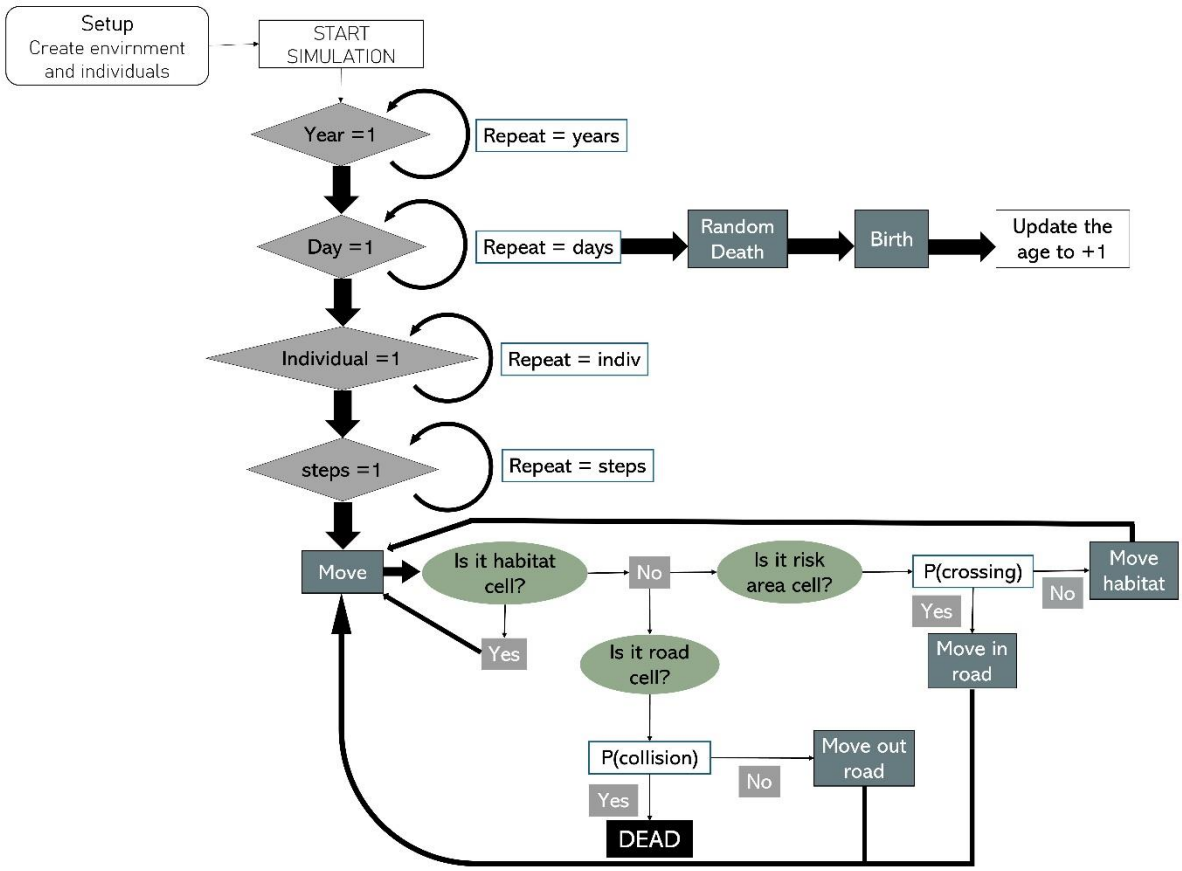
5. After the completion of all the days in the year, a stochastic mortality process is applied to the individuals that are still alive.

6. Individuals alive that have the minimum age for reproduction and are within the reproductive period can create new individuals.

7. Alive individuals increase their age by one year. This final process is the end of the year, and the sequence repeats for the next years until the simulation completes the predefined number of years.

The processes are organized sequentially: all individuals' movements are performed by correlated Lévy walk based on truncated Pareto distribution (Ríos-Uzeda et al., 2019), and their movement is updated at each simulation step. The alive status is updated immediately upon a collision event or after annual stochastic mortality. Movement and cell type verification are repeated at each simulation step, which occurs within a day and represents the daily temporal scale. Stochastic mortality and reproduction events represent the annual temporal scale. The environment remains fixed throughout the simulations and does not change during the processes. This schedule was chosen to reflect the biological processes under study: daily movement distance and collision risk, followed by annual demographic events such as aging and reproduction.

Figure A2. Flow diagram of the model.



Design concepts

4. Design concepts

4.1. Basic principles

This model was developed to better understand how daily movement distance, reproductive strategy, and crossing probability influence population persistence under different traffic flow scenarios. It is based on the principle that individual's daily movement distance determines how frequently an animal reaches a road and crossing probability how frequently an animal attempt to cross, thereby directly affecting wildlife-vehicle collisions. Individuals within a population share the same tendency to cross a road, although the crossing probability is calculated individually. When many individuals within a population frequently attempt to cross the road and experience high roadkill rates, would be necessary a reproduction strategy, such as early maturation and high fecundity to maintain population stability; otherwise, it is expected that the population would decline over time.

The development of this model was inspired by findings from previous studies. For instance, Rytwinski and Fahrig (2011) demonstrated that road density negatively impacts mammal abundance depending on reproductive rate and body size. Similarly, Jaeger et al. (2005) simulated different road

configurations with equivalent traffic flow distributed among them and explored varying levels of road avoidance behaviour. Based on these foundational studies, our model integrates and extends these concepts by explicitly simulating how combinations of behavioural and life-history traits (*e.g.*, daily movement distance, reproduction strategy, and crossing probability) influence population persistence in relation to traffic flow. These principles are implemented through individual movement decisions, reproduction, stochastic mortality, and mortality due to vehicle collisions. Furthermore, this model is designed to provide insights into which combinations of behavioural and life-history traits make populations more vulnerable to decline under different traffic flow scenarios. Such knowledge can support decision-makers in identifying vulnerable species and implementing appropriate mitigation measures.

4.2. Emergence

The primary emergent result is population stability – either persistence or local extinction – that comes from the interaction of three population traits – daily movement distance, reproduction strategy, and crossing probability – with traffic flow. The population dynamics have births and deaths influenced by density dependence, meaning reproduction rates are affected by population size while stochastic mortality occurs randomly. Individual-level decisions, including daily movement distance and crossing or not the road. The intensity of traffic flow directly impacts the number of wildlife-vehicle collisions.

Individuals' initial positions are randomly classified, and their movement follows the correlated Lévy walk based on truncated Pareto distribution (Ríos-Uzeda et al., 2019). The decision to cross the road is made individually and stochastically. Although each population has predefined the minimum and maximum crossing probabilities. That means that individuals can decide their own probability to cross based on the minimum and maximum crossing probabilities for their population.

While all individuals within a population share the same trait values, variation in population-level outcomes emerge when comparing distinct populations under different traffic flow scenarios. This structure allows the model to explore how complex population-level dynamics – such as extinction thresholds or persistence – can arise from simple rules interacting with traffic flow.

4.3.Adaptation

Individuals do not adapt their behavior based on themselves or landscape or other elements, such as the road and traffic flow. Although the movement direction and the decision to cross the road follow predefined rules that lead to emergent population-level patterns.

At each simulation step, individuals move using the correlated Lévy walk based on truncated Pareto distribution. When an individual is in a risk area (*i.e.*, a cell adjacent to the road, classified as cell type = 2), it probabilistically decides whether to attempt crossing. This decision is based on a Uniform distribution with fixed minimum and maximum values for all individuals within a population. The decision process incorporates both randomness and prior parameters about populations-specific probability to cross the roads.

4.4. Objectives

This model does not include direct decision-making related to individual movement. As described above, all behaviors are modeled through predefined rules that represent indirect decision processes.

4.5. Learning

This model does not include any form of learning. Individuals do not change their behavior based on past experiences or environmental feedback.

4.6. Prediction

This model does not incorporate explicit prediction. Individuals do not estimate future environmental states or their actions. All decisions are based on predefined probabilistic rules and fixed parameters that do not change in response to new information or prior experience.

4.7. Sensing

The individuals can recognize their own current location (x and y coordinates), the cell type they occupy, and their reproduction parameters (*i.e.*, age, period, and frequency), which are used to determine whether they can reproduce. At each simulation step, individuals evaluate the cell type they occupy – habitat, risk area, or road – which determines their next behavior: whether to continue moving (cell type = 1), attempt to cross the road (cell type = 2), or evaluate the risk of vehicle-collision (cell type = 3). There is no perception of other individuals or dynamic environmental conditions.

4.8. Interaction

In this model, no interaction among individuals is implemented. Each individual moves, reproduces, and dies independently of the others.

4.9. Stochasticity

Several processes in this model are represented stochastically to incorporate individual variability and simplify complex mechanisms. Stochasticity is used to define some individual attributes at

initialization, such as initial position, age, and movement angle. Individual movement follows the correlated Lévy walk based on truncated Pareto distribution and new angles from a Gaussian distribution. The decision to attempt crossing the road when located in a risk cell (cell type = 2) is based on a Uniform distribution with predefined parameters that reflect population-specific traits. Additionally, mortality due to collisions is probabilistic, when an individual is on a road cell (cell type = 3), a roadkill probability is evaluated, and the individual dies if this value exceeds a randomly drawn number. At the end of each year, individuals undergo a probabilistic stochastic death event, and reproduction occurs based on Poisson distribution with predefined parameters.

4.10. Collectives

This model does not include collectives. Individuals act independently and are not grouped into any aggregations or collective behaviours.

4.11. Observation

The focus of this model is to evaluate the persistence and decline of each population under different traffic flow scenarios. For each simulated population, the model records annual outputs, including initial and final population size, number of roadkill, roadkill rate, number of crossings, crossing rate, random deaths, births, net growth, and relative growth.

Details

5. Initialization

The model is generic, and it does not represent any specific species. Although, it is based on some real information and can be adapted to any species. The simulation model requires some population dynamic parameters as: birth rate (*b*), stochastic death rate (*d*), carrying capacity (*K*), and initial number of individuals (N_0); temporal parameters like number of days (*days*) and years (*years*); environment parameters as number of rows (*nrow*) and columns (*ncol*), and resolution (*res*). Also, the user needs to inform the road width (*road_width*), which influences the collision probability (see details in Section 7.5), and a list of population parameter (*pars*) must be defined before beginning the simulation (**Table A2**). All parameters described here can be changed for each purpose of the user.

As mentioned in Section 2.1, to create the landscape, it is necessary to specify the number of rows (*nrow*) and columns (*ncol*), as well as the resolution of the cell size (*res*) and population parameter (*pars*) which include information on the maximum step length for each population. Environmental

values of habitat, risk area, and road are fixed and do not change during simulation; however, the risk area width in the landscape changes according to the maximum step length of each population.

To create the individuals which represent the animals in the population, the initial number of individuals (N_0), the landscape (*env*) and a parameter table (*pars*) must be provided. This parameter table (*pars*; **Table A2**) includes the following population-specific parameters: number of simulation steps (*steps*), minimum step length (*lmin*), maximum step length (*lmax*), distribution parameter (*mu*), mean of movement angle (*angle_ mean*), standard deviation of the angle (*angle_sd*), mature age (*mature*), reproduction period (*reprod_period*), reproduction frequency (*reprod_freq*), number of offspring (*num_offspring*), carrying capacity (*K*), speed mean (*speed_mean*), speed standard deviation (*speed_sd*), minimum crossing probability (*min_cross_prob*), and maximum crossing probability (*max_cross_prob*). All individuals start alive and are randomly placed within habitat cells only; their coordinates are stored in the individual's *x* and *y* attributes, as well as in their movement *track*. The initial age of individuals is randomly sampled as either 0 (juvenile) or 1 to 3 (adult). The initial movement angle (*angle_abs*) follows a Gaussian distribution with predefined mean (*mean_angle*) and standard deviation (*angle_sd*), which are defined in *pars*. The *pars* table also include the traffic flow (*traffic_flow*) parameter, which influences the collision probability (see details in Section 7.4).

Table A2. The parameter table to be defined before the model simulation. These parameters are important to specify each population in the model simulation and the traffic flow impacts to be evaluated.

Parameter	Type and units	Meaning
steps	Discrete value; steps	The number of simulation steps in the model that tracks the individual movement.
mu	Discrete value; null	Shape parameter that mainly controls the tail and concentration of values in the truncated Pareto distribution.
lmin	Continuous value; meter	The minimum step length that an individual can take during each simulation step. This value is used in the truncated Pareto distribution to define the step length for the next simulation step.
lmax	Continuous value; meter	The maximum step length that an individual can take during each simulation step. This value is used in the truncated Pareto distribution to define the step length for the next simulation step.
angle_mean	Continuous value; degree	This value is used in the Normal distribution to define *angle_abs* (see details Section 2.2) when the individual is created. Afterwards, it is used to calculate the new angle for each simulation step.
angle_sd	Continuous value; degree	This value is used in the Normal distribution to define *angle_sd* (see details Section 2.2) when the individual is created. Afterwards, it is used to calculate the new angle for each simulation step.
mature	Discrete value; years	The maturity age at which the individual can start to reproduce.
reprod_period	Discrete value; years	The number of years between reproductive events. An individual reproduces only if its age is a multiple of this value.

reprod_freq	Discrete value; events/year	The frequency which the individual can reproduce within a year. It represents how often reproduction events can occur.
num_offspring	Discrete value; number of individuals	The maximum number of offspring that an individual can produce per reproductive event.
K	Discrete value; null	The value represents the carrying capacity of the population. It refers to the maximum population size following the logistic growth.
speed_mean	Discrete value; meters/minute	This value is used in the truncated Normal distribution to define the speed when the individual decides to cross the road.
speed_sd	Discrete value; meters/minute	This value is used in the truncated Normal distribution to define the speed when the individual decides to cross the road.
min_prob_cross	Continuous value; probability	The minimum probability that an individual will attempt to cross the road when located in a risk area.
max_prob_cross	Continuous value; probability	The maximum probability that an individual will attempt to cross the road when located in a risk area.
traffic_flow	Continuous value; vehicle/minute	Mean number of vehicles passing through the road per minute.

6. Input data

The model does not use external input data such as empirical datasets or spatial maps. All necessary information to define the landscape structure and population traits is set through parameters prior to the simulation.

7. Submodels

7.1. Create landscape

To create an environment, the user must run the *create_landscape* function. The user defines four parameters: *nrow*, *ncol*, and *res* which represent the cells and whole area size (**Table A3**) and *pars* to obtain the maximum step length (*lmax*; **Table A2**), which is used to define the risk area width. Initially, all cells are given value 1 to represent habitat and afterwards a road is defined in the middle of the landscape and given value 3. Then, the risk area surrounding the road is defined considering the maximum step length of the population, with a value of 2. Additionally, three distinct colors are given to each category (habitat, risk area, and road) to facilitate visualization (**Figure A1**). The user can choose to plot the landscape for visualization, turning the parameter *plot* to TRUE.

Table A3. The necessary parameters to create a landscape.

Variable name	Variable type and units	Meaning
nrow	Discrete value; number of cells	The number of columns that define the horizontal dimension of the landscape grid.
ncol	Discrete value; number of cells	The number of rows that define the vertical dimension of the landscape grid.
res	Continuous value; meters/cell	The value represents the spatial resolution of each cell in the landscape, defining the area represented in the simulated environment.

7.2.Create individuals

To create the animals in the population, it requires the number of initial individuals (N_0), defined by the user, the landscape created (*env*), and the parameter table (*pars*) with the parameter for that population (**Table A2**). All individuals are placed randomly within habitat cells, and the coordinates are stored in *x*, *y* and *track* attribute of each animal. Each individual has a unique ID, which is a sequence number, they start alive (value = 1), the age is sampled between 0 to 3, the initial movement angle (*angle_abs*) is defined following the Normal distribution (*angle_mean* and *angle_sd* specified in *pars*; **Table A2**). The user can also opt to visualize the individuals plotted with blue color on the landscape, turning the parameter *plot_point* to TRUE.

7.3.Individuals' movement

Animal movement is modeled by the correlated Lévy walk based on truncated Pareto distribution. This function requires as input the previously created landscape (*env*), the set of individuals (*indiv*),

and the parameter table (*pars*; **Table A2**). The parameters used in this submodel are minimum step length (*lmin*), maximum step length (*lmax*), distribution parameter (*mu*), mean movement angle (*mean_angle*), and standard deviation of the angle (*angle_sd*). Each movement step follows a hierarchical sequence:

1. Step length calculation: The step length for the current movement is sampled from the truncated Pareto distribution using the parameters *lmin*, *lmax*, and *mu*;

2. Current angle: The current movement angle is obtained from the individual's *angle_abs* parameter (initial movement angle; explained in Section 5 and 7.2);

3. New angle calculation: A new turning angle is sampled from a Normal distribution with predefined mean and standard deviation (*angle_mean* and *angle_sd* specified in *pars*);

4. Turning angle update: The turning angle is calculated as the sum of the current angle (*angle_abs*) and the new sampled angle in previous stage;

5. Angle update: The *angle_abs* attribute of the individual is updated with the new turning angle calculated previously.

6. Coordinate update: New coordinates are calculated following: new x-coordinates + cos (turning angle) * step length calculated and new y-coordinates sin(turning angle) * step length calculated. The new coordinates are always adjusted to ensure the toroidal space;

7. Update individual position: The individual's *x* and *y* coordinates are updated with the new values;

8. Track recording: The new coordinates are attached to the individual's movement *track*;

This sequence is repeated for each simulation step and for each individual that is alive during the simulation.

7.4.Collision probability

To calculate the probability of a vehicle colliding with an animal who attempts to cross the road, we used the equation described by Litvaitis and Tash (2008): $P_{killed} = N*a/v$. The necessary variables are vehicle per minute (N), width of kill zone (a; meters) and velocity of animal moving through kill zone (v; meters/min). In our submodel, the vehicle/minute (*traffic_flow*) is informed by the user within the parameter table (*pars*; **Table A2**), while the width of kill zone, which we considered as the road width (*road_width*), is defined prior as a fixed parameter in the simulation. Since animal speed is rarely available in empirical studies, we calculated it using a truncated Normal distribution to estimate the

speed for each individual who tried to cross the road. The minimum and maximum values were set at 50 and 700 meters/minute, respectively. The user can specify the mean and standard deviation to be used in this distribution (*speed_mean* and *speed_sd* specified in *pars*; **Table A2**).

Wildlife-vehicle collision starts in sixth year and for each individual who decides to cross, an individual's speed is calculated using the truncated Normal distribution and stored. The collision probability is calculated according to the Litvaitis and Tash (2008) equation described above. This probability is compared against a random number: if the probability exceeds the random value, the individual dies, then the alive attribute is update to 0 and *death_type* attribute of the individual is updated to "collision"; otherwise, it successfully crosses the road.

7.5. Stochastic mortality

At the end of each year of simulation, individuals that remain alive (*i.e.,* those that did not die due to collision) may die due to stochastic mortality. This represents demographic stochasticity, a common feature in population dynamics, ensuring that even in stable environments, some individuals may die randomly over time due to other means than collision, such as predation, resource limitation, or disease.

This submodel requires as input the list of individuals and the stochastic death probability parameter (*d*), which is defined by the user as a fixed parameter in the simulation. For each individual that is still alive, a Binomial distribution is performed using the parameter *d*. If the outcome is 1, the individual dies, and the alive attribute is updated to 0. Additionally, the *death_type* attribute of the individual is updated to "random" to distinguish this cause of death from collision. Also, a counter tracks the number of individuals that died due to stochastic mortality in each year.

7.6. Birth

At the end of each year of simulation, individuals that remain alive (*i.e.,* those that did not die due to vehicle collision or stochastically) and have reproductive conditions may give birth to new offspring. This submodel represents population recruitment and demographic dynamics.

The parameters used in this submodel are the previously created landscape (*env*), the list of individuals alive, the set of dead individuals (to access the ID numbers and to not repeat), the parameter table (*pars*; **Table A2**), carrying capacity (*K*), and the birth probability (*b*). Parameter *b* is defined by the user as fixed parameter prior to the simulation. For an individual to reproduce, this submodel verifies two conditions: whether the individual has the minimum reproductive age (parameter *mature* in *pars*) and whether the current year coincides with the individual's reproductive period

(*reprod_period* specified in *pars*; **Table A2**). If both conditions are true, the submodel calculates the adjusted birth probability based on reproductive frequency (parameter *reprod_freq* specified in *pars*; **Table A2**). Posteriorly, the adjusted birth probability is readjusted based on the population density, following the logistic population growth, which reduces the probability of reproduction as population density approaches carrying capacity (*K*) of each population.

Poisson distribution determines how many individuals will be born. The lambda is calculated for each individual considering the readjusted birth probability multiplied by the offspring (*num_offspring* specified in *pars*; **Table A2**). For each offspring, a random habitat cell is selected within the landscape to determine its initial coordinates. Each new individual has a unique ID, starting at age 0, and it has all the same attributes following the process described in Submodel 7.2. All new individuals created in this process are appended to a list of new individuals (*new_indiv_list*); consequently, they are added into the overall population list. Additionally, a counter tracks the total number of births in each year.

7.7. Sub-submodels

7.7.1. Move habitat

This sub-submodel is applied when the individual positioned in the risk area decides not to cross the road. It is selected all adjacent cells from the last position on habitat cell (using an 8-direction neighborhood). Thus, it randomly sampled a cell that is habitat to be the new position and moves the individual there. Afterwards, the new *x*, *y* and *tracks* are stored in the attributes of that individual. Optionally, the user can choose to plot the new position with a red point, turning the parameter *plot_point* to TRUE.

7.7.2. Move in road

If the individual decides to cross the road, this sub-submodel is applied. The individual moves to the road cell in front of it. The new *x*, *y* and *tracks* are stored in the attributes of that individual. The user can also decide to plot the individual on the road with a black point, turning the parameter *plot_point* to TRUE.

7.7.3. Move out road

This sub-submodel is applied if the individual did not die while trying to cross the road (see Section 7.4). Thus, the individual successfully crosses the road and moves to a new habitat cell on the other side of the road. The process starts by identifying the current road cell and the previous cell in the individual's movement trajectory. Based on the previous cell, before going to the road, the model

335 determines whether the individual is crossing from north to south or from south to north. Accordingly,
336 the new cell is a habitat cell in the opposite direction to the previous one (it jumps the risk area). Once
337 the new cell is selected, its coordinates are stored and used for a subsequent movement step, following
338 the same procedures described in Section 7.3. Thus, the individual's position attributes (*x*, *y*, and *track*),
339 as well as *angle_abs*, are updated. The new position is also optionally plotted on the landscape as a
340 purple point, turning the parameter *plot_point* to TRUE.

Appendix B. Examples of potential real species for each category created

Table B1. Potential medium-large mammal species to represent each simulated category. Species were selected as illustrative examples that match the defined criteria of daily movement distance and reproductive strategy. References supporting movement and reproductive parameters are provided for each species.

Category	Potential species	Daily movement references	Reproduction references
1	*Hydrochoerus hydrochaeris* (capybara); *Nasua nasua* (South American coati)	*Hydrochoerus hydrochaeris*: Dias et al., 2020 *Nasua nasua*: Hirsch, 2010	*Hydrochoerus hydrochaeris*: Alvarez and Kravetz, 2006 *Nasua nasua*: Hirsch and Maldonado, 2011
2	*Chrysocyon brachyurus* (maned wolf); *Lynx* sp. (lynx); *Meles meles* (European badger)	*Chrysocyon brachyurus*: Bandeira de Melo et al., 2007 *Lynx* sp.: Jędrzejewski et al., 2002 *Meles meles*: Kowalczyk et al., 2006	*Chrysocyon brachyurus*: Carvalho et al., 2022 *Lynx* sp.: Fritts and Sealander, 1978 *Meles meles*: Rosen et al., 2019
3	*Leopardus pardalis* (ocelot); *Panthera onca* (jaguar); *Panthera pardus* (leopard);	*Leopardus pardalis*: Rowcliffe et al.,2016 *Panthera onca*: Nuñez-Perez and Miller, 2019 *Panthera pardus*: Odden and Wegge, 2005	*Leopardus pardalis*: de Magalhães and Costa, 2009 *Panthera onca*: de Magalhães and Costa, 2009 *Panthera pardus*: Balme et al., 2013
4	*Myrmecophaga tridactyla* (giant anteater); *Tapirus indicus* (Malayan tapir)	*Myrmecophaga tridactyla*: Bertassoni et al., 2017 *Tapirus indicus*: Mahathir et al., 2017	*Myrmecophaga tridactyla*: Gaudin et al., 2018 *Tapirus indicus*: de Magalhães and Costa, 2009

Appendix C. The population categories with their respective parameters

Table C1. Parameter used to define the four population categories in the individual-based models. For each category, we specified the minimum and maximum step length (meters), age at sexual maturity (years), litter size (number of individuals), and carrying capacity (*K*). Simulations were performed for each category using three road-crossing probability ranges representing low (0–0.33), intermediate (0.33–0.66), and high (0.66–1) crossing probability.

Category	Step length (min; m)	Step length (max; m)	Mature (age)	Litter (individuals)	Carrying capacity (*K*)	Crossing probability (min)	Crossing probability (max)
1	6.94	34.72	1	8	58	0	0.33
1	6.94	34.72	1	8	58	0.33	0.66
1	6.94	34.72	1	8	58	0.66	1
2	34.72	69.44	1	3	55	0	0.33
2	34.72	69.44	1	3	55	0.33	0.66
2	34.72	69.44	1	3	55	0.66	1
3	34.72	69.44	2	3	60	0	0.33
3	34.72	69.44	2	3	60	0.33	0.66
3	34.72	69.44	2	3	60	0.66	1
4	6.94	34.72	3	2	95	0	0.33
4	6.94	34.72	3	2	95	0.33	0.66
4	6.94	34.72	3	2	95	0.66	1

Appendix D. Test of carrying capacity to population stability.

To assess population stability, we tested different carrying capacity (*K*) values for each population category, without considering traffic flow, by simulating 100 years with 100 independent replicates. The first five years of each simulation were excluded as a burn-in period to avoid the influence of transient dynamics. For each replicate, we calculated the mean population size across the post–burn-in years. For each category and *K* value, we calculated the mean and standard deviation of these replicates means, representing the expected equilibrium population size and its variability among replicates. Temporal stability was quantified using two complementary metrics. First, we calculated the mean percentage deviation of population size from its own temporal mean within each replicate, which measures the typical magnitude of fluctuations around equilibrium. Second, we computed the coefficient of variation (CV = SD / mean × 100) for each replicate and summarized its mean and standard deviation across replicates, providing a standardized measure of temporal variability.

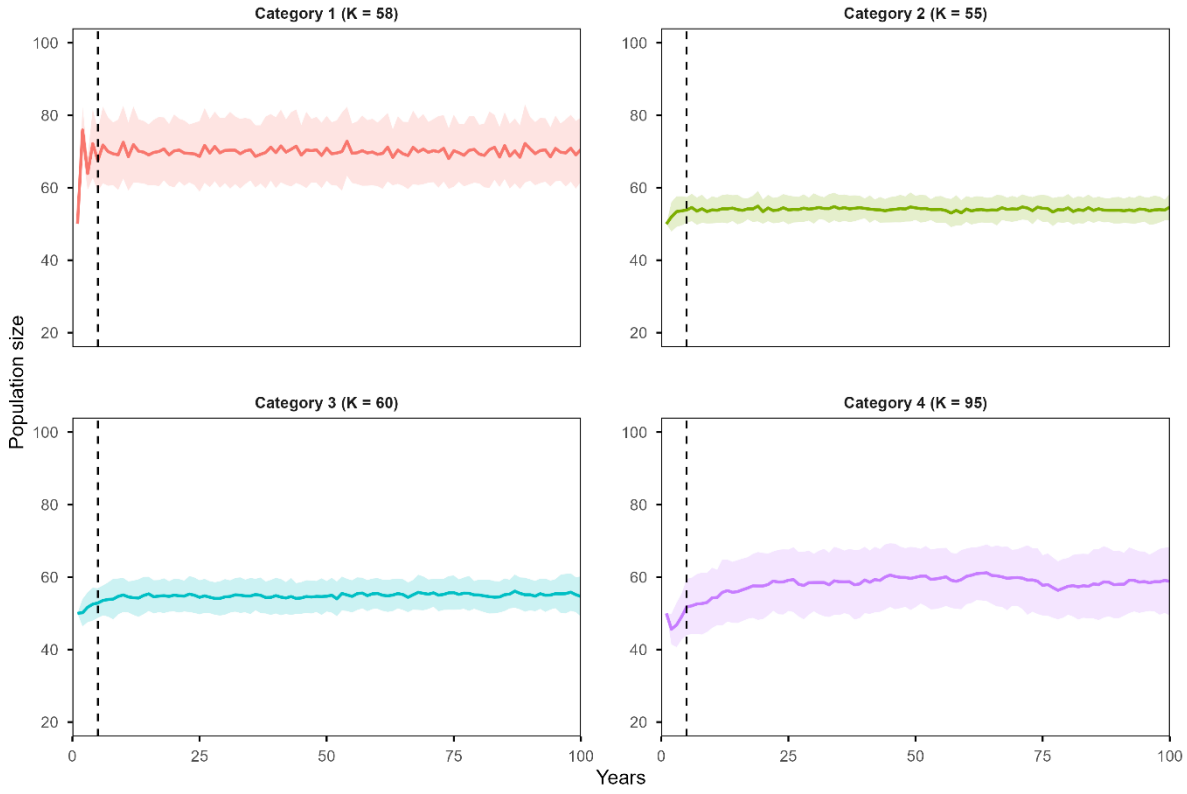
The criteria used to select *K* values included low temporal variability, low variation among replicates, and the absence of explosive or chaotic dynamics. The selected *K* values for all categories resulted in dynamically stable populations. Mean temporal fluctuations ranged from 5% to 11% around equilibrium across categories. The coefficient of variation indicated low temporal variability (CV range: 6.6–13.7%), with small standard deviations among replicates, indicating consistent convergence across simulations (SD ≤ 3.33 individuals). The full results for the selected carrying capacity values are presented in **Table D1**. The temporal dynamics of mean population size per year across replicates, along with the corresponding standard deviation, is shown in **Figure D2**.

Table D1. Population stability metrics for the selected carrying capacity (*K*) values in each population category. Simulations were run for 100 years with 100 independent replicates, excluding the first five years as burn-in. Mean population and its standard deviation represent the average equilibrium population size and its variability among replicates. Mean fluctuation (%) indicates the average percentage deviation of population size from its temporal mean within each replicate. The coefficient of variation (CV) provides a standardized measure of temporal variability.

Category	*K*	Mean population	SD population	Mean fluctuation (%)	SD fluctuation	Mean CV (%)	SD CV
1	58	70.02	0.62	10.73	0.74	13.11	0.84
2	55	54.04	0.49	5.18	0.53	6.57	0.63
3	60	54.91	0.84	6.41	0.88	8.13	1.17

Category	*K*	Mean population	SD population	Mean fluctuation (%)	SD fluctuation	Mean CV (%)	SD CV
4	95	58.36	3.33	11.13	2.54	13.72	3.01

Figure D2. Temporal dynamics of population size for the selected carrying capacity (*K*) values in each category. Solid lines represent the mean population size per year across 100 independent replicates, and shaded areas indicate standard deviation among replicates. The vertical dashed line marks the end of the 5-year burn-in period, which was excluded from stability analyses.



Appendix E. Model and Sensitivity analyses results

Table E1. ANOVA results for the effect of traffic flow on mean relative population growth. We fitted an analysis of variance model to assess the effect of traffic intensity on mean relative population growth, calculated as the average across 20 simulated years per replicate. Traffic flow was treated as an ordered factor with polynomial contrasts weighted by actual traffic values: 0, 1, 5, 10 vehicles/min; decomposing the effect into linear (L), quadratic (Q), and cubic (C) components. The values shown represent the estimates of the regression coefficients, the standard error (SE) and the p-value of significance (p<0.05). Model fit is indicated by the coefficient of determination $R^2 = 0.007$ ($F = 11.74$, $p < 0.001$).

Predictors	Estimate	SE	t-value	p-value
Intercept	0.01558	0.00029	54.382	< 0.001
traffic_flow.L	-0.00241	0.00057	-4.214	< 0.001
traffic_flow.Q	0.00172	0.00057	2.996	0.003
traffic_flow.C	-0.00167	0.00057	-2.913	0.004

Table E2. ANOVA results for the effect of traffic flow on mean relative population growth, including population categories and crossing probability as interacting factors. We fitted an analysis of variance model to assess the effects of traffic intensity, population category, crossing probability, and their interactions on mean relative population growth, calculated as the average across 20 simulated years per replicate. Traffic flow was treated as an ordered factor with polynomial contrasts weighted by actual traffic values: 0, 1, 5, 10 vehicles/min; decomposing the effect into linear (L), quadratic (Q), and cubic (C) components. Crossing probability levels: low (0–0.33), medium (0.33–0.66), and high (0.66–1). The values shown represent the estimates of the regression coefficients, the standard error (SE) and the p-value of significance (p<0.05). Model fit is indicated by the coefficient of determination $R^2 = 0.841$ ($F = 535.1$, $p < 0.001$).

Predictors	Estimate	SE	t-value	p-value
Intercept	0.04752	0.00040	119.150	< 0.001
traffic_flow.L	-0.00072	0.00080	-0.902	0.367
traffic_flow.Q	-0.00051	0.00080	-0.641	0.522

Predictors	Estimate	SE	t-value	p-value
traffic_flow.C	0.00130	0.00080	1.631	0.103
crossing[low]	-0.00189	0.00056	-3.356	< 0.001
crossing[medium]	-0.00026	0.00056	-0.457	0.647
category [2]	-0.04196	0.00056	-74.402	< 0.001
category [3]	-0.04568	0.00056	-80.982	< 0.001
category [4]	-0.04120	0.00056	-73.038	< 0.001
traffic_flow.L * crossing[low]	0.00323	0.00113	2.863	0.004
traffic_flow.Q * crossing[low]	0.00091	0.00113	0.803	0.422
traffic_flow.C * crossing[low]	-0.00185	0.00113	-1.637	0.102
traffic_flow.L*crossing[medium]	0.00169	0.00113	1.502	0.133
traffic_flow.Q * crossing[medium]	-0.00009	0.00113	-0.076	0.939
traffic_flow.C * crossing[medium]	0.00005	0.00113	0.042	0.966
traffic_flow.L * category [2]	-0.00120	0.00113	-1.060	0.289
traffic_flow.Q * category [2]	0.00173	0.00113	1.532	0.126
traffic_flow.C * category [2]	-0.00341	0.00113	-3.020	0.003
traffic_flow.L * category [3]	-0.00362	0.00113	-3.212	0.001
traffic_flow.Q * category [3]	0.00477	0.00113	4.230	< 0.001
traffic_flow.C * category [3]	-0.00634	0.00113	-5.619	< 0.001
traffic_flow.L * category [4]	-0.00412	0.00113	-3.653	< 0.001
traffic_flow.Q * category [4]	0.00335	0.00113	2.971	0.003

Predictors	Estimate	SE	t-value	p-value
traffic_flow.C * category [4]	-0.00526	0.00113	-4.660	< 0.001
crossing[low] * category [2]	0.00248	0.00080	3.115	0.002
crossing[medium] * category [2]	0.00019	0.00080	0.242	0.809
crossing[low] * category [3]	0.00402	0.00080	5.034	< 0.001
crossing[medium] * category [3]	0.00108	0.00080	1.353	0.176
crossing[low] * category [4]	0.00315	0.00080	3.943	< 0.001
crossing[medium] * category [4]	0.00087	0.00080	1.086	0.277
traffic_flow.L * crossing[low] * category [2]	-0.00292	0.00160	-1.828	0.068
traffic_flow.Q * crossing[low] * category [2]	-0.00123	0.00160	-0.771	0.440
traffic_flow.C * crossing[low] * category [2]	0.00307	0.00160	1.924	0.054
traffic_flow.L * crossing[med] * category [2]	-0.00200	0.00160	-1.252	0.210
traffic_flow.Q * crossing[med] * category [2]	0.00027	0.00160	0.172	0.864
traffic_flow.C * crossing[med] * category [2]	0.00095	0.00160	0.599	0.550
traffic_flow.L * crossing[low] * category [3]	-0.00392	0.00160	-2.456	0.014
traffic_flow.Q * crossing[low] * category [3]	-0.00269	0.00160	-1.687	0.092
traffic_flow.C * crossing[low] * category [3]	0.00519	0.00160	3.255	0.001
traffic_flow.L * crossing[med] * category [3]	-0.00063	0.00160	-0.397	0.691
traffic_flow.Q * crossing[med] * category [3]	-0.00014	0.00160	-0.086	0.931
traffic_flow.C * crossing[med] * category [3]	0.00164	0.00160	1.031	0.303
traffic_flow.L * crossing[low] * category [4]	-0.00268	0.00160	-1.680	0.093

Predictors	Estimate	SE	t-value	p-value
traffic_flow.Q * crossing[low] * category [4]	-0.00177	0.00160	-1.109	0.267
traffic_flow.C * crossing[low] * category [4]	0.00450	0.00160	2.818	0.005
traffic_flow.L * crossing[med] * category [4]	-0.00106	0.00160	-0.664	0.506
traffic_flow.Q * crossing[med] * category [4]	-0.00055	0.00160	-0.347	0.729
traffic_flow.C * crossing[med] * category [4]	0.00121	0.00160	0.758	0.448

Table E3. First-order (S_i), Total-order (T_i), and Second-order (S_{ij}) of Sobol' sensitivity indices for the eight parameters included in the global sensitivity analysis. S_i quantifies the contribution of each parameter individually to relative growth variability; T_i quantifies the total contribution of each parameter including interactions with all other parameters; S_{ij} quantifies the contribution of pairwise parameter interactions. Estimate values (original), bootstrap bias (bias), standard error (se), and 95% bootstrap confidence intervals (low.ci, high.ci) are reported for each index ($R = 10^5$ resamples, N = 100 samples per matrix). Parameter abbreviations: lmin/lmax = minimum and maximum step length (m); mature = age at first reproduction (years); offspring = number of offspring per reproductive event; K = carrying capacity; traffic_flow = vehicles/min; min_probCross/max_probCross = minimum and maximum road-crossing probability.

original	bias	se	low.ci	high.ci	sensitivity	parameters
-0.124	-0.003	0.156	-0.428	0.185	Si	lmin
0	-0.003	0.15	-0.291	0.297	Si	lmax
0.046	-0.004	0.135	-0.215	0.314	Si	mature
0.171	0	0.147	-0.118	0.46	Si	K
-0.053	-0.001	0.152	-0.35	0.247	Si	offspring
-0.191	-0.004	0.132	-0.447	0.071	Si	traffic_flow
-0.155	-0.003	0.132	-0.411	0.105	Si	min_probCross
0.116	-0.001	0.134	-0.146	0.38	Si	max_probCross
1.015	0.009	0.14	0.732	1.281	Ti	lmin
1.008	0.008	0.144	0.716	1.283	Ti	lmax
0.967	0.008	0.126	0.712	1.206	Ti	mature
0.855	0.008	0.132	0.587	1.106	Ti	K

original	bias	se	low.ci	high.ci	sensitivity	parameters
0.759	0.004	0.125	0.51	1	Ti	offspring
1.062	0.011	0.146	0.765	1.338	Ti	traffic_flow
0.956	0.007	0.149	0.657	1.242	Ti	min_probCross
0.902	0.007	0.109	0.682	1.108	Ti	max_probCross
0.254	0.002	0.218	-0.174	0.679	Sij	lmin.lmax
0.213	0.003	0.183	-0.15	0.568	Sij	lmin.mature
-0.147	0.001	0.231	-0.601	0.305	Sij	lmin.K
0.112	0.004	0.234	-0.352	0.567	Sij	lmin.offspring
0.438	0.006	0.196	0.047	0.816	Sij	lmin.traffic_flow
0.283	0.003	0.229	-0.169	0.73	Sij	lmin.min_probCross
0.1	0.001	0.192	-0.277	0.475	Sij	lmin.max_probCross
-0.076	0.006	0.197	-0.468	0.304	Sij	lmax.mature
-0.322	-0.001	0.181	-0.675	0.033	Sij	lmax.K
0.02	0.001	0.241	-0.453	0.49	Sij	lmax.offspring
0.052	0.002	0.182	-0.308	0.407	Sij	lmax.traffic_flow
-0.1	0.002	0.176	-0.447	0.243	Sij	lmax.min_probCross
-0.144	0.002	0.157	-0.454	0.161	Sij	lmax.max_probCross
-0.258	0.002	0.195	-0.642	0.122	Sij	mature.K
-0.171	0.003	0.202	-0.57	0.22	Sij	mature.offspring
0.076	0.007	0.193	-0.309	0.448	Sij	mature.traffic_flow
0.183	0.003	0.185	-0.182	0.542	Sij	mature.min_probCross
-0.254	0.003	0.2	-0.649	0.133	Sij	mature.max_probCross
-0.085	-0.001	0.245	-0.565	0.397	Sij	K.offspring
-0.051	0.002	0.21	-0.465	0.359	Sij	K.traffic_flow
-0.074	0.004	0.19	-0.45	0.295	Sij	K.min_probCross
-0.349	0	0.19	-0.722	0.024	Sij	K.max_probCross
0.137	0.001	0.198	-0.252	0.525	Sij	offspring.traffic_flow
0.203	0.004	0.199	-0.192	0.589	Sij	offspring.min_probCross
-0.078	0.003	0.222	-0.516	0.354	Sij	offspring.max_probCross
0.313	0.006	0.23	-0.143	0.758	Sij	traffic_flow.min_probCross
0.201	0.005	0.175	-0.146	0.538	Sij	traffic_flow.max_probCross
0.157	0.004	0.198	-0.235	0.541	Sij	min_probCross.max_probCross

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Capítulo III

A systematic map of the terms and methods used to identify spatial patterns of roadkill concentration on roads

Esse capítulo será submetido a revista "*Conservation Biology*" e foi realizado em colaboração com Andreas Kindel, Vinicius A. G. Bastazini, Igor Pfeifer Coelho e Fernanda Zimmermann Teixeira.

Conservation Biology

A systematic map of the terms and methods used to identify spatial patterns of roadkill concentration

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Author Contributions

Ingridi Camboim Franceschi: Conceptualization; Methodology; Investigation; Formal analysis; Visualization; Writing – original draft; Writing – review & editing. **Andreas Kindel**: Conceptualization; Investigation; Writing – review & editing; Supervision. **Vinicius Augusto Galvão Bastazini**: Conceptualization; Formal analysis; Visualization; Writing – review & editing. **Igor Pfeifer Coelho**: Conceptualization; Writing – review & editing. **Fernanda Zimmermann Teixeira**: Conceptualization; Investigation; Writing – review & editing.

Authors Statement

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Abstract

Wildlife-vehicle collisions on roads threaten species persistence, compromise human safety, and generate significant economic losses. Identifying road segments with higher concentration of roadkill is essential for planning mitigation measures to reduce this impact. Two complementary questions are commonly used to prioritize such segments: first, whether roadkill data is spatially concentrated, and second, where are the segments with roadkill concentration located. However, the terminology and methods associated with these questions are frequently misunderstood and misapplied. This systematic map aimed to identify the terminology and statistical spatial methods used to evaluate roadkill spatial patterns, and to explore whether methodological choices vary by continent, taxonomic group, and publication year. We searched for peer-reviewed articles published in English between 2000 and 2022 in Web of Science and Google Scholar, retrieving 2,051 records. A three-stage blind screening protocol was conducted independently by two reviewers. Inclusion criteria required studies to report statistical spatial methods for assessing roadkill spatial patterns. We selected 120 studies and extracted methodological information, terminology, taxonomic groups, continents, and publication years. Associations between the data extracted were assessed using Fisher's test, and Multiple Correspondence Analysis was used to visualize methodological patterns. Terminological confusion was evident, as terms such as "*aggregation*", "*cluster*", and "*hotspot*" were frequently used interchangeably to describe both questions with distinct analytical approaches. We identified eight methods for assessing detection of roadkill concentration, the most common being 2D-Ripley's K and Ripley's K functions, and 19 methods for identifying the location of roadkill concentration, with Kernel Density Estimation used in 49% of studies. Most studies (69) identified the location of roadkill concentration without testing for detection of roadkill concentration, whereas 43 applied both question approaches sequentially. Our synthesis reveals geographically biased methodological choices, and lack of clarity about which spatial question was being addressed. These patterns have practical implications for the planning and evaluation of mitigation actions that depend on spatial and temporal comparisons. Future studies comparing the performance of spatial methods under different data distributions are needed to support method selection, enabling researchers and practitioners to make analytically informed choices rather than tradition-driven ones.

Keywords: Gap analysis; Geographic bias; Hotspot; Research bias; Road Ecology; Spatial analysis; Spatial methods; Wildlife-vehicle collision

Introduction

Wildlife-vehicle collisions on roads have impacts on both wildlife populations and human health. Roadkills can influence the persistence of ecological populations (Grilo et al., 2021) and communities (Mestre et al., 2025), and compromise user safety (Balčiauskas et al., 2025; Bíl et al., 2025), in addition to causing significant economic losses (Abra et al., 2019; Huijser et al., 2022). Hence, identifying road segments with high numbers of roadkills is a key step in guiding the prioritization of mitigation measures (Spanowicz et al., 2020). Choosing appropriate statistical methods is essential to accurately identify priority road segments to save wildlife and human lives, as well as efficiently allocating resources to these ends (Spanowicz et al., 2020; Karanasios et al., 2021).

The spatial location of road segments with higher concentration of roadkill records is commonly referred as "roadkill hotspots" (e.g., Gunson and Teixeira, 2015). However, researchers use different terms to refer to that as synonymous (e.g., Yamashita et al., 2021; Chamling et al., 2020; Brockie, 2007). Here, we will use a generic term to mention it to avoid misunderstandings throughout the text and to ensure readability for anyone: "location of roadkill concentration". Similarly, there are multiple statistical methods to evaluate spatial patterns of higher concentration of roadkill along the roads. Although those methods are complementary, which can lead to frequent misunderstanding and misapplication, they address different questions, analytical purposes, and rely on distinct statistical outcomes. Considering that, we will address these spatial pattern methods in two distinct analytical questions: (1) methods that seek to evaluate whether roadkill events are spatially concentrated or not (e.g., Clevenger et al., 2003; Coelho et al., 2008), as detection of roadkill concentration methods; (2) methods that aim to identify the specific spatial location of road segments where roadkill is concentrated (e.g., Coelho et al., 2014; Malo et al., 2004; Okabe et al., 2006), as the location of roadkill concentration. As a result, terminology is applied across those spatial pattern methods without a clear distinction between the method and purposes. Terminology diversity is natural in science and may evolve as the field advances, however conceptual clarity and transparent use of terms is essential for scientific communication and ecological application (Parker et al., 2016; Moore et al., 2021). Therefore, we will consider distinct terms for both analytical approaches based on the questions.

Terminological and methodological choices in scientific research may be influenced by multiple factors, which could explain the diversity observed in the roadkill literature. First,

temporal bias may arise as research priorities, analytical methods, and scientific paradigms evolve over time, influencing which questions are addressed and how studies are conducted (Culumber et al., 2019). Second, most studies in biodiversity conservation, ecology, and evolution are concentrated in North America and Europe, incurring in geographical bias (Trimble and van Aarde, 2012; Stroud and Feely, 2017). Third, taxonomic bias may be driven by preferences towards charismatic species (Sumner et al., 2018) or related to human safety and human-wildlife conflict (Hoffmann and Montgomery, 2022). Beyond these broader patterns, method selection may also be influenced by practical considerations such as study scope, sample size, and the type of available data (Mwita, 2022). Thus, analytical decisions can influence research outcomes, since different methods applied to the same dataset may lead to different results, emphasizing the importance of transparency in methodological choices (Sarstedt et al., 2024; Sutherland et al., 2018). These factors may explain variation in the terminology and methods used to assess the spatial patterns of roadkill across studies. Despite the expanding literature on wildlife-vehicle collision (Pagany, 2020; Su et al., 2026), it remains unclear whether authors' methodological choices are based on data or reflect research bias. Although some studies have compared roadkill spatial methods (e.g., Gomes et al., 2009; Borda-de-Água et al., 2019), the relative performance of different methods under varying sampling conditions has not been systematically evaluated. A global synthesis of these terms and methods could promote more consistent use of terminology and analytical approaches, but also identify priorities for future methodological development, including simulation-based comparisons of method performance across different data conditions.

Objective of the review

We performed a systematic mapping review to identify the terminology and statistical spatial methods applied to identify spatial patterns of roadkill, focusing on analytical methods that (1) detect of roadkill concentration and (2) identify the location of roadkill concentration. We tested whether terminological and methodological choices are associated with continent, taxonomic group, or year of publication, to explore potential tradition-driven research bias. Additionally, we also aimed to identify research gaps, particularly the need for studies exploring the performance of different analytical methods under varying roadkill spatial distributions, spatial scales, and road configurations.

Primary question and Components

Our primary question was: What terms and spatial methods are used to evaluate spatial patterns of roadkill, considering two analytical approaches regarding roadkill patterns: (1) detection of roadkill concentration, and (2) location of roadkill concentration?

To address our question of mapping terminology and statistical approaches, we structured our review as a scoping review/systematic mapping. We adopted a PCC framework (Population – Concept – Context; Peters et al., 2022) to define the review scope and eligibility criteria:

- Population: wildlife-vehicle collision studies.
- Concept: terminology and statistical methods to evaluate detection of roadkill concentration and identify the location of roadkill concentration.
- Context: road ecology.

Methods

This review followed the Collaboration for Environmental Evidence Guidelines (CEE, 2022) and ROSES reporting standards (James et al., 2016; Haddaway et al., 2018; SM1), which include article searching, screening protocol, eligibility criteria, study validity assessment, data extraction, and descriptive analysis.

Article searching

We selected keywords by combining infrastructure type, terminology, and taxonomic group (**Table 1**). Components were linked by the Boolean operator "AND" to combine components between components and the operator "OR" within components.

Table 1. Components used in the literature search with corresponding components and search string structure. The asterisk (*) denotes truncated components to retrieve plural forms.

Components	Strings	Search string
Infrastructure	road, highway, motorway, freeway, train, rail	road* OR highway* OR motorway* OR freeway
		AND
Terminology	hotspot, aggregation, cluster, blackspot	hotspot* OR aggregation* OR *cluster* OR blackspot*
		AND

Taxon	wildlife, vertebrate, mammal, bird, amphibian, reptile, anuran, species, invertebrate, insect, animal	wildlife OR vertebrate* OR mammal* OR bird* OR amphibian* OR reptile* OR anuran* OR species OR invertebrate* OR insect* OR animal*

We conducted literature searches using Web of Science (WoS) Core Collection accessed from Universidade Federal do Rio Grande do Sul's institutional subscription and the search engine Google Scholar (GS) as complementary information (Haddaway et al., 2015). In both platforms, we used the same strings and temporal filter, looking only for publications in English.

For Web of Science, the first search was conducted on November 10, 2022, using a temporal filter from January 1, 2000, to June 30, 2022, and the Topic Search (TS) field, which retrieves records from titles, abstracts, and author keywords. This search yielded 2,096 articles. After retaining only research and review articles, 1,949 articles remained. Subject area filters, such as "Biodiversity Conservation", "Biology", "Ecology", "Environmental Sciences", "Environmental Studies", "Transportation", "Urban Studies", and "Zoology", were then applied, resulting in 767 articles. A second search was conducted on June 9, 2023, covering January 1 to December 31, 2022, and applying the same publication type and subject area filters. This search yielded 106 articles, of which seven fell outside the temporal range and one was a duplicate (see **SM2**). Across both searches, 48 duplicate articles were identified and removed. In total, 817 Web of Science articles were reviewed.

For Google Scholar, the first search was conducted on November 14, 2021, covering 2000–2021 and yielding 17,600 articles, and a second search on June 9, 2023, identified articles published in 2022, returning 4,920 articles. In both searches, we captured the first 40 pages (20 articles per page) sorted by relevance and exclude citations to be screened. After screening, 790 and 797 articles were retained from the first and second searches, respectively (see **SM2**). From the second search, 239 out-of-range articles and four duplicates were excluded. In total, 1,344 Google Scholar articles were screened.

After performing the searches, all articles retrieved from the Web of Science were exported as Excel files (.xlsx), while Google Scholar results were exported as a CSV file. Despite differences in metadata structures between platforms, the following common fields were used

for data harmonization and duplicate removal: authors, title, publication/journal, year, and DOI (when available).

Screening protocol

We followed a systematic blind protocol with two independent reviewers (Stoll et al., 2019). Both reviewers screened all articles at three sequential stages: title, abstract, and full text (**Fig. 1**). Duplicate articles were removed prior to screening, including duplicates between platforms (Google Scholar n = 110), within the same search and platform (n = 5), and between searches of the same platform (n = 48). Details of the duplicate removal procedure are provided in **SM2**.

Eligibility criteria

We only included studies aimed at identifying spatial pattern of roadkill, considering at least one of the analytical approaches: (1) detection of roadkill concentration, and (2) the location of roadkill concentration. During the screening process we excluded: non-English literature, grey literature, simulation-based studies, studies using predictive or explanatory variables to model spatial patterns, and reviews. The reason for exclusion of each article is presented in SM2. Below we describe each screening stage:

Stage 1 – Title screening

Both reviewers independently assessed all titles based on the question: "Does the article involve, or could it potentially involve spatial patterns of roadkill on roads?" If the answer was clearly yes or potentially yes, the article was taken for the second stage (abstract screening). In this initial stage, we excluded articles only if we were certain they were unrelated to the topic for both reviewers.

Stage 2 – Abstract screening

Abstracts were evaluated according to the question: "Does the article describe or clearly present the method used to detect roadkill concentration, and/or the localization of roadkill concentration?". Articles meeting this criterion were selected for inclusion and did not follow for next stage. If one or both reviewers were uncertain, the study advanced to third stage (full text screening).

Stage 3 – Full text screening

We only included articles when the authors applied a method to evaluate spatial patterns of roadkill. Disagreements between the main reviewers were resolved by consulting a third independent reviewer who acted as the tiebreaker (n = 25).

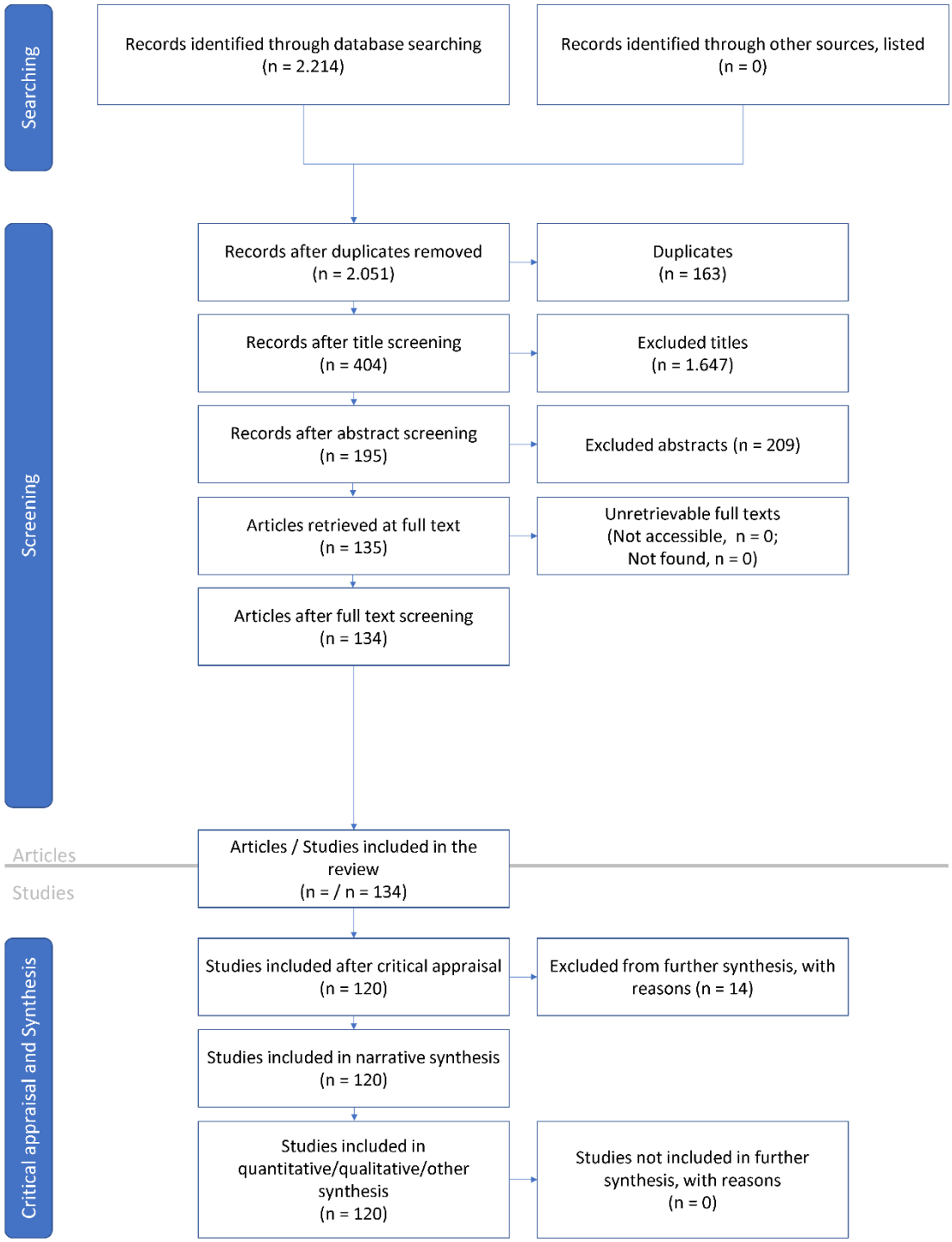


Figure 1. ROSES flow diagram to represent the sequence of the screening protocol and selected number of studies in the systematic review.

Study validity assessment

Studies were only included when methodological transparency was sufficient to identify the spatial method used to detect roadkill concentration or the location of roadkill concentration. This exclusion criterion ensured that all included studies provided sufficient methodological information for our purpose. Studies unclear or missing methodological description were excluded from further synthesis without contacting authors. During the data extraction stage, seven studies were excluded because we could not identify the analytical method or determine what was considered a location of roadkill concentration in the full text, although these studies presented results and, in some cases, discussed their findings.

Data extraction

Data were extracted manually by a single reviewer (I.C.F.) using a standardized data sheet designed prior to the extraction phase (see **SM3**). As described above, we classified the statistical methods into two analytical approaches: (1) detection of roadkill concentration, and (2) the location of roadkill concentration along the road. We extracted information related to terminology and spatial methods aspects of each study for each question, whether the study addressed both questions or only one of them, and the software used for each method. As well as information about country, year, and taxonomic group studied were also recorded as categorical data (**SM3**). When methodological descriptions were ambiguous or difficult to classify, the primary reviewer consulted the second and third reviewers to reach consensus on method identification and consistency in classification. The extraction focused on analytical methods rather than quantitative information; hence, no values of spatial patterns or statistical measures were collected.

As described above, we classified the statistical methods into two question approaches: (1) detection of roadkill concentration, and (2) the localization of roadkill concentration along the road. We extracted the analytical methods name, terminology used to refer each question, whether the study addressed both questions or only one of them, and the software used for each method. Information such as country, year, and taxonomic group were also recorded as categorical data (**SM3**).

Descriptive analysis

Inter-reviewer agreement was assessed using Cohen's Kappa coefficient (Cohen, 1960) calculated with the “cohen.kappa” function in ‘psych’ package (Revelle, 2025). Kappa values

were interpreted according to Landis and Koch (1977) and described in McHugh (2012): values of 0.00–0.20 are considered as no agreement, 0.21–0.39 as minimal, 0.40–0.59 are weak, 0.60–0.79 as moderate, 0.81–0.90 are considered strong, and above 0.90 as almost perfect agreement.

The temporal trend in scientific publication was analysed by fitting four models describing the relationship between the number of published articles and publication years: linear, asymptotic, exponential, and a null model (intercept only). Null and linear models were fitted using the "lm" function, whereas asymptotic and exponential models were fitted using the "nls" function both from the 'stats' package (R Core Team, 2025). The shape of these curves indicates the nature of temporal growth (e.g., constant, accelerated, stabilizing, or no trend). Models were compared using second-order Akaike Information Criterion (AICc), which estimates information loss while accounting for sample size (Johnson and Omland 2004; Anderson 2008). We then calculated delta AICc (ΔAICc) and Akaike weights to estimate the relative support for each candidate model (Burnham and Anderson 2002; Johnson and Omland 2004).

We performed Fisher's test for count data with Monte Carlo simulation (B = 100,000 replicates) to assess associations between spatial methods, terminology, continents, taxonomic groups, and publication years, using the 'stats' package (R Core Team, 2025). For each analytical approaches (detection of roadkill concentration, and the location of roadkill concentration), we executed, separately, pairwise combinations with the following variables: methods × terms, methods × continent, methods × taxonomic group, and methods × publication year. Additionally, for each question, we tested associations between terminology × continent and terminology × publication year. Multiple Correspondence Analysis (MCA) was performed for each analytical approaches with three categorical variables (method, terminology, and continent) to visualize patterns, using the 'FactoMineR' package (Le et al., 2008). For MCA analysis, we used only terms applied more than once to avoid outliers that could wrest the patterns. All analyses were conducted in R version 4.5.2 (R Core Team, 2025).

Results

We reviewed 2,051 articles from both Web of Science and Google Scholar, and after the screening steps we maintained 120 studies (WoS = 93, GS = 27; Fig. 1). Inter-reviewer agreement was mostly moderate, with 55.6% (5 of 9) across all screening stages, considering the platforms separately and combined. The agreement was classified as weak in 33.3% of the cases (3 of 9), one study in abstract screening for WoS and for two studies in text screening

242 step for GS and combined platforms. While one estimate (11.1%) was classified as almost
243 perfect (**Table SM4**).

244 Our dataset was concentrated in the American continent, with most studies from Brazil,
245 United State and Canada, followed by the European continent, with most studies from Spain,
246 Czech Republic, Portugal, and Australia in Oceania (**Figure 2**). Study publication years ranged
247 from 2003 to 2022. Most of the studies were published after 2011, supported by linear and
248 asymptotic models (AICc = 86.5 and 86.6, respectively), indicating an increase in the last
249 decade (**Figure 3**; **Table SM5**)

250 The most frequently studied taxonomic group was mammals (n = 87), followed by reptiles
251 (n = 35), birds (n = 31), and anurans (n = 25), respectively (**Figure SM6**). Studies focusing
252 exclusively on mammals, reptiles, birds, and anurans totalled 60, nine, seven, and six,
253 respectively. Only one study focused on invertebrates, assessing the location of roadkill
254 concentration for butterflies. Additionally, four studies did not clearly report which taxonomic
255 groups or species were analysed, referring only to wildlife-vehicle collisions.

256 We found four terms referring to detection of roadkill concentration and seven terms for
257 location of roadkill concentration (**Figure 4**). Moreover, the most used terms for both analytical
258 approaches were the same: *aggregation*, *cluster*, and *hotspot* (**Figure 4**). The term *cluster*
259 increased over time, especially to refer to the detection of roadkill concentration methods, while
260 the term *hotspot* highly increased among the location of roadkill concentration methods, and
261 other terms occasionally were used (**Figure SM7**). The terms ranking was the same between
262 the continents (**Figure SM8**). We found no statistically significant association between the
263 terms and the continents (detection of roadkill concentration: *p-value* = 0.405; location of
264 roadkill concentration: *p-value* = 0.055), nor between the terms and the publication years
265 (detection of roadkill concentration: *p-value* = 0.998 location of roadkill concentration: *p-value*
266 = 0.589), indicating consistent use of terminology across time and geographical regions.

267 We identified eight studies that only evaluated detection of roadkill concentration, 69
268 studies that only identified the location of roadkill concentration along the road, and 43 studies
269 that employed both analytical approaches. The use of detection of roadkill concentration
270 methods was consistently low and showed no temporal change (**Figure SM9**). In contrast, the
271 use of methods to identify the location of roadkill concentration increased after 2011, with a
272 more pronounced rise following 2018, and studies combining both analytical approaches
273 showed a slight increase but remained relatively stable (**Figure SM9**).

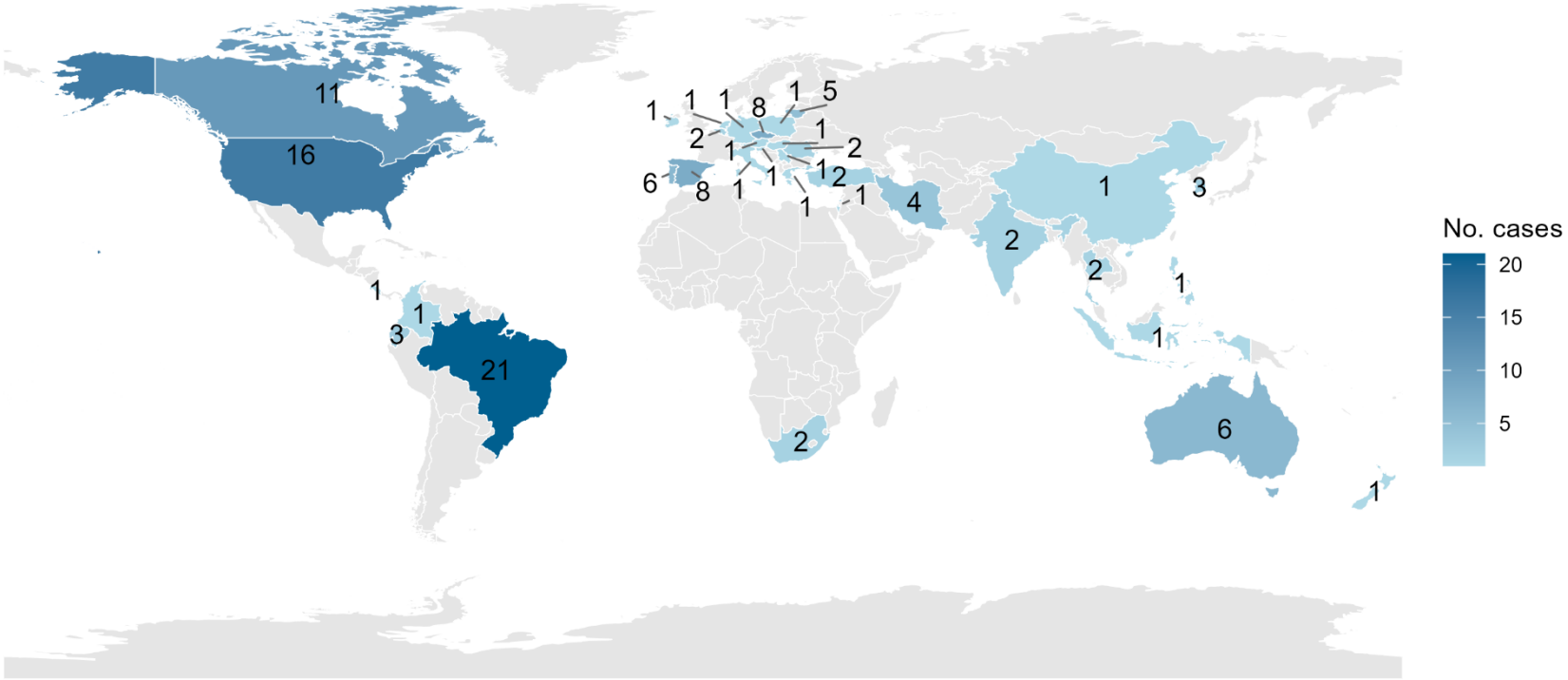


Figure 2. Geographic distribution of number of selected studies per country.

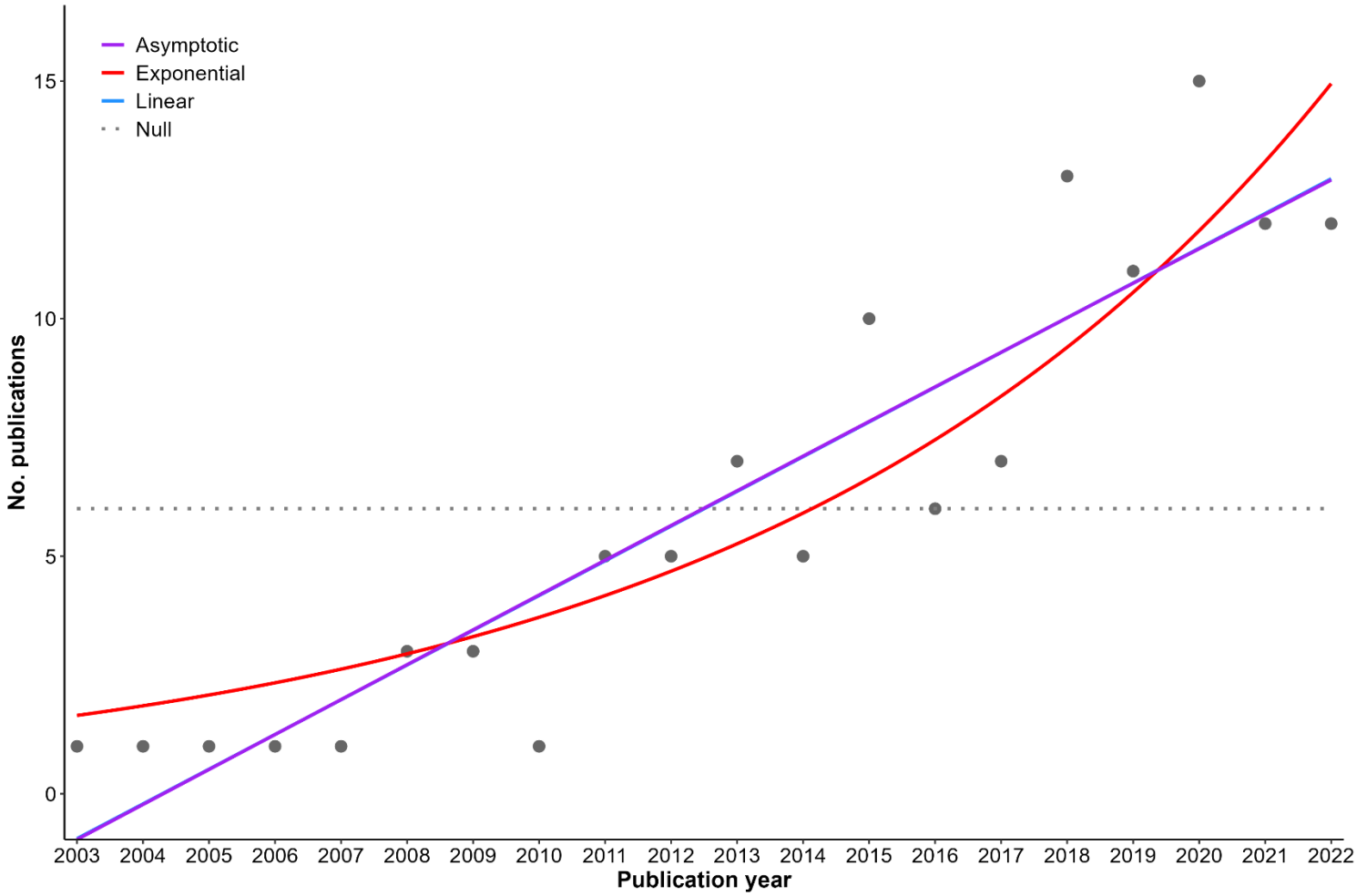


Figure 3. Annual number of included studies (n = 120) by publication year, based on searches in Web of Science and Google Scholar. The time series spans from 2000 to 2022; however, years with zero publications at the beginning of the period are not shown. Lines represent fitted models

describing temporal trends: linear, asymptotic, exponential, and null (intercept-only). The linear model (blue line) provided the best fit (AICc = 86.5), closely followed by the asymptotic model (purple line; AICc = 86.6), whose curve largely overlaps and obscures the linear fit.

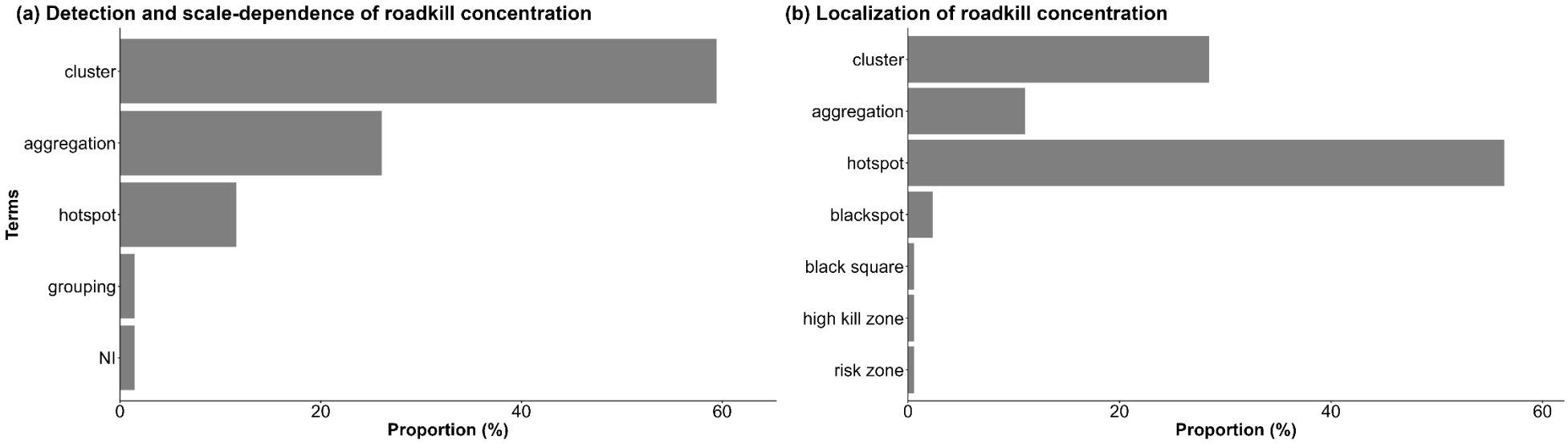
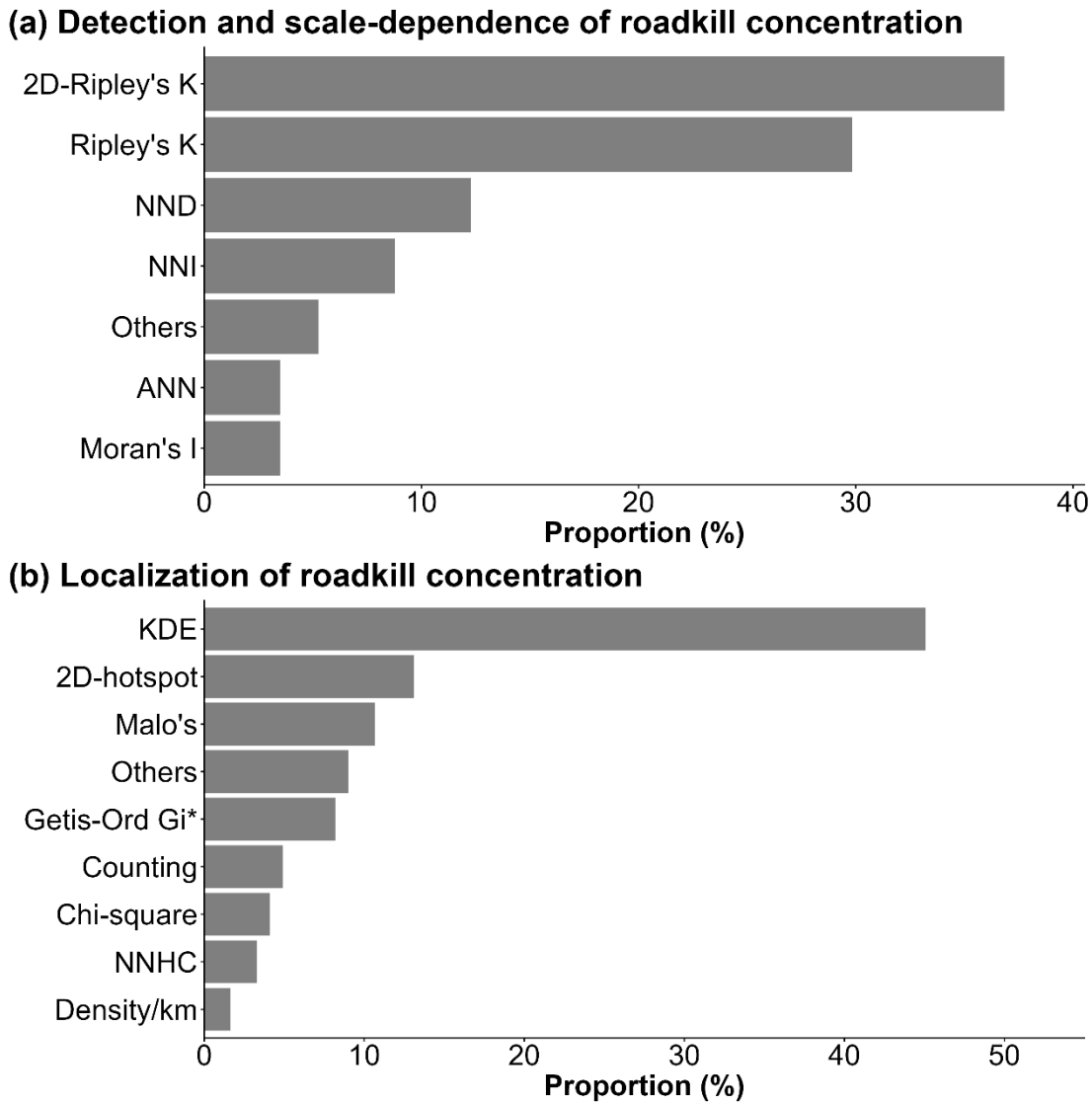


Figure 4. Proportion of studies using each different terminology to describe (a) detection of roadkill concentration and (b) localization of roadkill concentration. Bars indicate the percentage of use for each term. The terms 'NI' indicates no clear definition to refer it.

We identified eight statistical methods to analyse detection of roadkill concentration (**Figure 5**). The most used methods were 2D-Ripley's K (n = 21) and Ripley's K function (n = 17). The use of 2D-Ripley's K had a slight increase after 2015; otherwise, Ripley's K showed a constant use through time (**Figure SM10**). For the location of roadkill concentration, we identified 19 methods (**Figure 5**). The most used method was Kernel density estimation (KDE; n= 55 studies). The use of KDE method showed an increase over years, otherwise the use of 2D-hotspot demonstrated a minor increase, and the others were more constant and occasionally used (**Figure SM10**).

Statistically significant associations were detected between the methods (for both questions approaches) and the continents (detection of roadkill concentration: *p-value* = 0.001, localization of roadkill concentration: *p-value* = 0.0001; **Figure 6**). As well, the multiple correspondence analysis (MCA) revealed spatial segregation of statistical methods by continent along the first two dimensions (23.7% cumulative variance), indicating regional preferences in the statistical methods used (**Figure 7**). For localization of roadkill concentration methods, there was also a significant association between the chosen method and the terms employed to describe it (*p-value* = 0.0002; **Figure 8**). The relation between detection of roadkill concentration methods and terms was not statistically confirmed (*p-value* = 0.478). In contrast, no significant associations were found between the statistical methods (for both question approaches) and the taxonomic groups, nor between the methods and the publication years (detection of roadkill concentration: *p-value* = 0.476, location of roadkill concentration: *p-value* = 0.287).



306

307 **Figure 5.** Proportion of methods used to evaluate (a) detection of roadkill concentration and
308 (b) localization of roadkill concentration. Bars indicate the percentage of use for each method
309 with the corresponding absolute frequency in parentheses. Methods used only once were
310 grouped in represented by 'Others'. Note: 'NND' refers to 'Nearest neighbour distance'; 'NNI'
311 indicates 'Nearest neighbour index'; 'ANN' represents 'Average nearest neighbour'; and
312 'NNHC' correspond to 'Nearest neighbour hierarchical cluster'.

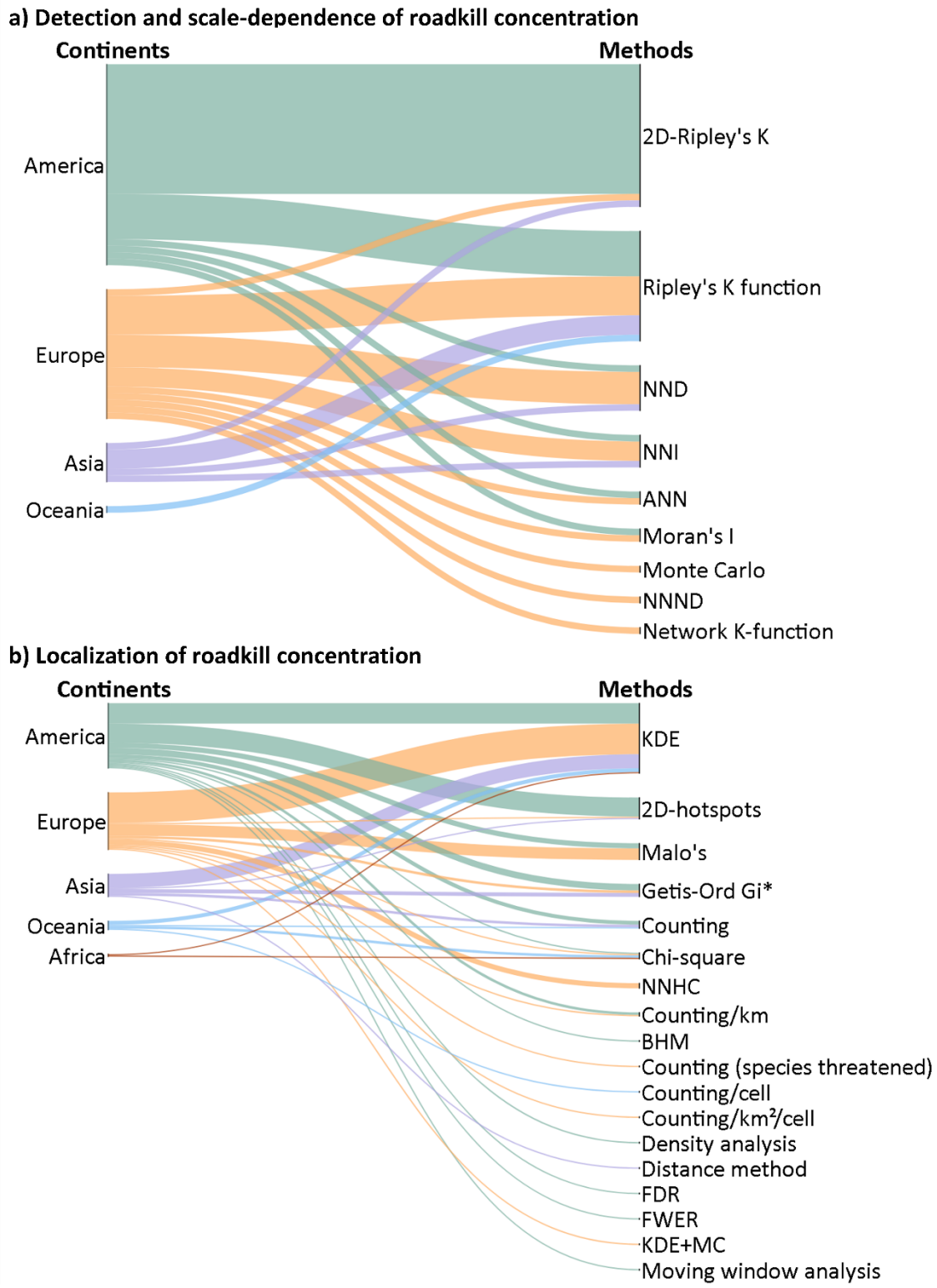


Figure 6. Sankey diagrams illustrate the relationship between geographic distribution of studies and the methods used. (a) Methods used to detect roadkill concentration and (b) methods used to localize roadkill concentration. Flow widths represent the number of studies applying each method in each continent.

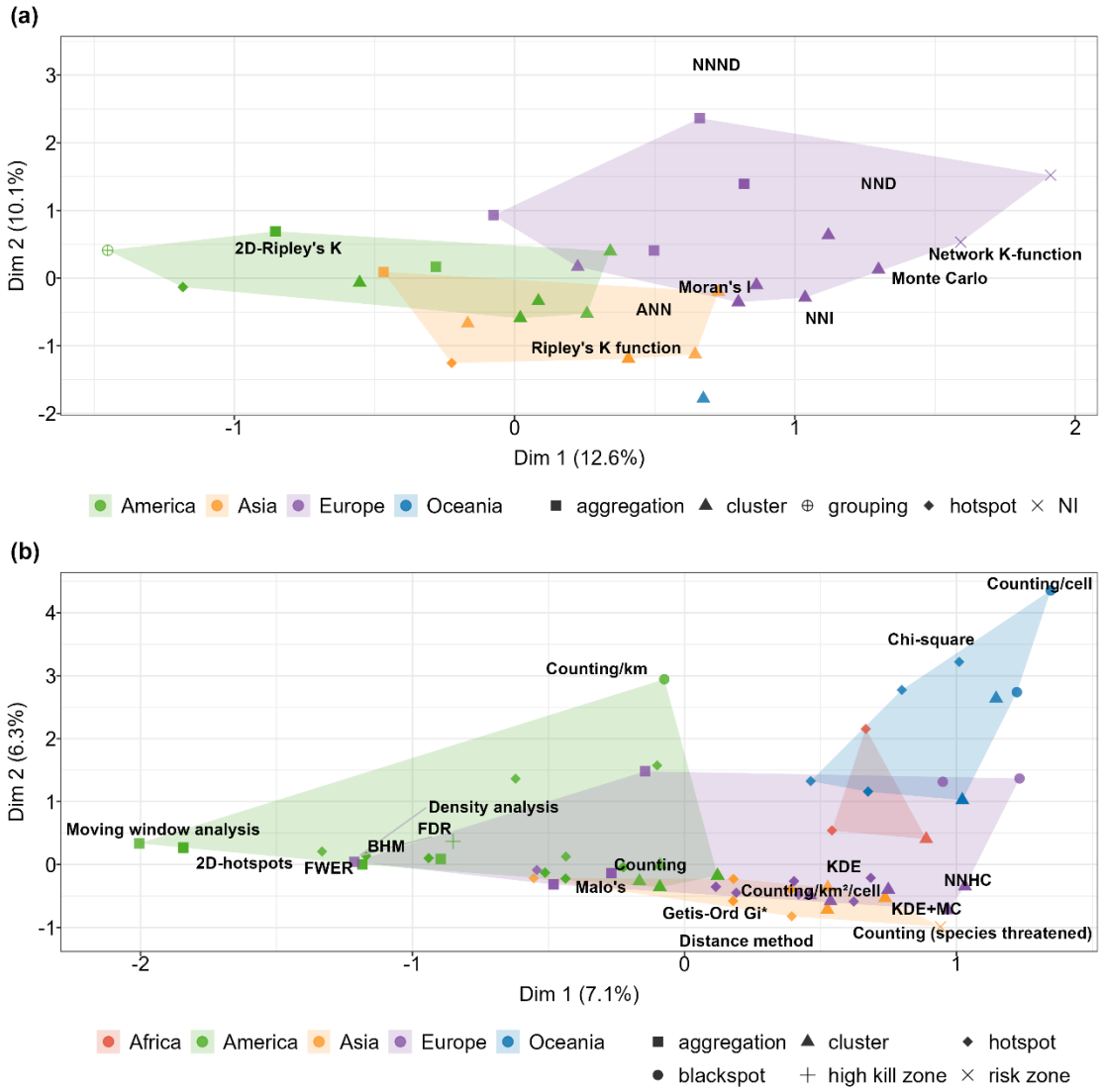


Figure 7. Multiple Correspondence Analyses (MCA) showing associations between continents, methods, and terminology. (a) Detection of roadkill concentration methods (cumulative variance: 23.7%) and (b) location of roadkill concentration methods (cumulative variance: 13.4%). Polygons represent convex hulls for each continent; points indicate individual studies coloured by continent and shaped by terminology used. Note: 'BHM' refers to 'Bayesian hierarchical modelling', 'FDR' indicates 'The false discovery rate correction', 'FWER' correspond to 'The family wise error rate correction', 'KDE' indicates to 'Kernel density estimation', 'NND' refers to 'Nearest neighbour distance'; 'NNI' indicates 'Nearest neighbour index'; and 'NNHC' correspond to 'Nearest neighbour hierarchical cluster'.

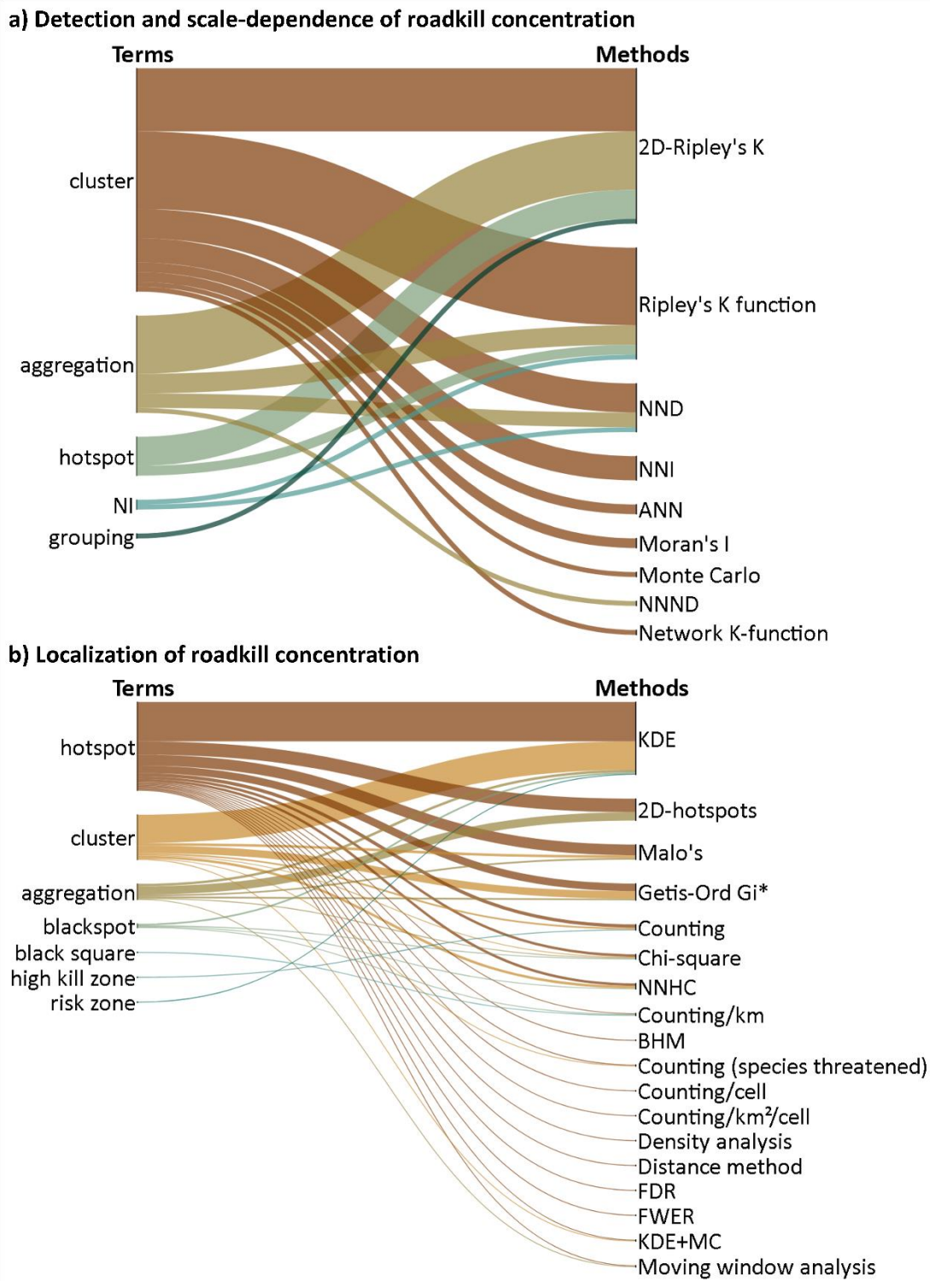


Figure 8. Sankey diagrams illustrating the relationships between terminology and analytical methods used in roadkill spatial analyses. (a) Connections between terms and methods applied to detect roadkill concentration (b) Connections between terms and methods used to localize of roadkill concentration. The width of each flow is proportional to the number of studies linking a term to a specific method. Note: 'BHM' refers to 'Bayesian hierarchical modelling', 'FDR' indicates 'The false discovery rate correction', 'FWER' correspond to 'The family wise

error rate correction', 'KDE' indicates to 'Kernel density estimation', 'NND' refers to 'Nearest neighbour distance'; 'NNI' indicates 'Nearest neighbour index'; and 'NNHC' correspond to 'Nearest neighbour hierarchical cluster'.

Discussion

Road ecology has grown in the last two decades (Sukhontapatipak et al., 2025), as well as studies on roadkill spatial patterns to support mitigation measures. Our review of 120 studies identified two interconnected challenges in this growing literature: inconsistent terminology across spatial analytical questions, and regionally biased method selection apparently driven more by tradition than by analytical suitability or performance. These patterns have practical implications related to the planning and evaluation of mitigation actions that depend on spatial and temporal comparisons within the same infrastructure and between infrastructures.

We recognize some limitations that should be considered when interpreting results. Our review was restricted to English-language publications and studies published between 2000 and 2022; however, we believe that it captures the variability and dominance of both the terminology and statistical methodology. Previous studies have shown that excluding non-English literature can introduce systematic biases and omit region-specific knowledge (Konno et al., 2020; Hannah et al., 2024). Although we recognize that inclusion of other languages may result in additional terminology or spatial methods, we do not expect changes in regional bias due to our sample sizes (Morrison et al., 2012). Despite this possible limitation, our synthesis provides the first comprehensive overview of terminology and methodological practices in roadkill spatial analysis, providing key information for improvement of research and conservation application.

The use of the same three terms – aggregation, cluster, and hotspot – across two distinct questions represents a specific conceptual problem in road ecology. Although terminological diversity is not inherently problematic (Hodges, 2008) the issue here goes beyond simple lexical variation**.** The term “hotspot” has become a broad and often undefined concept, functioning as an umbrella term to represent the assessment of detection of roadkill concentration, and location of roadkill concentration**.** When identical terms are used to describe distinct questions and outcomes of distinct analytical methods, the result was semantic fragmentation rather than conceptual innovation (Zhu et al., 2026). This type of terminological inconsistency undermines research comparability and knowledge synthesis (Golgolnia et al., 2024), challenges evidence-based policy making (Moore et al., 2021) and compromises effective literature retrieval in systematic reviews (Zhu et al., 2026). For instance, in climate change mitigation, the rapid diffusion of concepts without shared definitions has been identified as a major barrier to both scientific progress and policy implementation (Moore et

al., 2021). Road ecology has increased large-scale syntheses that integrate findings across studies and regions (Schwartz et al., 2020; Grilo et al., 2021; Medrano-Vizcaíno et al., 2022), making terminology not only an academic concern but a practical requisite for knowledge exchange and knowledge-based decision making. Without clear definitions, studies using the same term to describe methodologically distinct analyses become difficult to integrate, limiting the potential of such syntheses to inform road mitigation policies at broader scales. We do not argue for rigid standardization, but rather for explicit conceptual and methodological transparency. Researchers should clearly state which term they are adopting for each spatial questions they are addressing – detection of roadkill concentration, or location of roadkill concentration. For example, if hotspot is still a choice, differentiating hotspot existence or detection from hotspot location and clearly stating what each term means may be sufficient to avoid confusion.

Beyond terminology, our results also revealed that most studies explored only the identification of location of roadkill concentration. However, testing for detection of roadkill concentration (e.g., Ripley's K: Clevenger et al., 2003) is important to inform the resolution to be selected for analyses to locate roadkill concentrations (Spanowicz et al., 2020). Identifying the location of roadkill concentration without prior detection of roadkill concentration may simply reflect random variation in an otherwise uniform distribution (Teixeira et al., 2013; Spanowicz et al., 2020). The two-step analysis is common to other research fields, such as road safety, public health, and species distribution, that mostly use the same general spatial methods (Abdulhafedh, 2017; Lan and Delmelle, 2023; Zevgolis et al., 2025). Despite the recurrent recommendations for the adoption of the two-step approach (see Getis and Ord, 1992; Abdulhafedh, 2017; Columbia University, 2024; Guinard et al., 2023), our review revealed that this is still not the regular practice in road ecology. We identified several statistical methods used for each roadkill spatial pattern with a small number of methods widely adopted within each one. Method selection is important because subtle differences between them could have important consequences on detection and location of roadkill concentrations. For example, and Ripley's K statistics and 2D-Ripley's K differ in how road distances are considered for counting roadkill events within each scale of analysis to detect roadkill concentrations (Clevenger et al., 2003; Coelho et al., 2008).

The analytical question approaches reviewed here – detection of roadkill concentration and or the location of roadkill concentration – implicitly assume a spatially homogeneous of

roadkills distribution along the road. However, roadkill surveys involve three main sampling errors: searcher efficiency by observers, carcass availability in sampling area, and carcass persistence on the road (Korner-Nievergelt et al., 2015; Barrientos et al., 2018). There are valuable reasons to suspect these errors differ across a road's length, as searcher efficiency rates and carcass persistence are known to vary with sampling intervals, traffic volume, weather conditions, and taxonomic group (Santos et al., 2011; Teixeira et al., 2013). For instance, carcasses on the road surface may be more easily detected but are also more rapidly removed by traffic and scavengers, whereas carcasses on vegetated road margins may persist longer but be less visible (Santos et al., 2011; Barrientos et al., 2018). Few studies have explicitly examined spatial heterogeneity of these errors and found that both searcher efficiency and carcass persistence vary considerably among road (e.g., Franceschi et al., 2021; Gonçalves et al., 2023). Despite this evidence, analytical approaches considering these errors spatially heterogeneous across the road still represents a research gap with direct implications for the reliability of spatial prioritization of mitigation measures (see Gonçalves et al., 2023).

The association between analysis methods and continents may indicate that methodological choices are driven more by regional research traditions or influences than by informed analytical choices. Several mechanisms may explain this geographic pattern, such as regional influential research groups that use specific approaches, collaborative networks, and software availability with some tools are more accessible in certain countries (Sukhontapatipak et al., 2025). For instance, KDE is the most used method possibly since it is available in multiple software (e.g., ArcGIS, QGIS, R and KDE+), follows visual intuition (heat maps), has less complex statistical assumptions, and is widespreadly cited (Pagany, 2020). Methodological diversity and improvement of methods are important, but it is essential to clearly understand the purpose, assumptions, and weaknesses of each approach and how to use it appropriately.

The geographical pattern in method selection raises questions about whether mitigation planning is guided by the most suitable methods for each roadkill pattern and data context. Despite a few attempts to evaluate and compare performances of different analytical methods (e.g., Gomes et al., 2009; Borda-da-Água et al., 2019; Habib et al., 2023) this remains a research gap that should be explored in future studies to better inform methodological choices. It is important that these studies compare methods performance using simulations and empirical datasets to evaluate which methods have best accuracy and precision under different

conditions (e.g., data amount and distribution, spatial scales, taxonomic group, and road geometry). An inappropriate method choice or spatial scale may lead to both false positives and false negatives, failing to detect meaningful spatial patterns (Borda-da-Água et al., 2019; Spanowicz et al., 2020) and compromising mitigation planning and effectiveness.

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Conservation Biology

Supplementary Material

A systematic map of the terms and methods used to identify locations of roadkill concentrations on roads

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Summary

SM1. ROSES Systematic for Map Reports (separate .xlsx file)

SM2. Data review information (separate .xlsx file)

SM3. Data extraction information (separate .xlsx file)

SM4. Cohen's Kappa table result

SM5. Model temporal trend result

SM6. Number of papers for each taxonomic group

SM7. Terminology reported in the selected studies over years

SM8. Terminology and geographic distribution relationship

SM9. Number of papers for each methodological approach over years

SM10. Methods reported for each methodological approach over years

Table SM4. Cohen's Kappa coefficients for inter-rater agreement across the three screening stages, considering Web of Science, Google Scholar, and combined platforms. N represents the total number of papers evaluated at each stage associated with its respective Cohen's Kappa unweighted coefficient estimated (κ) and 95% confidence interval (CI); and Interpretation follows Landis and Koch (1977), as described in McHugh (2012).

Stage	Platforms	N	κ	95% CI	Interpretation
Title	Web of Science	817	0.91	0.87–0.95	Almost Perfect
	Google Scholar	1234	0.68	0.62–0.74	Moderate
	Combined	2051	0.79	0.75–0.83	Moderate
Abstract	Web of Science	179	0.52	0.42–0.62	Weak
	Google Scholar	225	0.67	0.56–0.78	Moderate
	Combined	404	0.64	0.58–0.71	Moderate
Text	Web of Science	69	0.62	0.46–0.78	Moderate
	Google Scholar	41	0.45	0.23–0.68	Weak
	Combined	110	0.58	0.45–0.71	Weak

Table SM5. Model selection results for temporal trends in scientific production. Models describing the relationship between the number of published studies and publication year (linear, asymptotic, exponential, and null) were compared using the corrected Akaike Information Criterion (AICc). df represents the number of estimated parameters in each model, AICc values indicate relative model fit, ΔAICc is the difference from the best-supported model, and Akaike weights (wi) indicate the relative likelihood of each model being the most plausible among those considered.

Model	AICc	ΔAICc	df	wi
Linear	86.5	0.0	3	0.43
Asymptotic	86.6	0.1	3	0.42
Exponential	88.6	2.1	3	0.15
Null	122.2	35.7	2	<0.001

Figure SM6. Number of studies by taxonomic group. Bars represent the number of studies evaluating each taxonomic group, partitioned into studies focusing exclusively on a single taxon and those including multiple taxonomic groups.

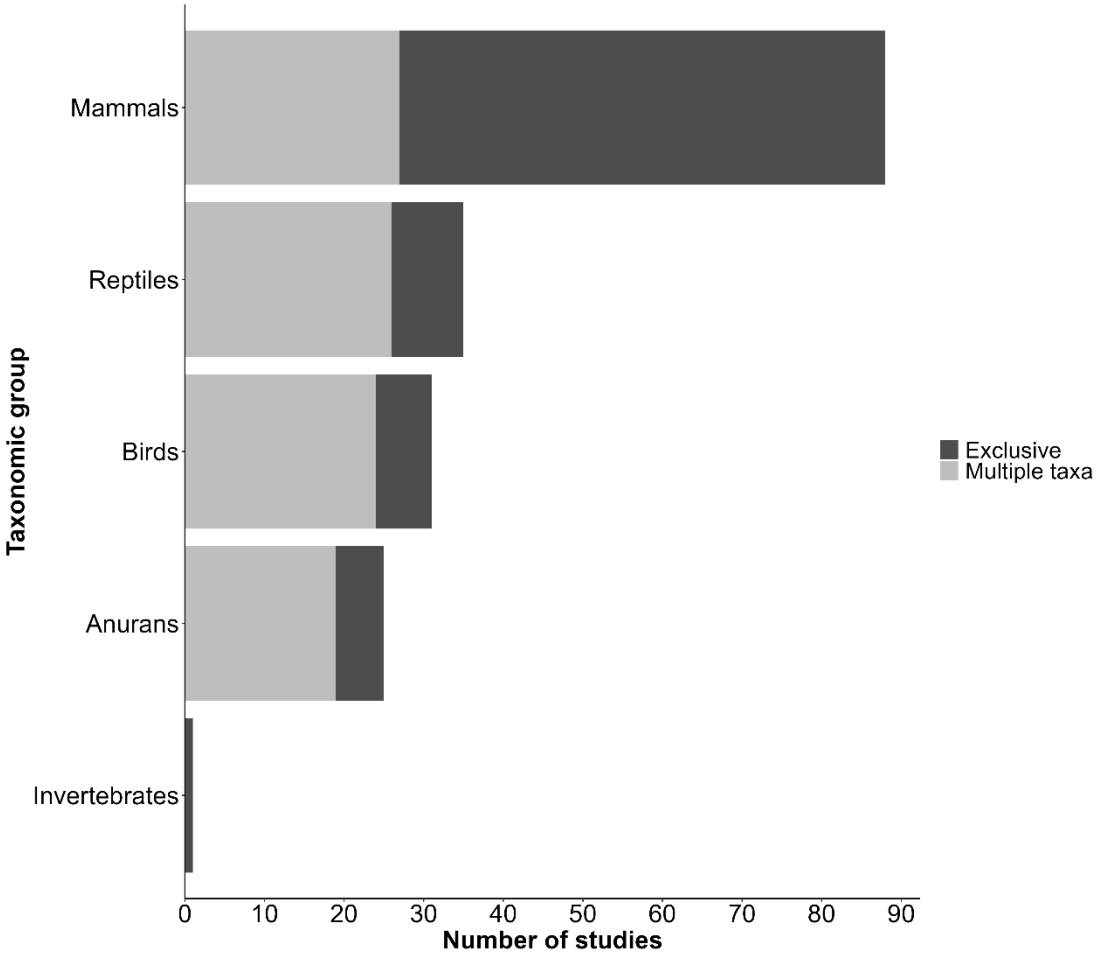


Figure SM7. Temporal distribution of (a) terms referring detection and scale-dependence of roadkill concentration and (b) terms referring the localization of roadkill concentrations that were reported in the selected studies. Each panel displays the annual frequency of studies mentioning a specific term between 2003 and 2022. Only the most frequently used terms are shown; rarely used terms or unclear terms were excluded.

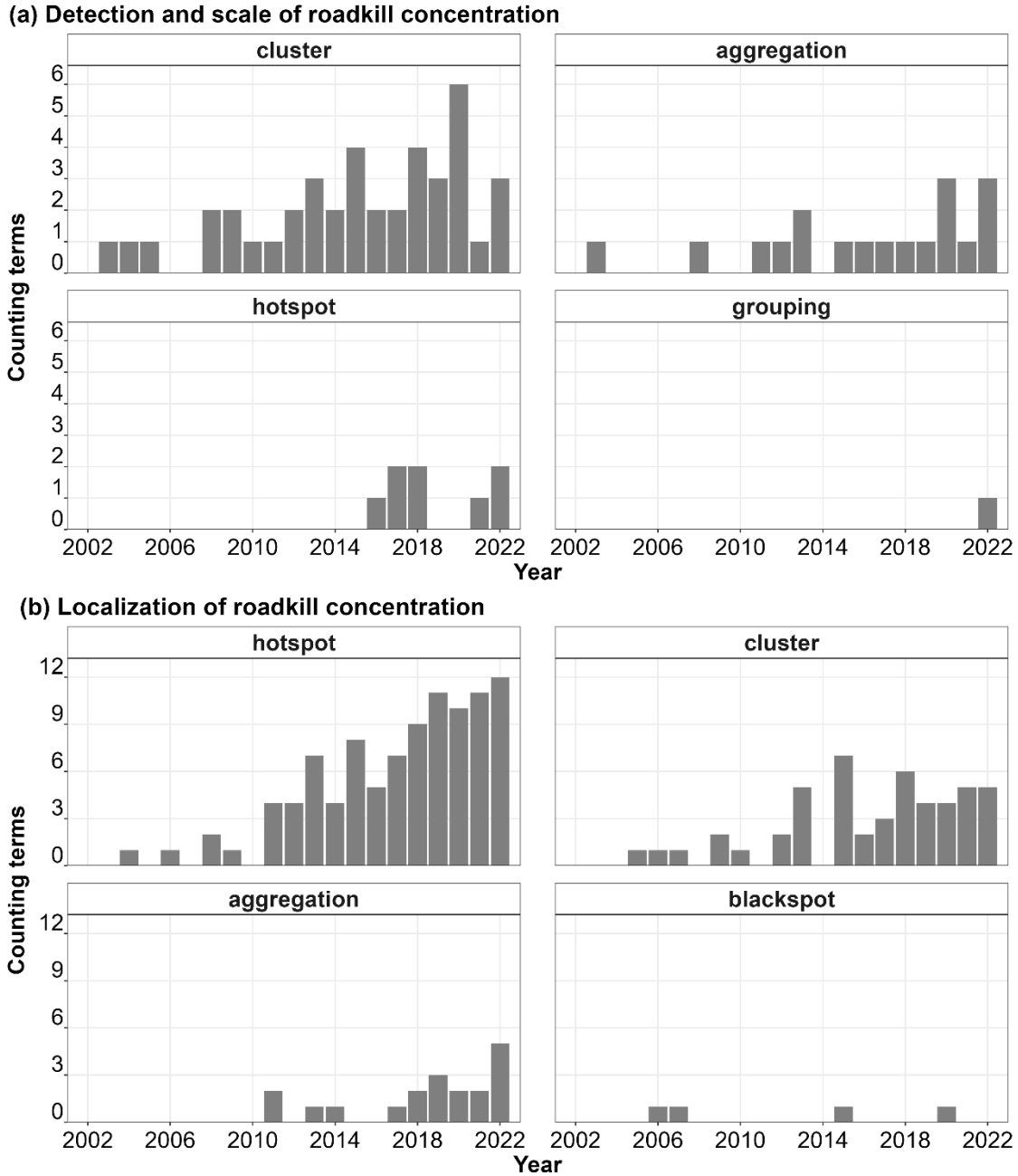


Figure SM8. Sankey diagrams illustrating the relationship between terminology and geographic distribution of studies. (a) Terms used to detect and assess scale-dependence of roadkill concentration and their continents distribution. (b) Terms used to describe the localization of roadkill concentrations and the continents distribution. The width of each flow is the number of studies linking a given term to each continent.

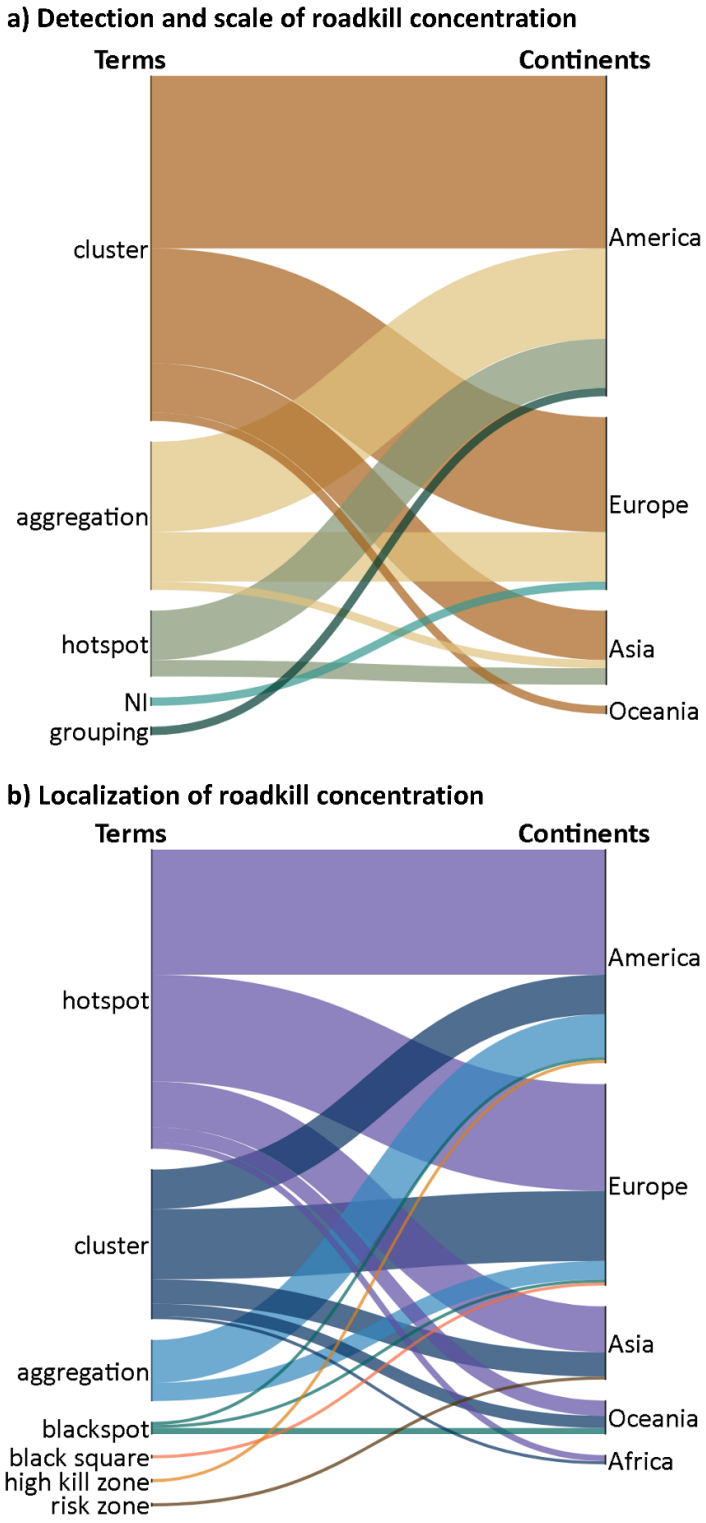


Figure SM9. Number of papers for each methodological approach by year. Bars represent the total number of selected papers in each year for each methodological approach. The category "Both" indicates the used of the two approaches: statistical analyses to determine the detection and scale-dependence of roadkill concentration and the localization of roadkill concentrations.

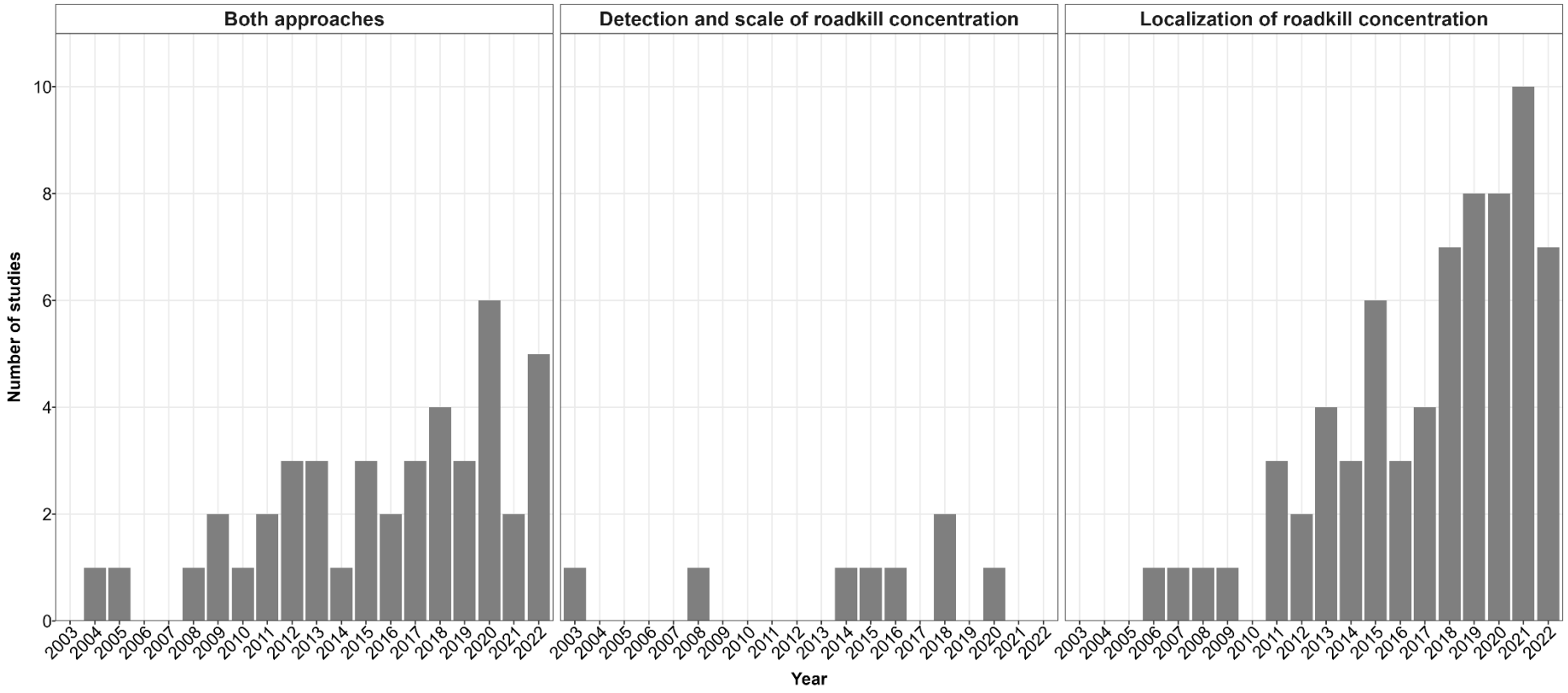
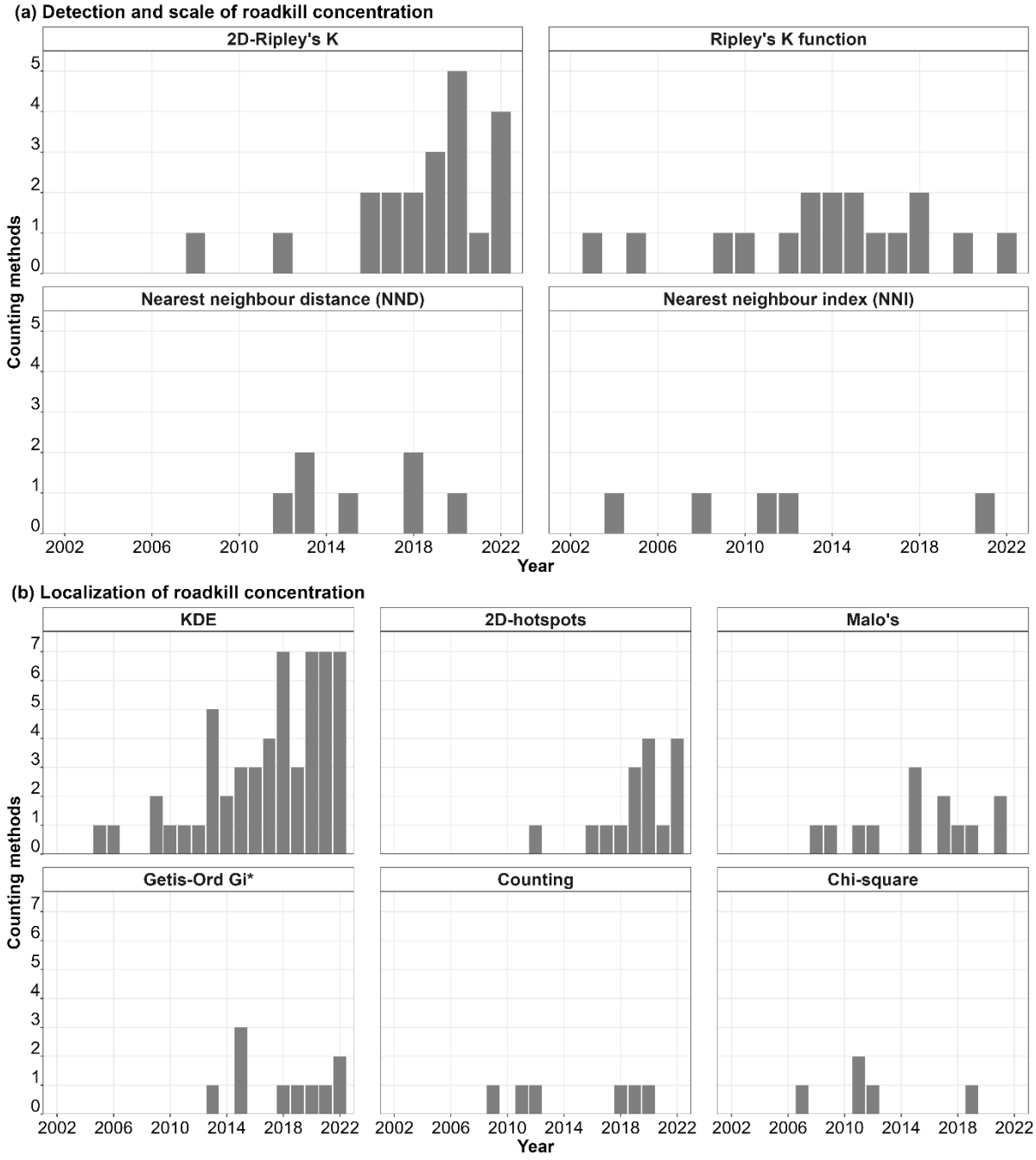


Figure SM10. Temporal distribution of (a) detection and scale-dependence of roadkill concentration methods and (b) the localization of roadkill concentrations methods used in the selected studies. Each panel shows the annual frequency of each method between 2003 and 2022. Bars represent the number of studies published per year using each method. Only methods applied more than once are shown; methods used a single time were excluded from the panels.



Considerações Finais

A presença de rodovias é crescente em todo o mundo, assim como os inúmeros impactos associados à biodiversidade. Esse cenário reforça a necessidade de compreender melhor tais impactos e a dimensão desses impactos no tempo e no espaço. Em muitos casos, a construção de uma estrada é inevitável, tornando necessário avaliar e prever os impactos e propor medidas de mitigação adequadas para cada contexto. Nesta tese, busquei compreender alguns dos impactos das rodovias sobre a biodiversidade utilizando diferentes abordagens analíticas. Para isso, utilizei: imagens geoespaciais de plataformas de dados abertos para investigar as mudanças na vegetação nativa considerando abordagem antes-depois-gradiente à pavimentação das estradas; modelo mecanístico, como modelo baseado em indivíduos, para avaliar os impactos do tráfego sobre populações de fauna silvestre; e mapeamento sistemático das terminologias e dos métodos estatísticos utilizados na literatura para avaliar os padrões espaciais de colisões veículos-fauna.

A pavimentação de estradas pode intensificar a atividade humana, resultando em maiores mudanças na vegetação nativa em áreas ao entorno. No Capítulo I, busquei compreender os efeitos da pavimentação sobre a vegetação nativa ao longo do tempo e do espaço, utilizando o Brasil como estudo de caso. Os resultados revelaram que esses efeitos são dependentes da escala temporal analisada e que, contrariamente ao esperado, a análise em nível nacional indicou um aumento ou uma desaceleração na perda de vegetação nativa, dependendo da escala temporal, após a pavimentação. Contudo, esses resultados mascaram a variação espacial entre os biomas: a perda de vegetação nativa continuou na Amazônia, no Cerrado e no Pampa, enquanto a Mata Atlântica e a Caatinga exibiram ganhos. Esses achados enfatizam que os impactos da pavimentação de estradas são dependentes da vegetação na região e que avaliações em múltiplas escalas espaciais e temporais, bem como análises por bioma, são essenciais para suportar políticas públicas e decisões relacionadas ao licenciamento ambiental.

As colisões veículos-fauna silvestres representam uma causa importante de mortalidade direta da fauna e pode levar ao declínio populacional de diversas espécies. No Capítulo II, desenvolvi um modelo teórico mecanístico para explorar como o fluxo de veículos influencia o crescimento relativo populacional de populações com diferentes combinações de distância de deslocamento diário, estratégia reprodutiva e probabilidade

de travessia de rodovias, utilizando mamíferos terrestres de médio e grande porte como exemplo. Os resultados confirmaram que os impactos do fluxo de veículos sobre as populações não são lineares e dependem da combinação das características. As populações que combinam grande distância de deslocamento diário com maturação tardia apresentaram crescimento relativo negativo em todos os cenários de tráfego, representando a combinação de características mais vulnerável. Em contraste, populações com baixa distância de deslocamento diário e maturação precoce mantiveram crescimento populacional mesmo sob alto fluxo de veículos. Esses resultados fornecem uma base teórica para prever a vulnerabilidade populacional a diferentes cenários de fluxo de veículos, além do modelo permitir adaptações para diferentes contextos que se desejar avaliar.

As colisões veículo-fauna em rodovias também comprometem a segurança humana e geram perdas econômicas significativas. Dessa forma, identificar segmentos das rodovias com maior concentração dessas colisões é fundamental para o planejamento de medidas de mitigação. No entanto, a identificação dessas concentrações envolve duas perguntas: (1) as colisões veículo-fauna são espacialmente concentradas e, se sim, em que escala estão concentradas; e (2) em quais segmentos na estrada as colisões estão mais concentradas. No Capítulo III, realizei uma revisão do tipo mapa sistemático com o objetivo de identificar a terminologia e os métodos estatísticos utilizados para avaliar padrões espaciais de colisões veículo-fauna e explorar se as escolhas metodológicas variam entre continentes, grupos taxonômicos e ao longo do tempo. A síntese revelou uma confusão terminológica generalizada, viés geográfico nas escolhas metodológicas e falta de clareza sobre qual pergunta estava sendo respondida. Consideramos que é essencial que haja maior clareza terminológica e transparência metodológica, pois têm implicações práticas relacionadas ao planejamento e à avaliação de mitigação. Além disso, destacamos a necessidade de estudos comparando o desempenho dos métodos sob diferentes distribuições espaciais para apoiar as escolhas metodológicas.

De forma geral, os resultados apresentados nesta tese contribuem para ampliar a compreensão sobre os impactos das rodovias na biodiversidade, abordando esses impactos em diferentes escalas e contextos: da vegetação nativa à fauna silvestre; da escala regional à nacional. Os resultados indicam que compreender esses impactos não é uma tarefa trivial – os padrões podem depender do cenário abordado, seja o bioma, as espécies-alvo ou o método estatístico escolhido –, reforçando que avaliações

generalizadas podem mascarar padrões importantes e levar a decisões equivocadas. Espero que os achados aqui apresentados inspirem novos estudos sobre os impactos das rodovias e contribuam para decisões mais embasadas tanto no planejamento viário quanto na implementação de medidas mitigadoras.

Além dos capítulos que compõem esta tese, durante o doutorado também tive a oportunidade de realizar atividades acadêmicas no exterior. Em 2023, realizei um doutorado-sanduíche de quatro meses na Universidade de Birmingham, na Inglaterra, onde desenvolvi o Capítulo I desta tese sob orientação do Dr. Juliano. Posteriormente, em 2024, realizei uma visita de um mês à Universidade de Saskatchewan, no Canadá, onde iniciei o Capítulo II sob orientação da Dra. Érika. Além de ter viabilizado parte do desenvolvimento da minha tese, essas experiências permitiram ampliar a minha rede de colaboração dentro da área da ecologia, conhecer outros grupos de pesquisa, e aprimorar minhas habilidades em inglês, em programação em R e escrita científica. Durante o período do doutorado também tive a oportunidade de publicar trabalhos acadêmicos: Franceschi *et al*., 2022; Franceschi *et al*., 2023; Franceschi *et al*., 2024; Brack *et al*., 2024, Dasoler *et al*., 2026b, Dasoler *et al*., 2026c; participar de eventos em congressos nacionais e internacionais, podendo divulgar resultados parciais dos meus capítulos, bem como resultados de trabalhos publicados; participar de cursos de formação continuada para consultores, ministrando sobre como analisar os dados dos monitoramentos de fauna atropelada; participar do Ciclo de Workshops para a Revisão da Diretriz Técnica de Avaliação de Mortalidade de Vertebrados em Rodovias do RS e no Planejamento da Mitigação, participando na construção da nova proposta de diretriz; também pude realizar uma palestra na Semana Acadêmica da Biologia da Universidade Federal de Santa Maria, abordando os impactos das rodovias na fauna silvestre; e compor uma banca de Trabalho de Conclusão de Curso e de duas bancas do Salão de Iniciação Científica da UFRGS, avaliando trabalhos dentro da temática de ecologia. Cada uma das atividades desenvolvidas e das oportunidades vivenciadas contribuiu para o meu desenvolvimento como pesquisadora e foi fundamental para a minha formação acadêmica.

“The road is a visitor,” the tribes insisted, that should “respond to and be respectful of the land and the Spirit of Place.”

“A estrada é uma visitante”, insistiram as tribos, que deveria “responder ao território e respeitar o Espírito do Lugar.”

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