Rethinking the Road Effect Zone: The Probabilistic Effect of Roads on Ecosystems

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Abstract

Roads are important for human socio-economic growth, but they carry substantial ecological impacts that can extend far beyond their physical footprint. These impacts have given rise to the so called 'Road Effect Zone'. Although the foundational concept of the Road Effect Zone has proven useful in measuring patterns of biodiversity loss near roads, it focuses on changes in species presence/abundance, rather than the potential effects on ecological interactions. Here, we introduce a more mechanistic approach to the road effect zone that brings together the probability of a wildlife-vehicle collision with the probability of an ecological interaction occurring across an animal's home range. We demonstrate the utility of a probabilistic representation of the road effect for giant anteaters living near a highway in Brazil. We then conclude with a brief discussion of how this probabilistic road effect can be employed in practice to inform species conservation.

Introduction

The ca. 64,000,000 km of roads distributed across the globe are important for human socio-economic growth (Ibisch et al., 2016). Yet, while the area that roads occupy might be small, the ecological impacts they carry are substantial (Ascensão and Desbiez, 2022; Coffin, 2007; Fahrig and Rytwinski, 2009), and can extend far beyond their physical footprint (Forman and Alexander, 1998; Forman et al., 2003). From an ecological perspective, roads and roadside ecotones are considered high disturbance systems with non-natural chemical, physical, hydrological, and auditory properties (Brady and Richardson, 2017; Forman and Alexander, 1998; Reijnen et al., 1996). Roads have been shown to alter population densities (Andrasi et al., 2021; Fahrig and Rytwinski, 2009; Reijnen et al., 1996), community composition (Truscott et al., 2005), evolutionary trajectories (Brady and Richardson, 2017; Brown and Brown, 2013), and are a serious source of non-natural mortality for many species (Ascensão and Desbiez, 2022; Carter et al., 2020; Desbiez et al., 2020; Silva et al., 2020). Fully understanding the ecological footprint of roads is thus of the utmost importance if we are to design well-informed ecological mitigation strategies.

Roads can cause a broad range of ecological impacts, but their effects are usually considered strongest with increasing proximity to the road surface. The strength or impact of these road effects decay at varying rates with increasing distance from the road. This relationship between the strength of effect and proximity to the road forms the basis for the concept of the 'Road Effect Zone' (Forman, 2000; Forman and Alexander, 1998), hereafter referred to as the REZ (Fig. 1). Ecologists and conservation practitioners regularly quantify the REZ for different species (e.g., Andrasi et al., 2021; Eigenbrod et al., 2009; Semlitsch et al., 2007), and these distances are often used to make conservation recommendations (e.g., Ford et al., 2020; Forman and Deblinger, 2000; Peaden et al., 2015).

Although the REZ has proven useful in measuring patterns of biodiversity loss, it's correlative basis combines several mechanisms that shape where and why roads affect nature. The REZ concept is also a static measure that does account for the dynamic effects animal movement

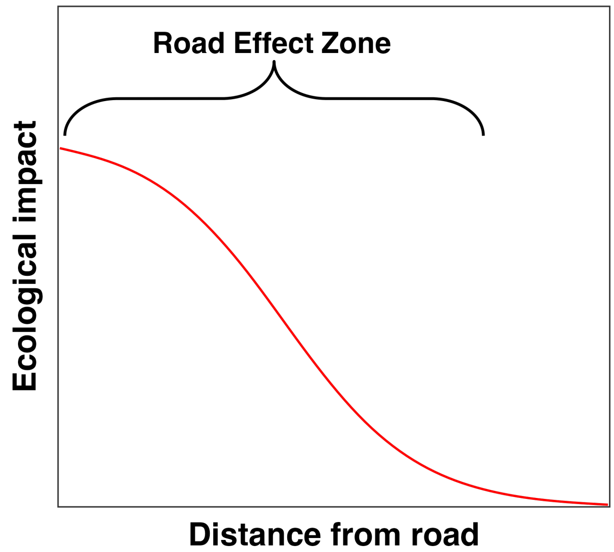

Figure 1: Theoretical depiction of the road effect zone as originally defined by Forman and Alexander (1998).

and species interactions. This is a noteworthy limitation. Consider for instance, migratory ungulates that move over vast distance between seasonal home ranges (Kauffman et al., 2020, 2021). The effects of road mortality on these highly vagile animals might decrease nutrient transfer (Subalusky et al., 2017), prey densities (Walton et al., 2017), and/or grazing pressure (Augustine and McNaughton, 1998) hundreds or even thousands of kilometers away from the road, yet these effects would not be captured within the current REZ framework. Similarly, for territorial species, the death of a roadside animal can have a cascading effect on the species' socio-spatial arrangement over vastly larger distances than the conventional REZ might suggest as individuals disperse and restructure themselves around newly unoccupied territories (Mumme et al., 2000). The reduction in density of frugivorous and/or seed-caching animals around roads can also have cascading effects on seed dispersal over larger areas than described by the REZ (Tucker et al., 2021). Here, we introduce a more mechanistic probabilistic road effect (PRE) that describes the broader ecological impacts that the mortality of an animal might have on the landscape.

The Road Effect as a Joint Probability

As noted above, our focus is on the ecological impact of a wildlife mortality caused by a collision with a vehicle. Our framework begins from the concept of animal space use and movement ecology. An individual's home range describes the space it uses to undergo '*its normal activities of food gathering, mating, and caring for young*' (Burt, 1943). Ecologists have long recognised the utility of the home-range concept in describing patterns of space use (e.g., Kie et al., 2010), and routinely estimate home ranges from animal tracking data (see Noonan et al., 2019). Statistically, home-range estimation results in a probability distribution function ($\mathrm{PDF}_{\mathrm{HR}}$) satisfying

$$\iint_{-\infty}^{\infty} \mathrm{PDF}_{\mathrm{HR}}\, dxdy = 1. \tag{1}$$

The $\mathrm{PDF}_{\mathrm{HR}}$ provides information on the locations where an animal is likely to be found. Importantly for the context of understanding the effects of roads on ecological processes, $\mathrm{PDF}_{\mathrm{HR}}$ also represents the sample space over which an individual's ecological interactions (e.g., foraging, mating, defecating, engaging in territorial defence, etc.) are expected to occur. This PDF can thus be considered to be proportional to an animal's impact on or from the ecosystem, with core (i.e., high probability) areas of the PDF being more heavily impacted by or from an animal than tail (i.e., low probability) areas. Under the assumption that the probability of an animal being roadkilled $P\{\text{Roadkilled}\}$ is proportional to the amount of time it spends on the road, we can quantify $P\{\text{Roadkilled}\}$ by integrating $\mathrm{PDF}_{\mathrm{HR}}$ over the area the falls on road surfaces

$$P\{\text{Roadkilled}\} = \iint_{r}^{r^i} \mathrm{PDF}_{\mathrm{HR}}\, dxdy, \tag{2}$$

where r and r^i represent the road margins. Similarly, the probability of an animal engaging in normal ecological interactions, $P\{\text{Ecological Interactions}\}$, is proportional to the amount of time it spends in locations other than on the road

$$P\{\text{Ecological Interactions}\} = \iint_{-\infty}^{\infty} \text{PDF}_{\text{HR}}\, dxdy - P\{\text{Roadkilled}\}. \tag{3}$$

The ecological impact of wildlife vehicle collision is equivalent to the outcome of an animal not being able to engage in normal behaviour across its home range. This impact can thus be quantified via the joint probability of (1) an animal encountering a vehicle on a road and it being killed on the road, $P\{\text{Roadkilled}\}$, and (2) the probability of an animal engaging in ecologically relevant behaviour, $P\{\text{Ecological Interactions}\}$, or $P\{\text{Roadkilled}, \text{Ecological Interactions}\}$. Assuming independence, the PRE is given by the joint probability of these two events

$$P\{\text{Road Effect}\} = P\{\text{Roadkilled}, \text{Ecological Interactions}\} = P\{\text{Roadkilled}\}P\{\text{Ecological Interactions}\} \tag{4}$$

If an animal occupies a home range that is far away from a road $P\{\text{Roadkilled}\}$ will be ≈ 0, resulting no road effect. Similarly, if an animal spends all of its time on roads, $P\{\text{Roadkilled}\}$ may be high, but $P\{\text{Ecological Interactions}\}$ in areas away from the road will be ≈ 0, also resulting in no road effect. For animals where $P\{\text{Roadkilled}\} \neq 0$ and $P\{\text{Ecological Interactions}\} \neq 0$, however, the road effect will be some non-zero probability with a strength that is a function of how much time an animal spends on roads relative to the rest of its home range. Thus, the strongest PRE must occur for animals that strongly interact with both roads and areas away from roads. Similarly, organisms with large home ranges have more diffuse ecological interactions, whereas animals with smaller home ranges have denser interactions over an equivalent time period. While the general concept of a PRE is useful, we can also integrate over areas of interest to calculate the local PRE. For instance, the PRE within some distance threshold of a road can be quantified as

$$\iint_{z}^{z^i} P\{\text{Roadkilled}, \text{Ecological Interactions}\}\, dxdy, \tag{5}$$

where z and z^i represent distance thresholds from the road edge. For example, setting z to 0m and z^i to 1m would provide the probability of a road effect within 1m of the road edge. Defining the road effect zone in this way allows it to flexibly take individual-specific forms based on each animal's movement ecology (Fig. 2). Notably, although our focus here is on the ecological impacts of roadkilled animals, the concepts presented herein can be readily extended to other spatially explicit ecological processes, such as the area a root or mycelial network diffuses through (Bielčik et al., 2019).

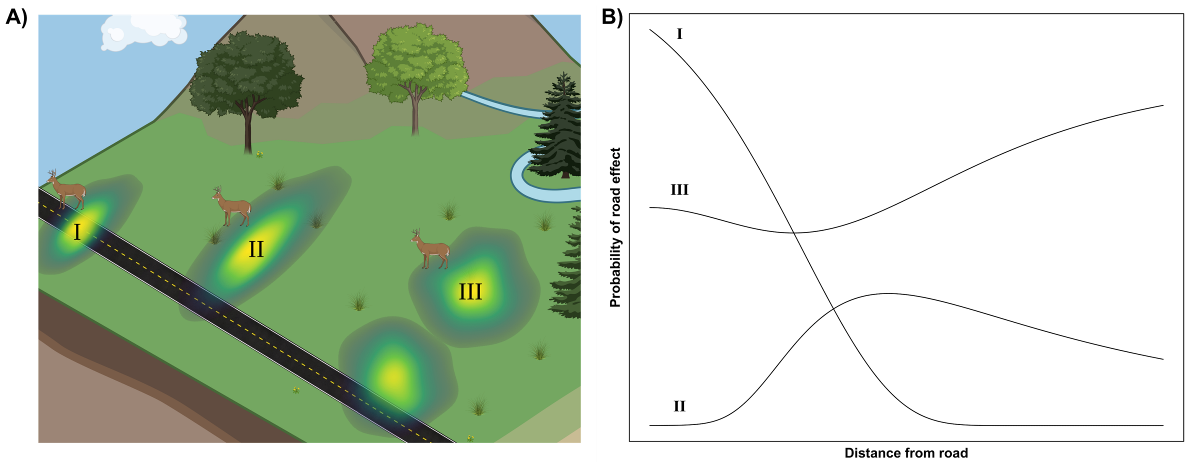

Figure 2: Theoretical depiction of the probabilistic road effect (PRE). Panel A shows three animal home ranges that vary in extent and overlap with a road. Animal I has a small home range with high road overlap, Animal II has a small home range with low road overlap, and Animal III has a large home range with intermediate overlap. Note how the three different patterns of space use shown in A result in different PREs in B. As more home range area overlaps with roads, the probability of a road mortality increases, thereby increasing the probability of a road effect occurring. Similarly, as an animal's home range increases, its ecological effects become more diffuse and the effects of a road mortality may be felt over a larger area. Panel A was created with BioRender.

The Probabilistic Road Effect for Giant Anteaters

Here, we demonstrate the utility of a probabilistic representation of the road effect on a pair of giant anteaters (*Myrmecophaga tridactyla*) from the Brazilian Cerrado. Giant anteaters are the largest extant anteater, reaching over 2m and weighing up to 50kg (McNab, 1984) and are distributed throughout Central and South America (Gardner, 2008). Giant anteater populations have suffered severe reductions and wildlife-vehicle-collisions are a major threat to their survival (Ascensão et al., 2021; Noonan et al., 2022). Wild giant anteaters were captured between 2017 and 2018, in the vicinity of the three paved highways in the state of Mato Grosso do Sul, in the Cerrado biome, and equipped with tracking collars that obtained GPS fixes at 20-min intervals (for full details see Noonan et al., 2022). A preliminary analysis on these data suggested that these individuals occupied fixed home ranges that regularly overlap paved highways. Following the workflow described above, we estimated the PRE for these two individuals in `R` (ver. 4.2.1, R Core Team, 2016). Home range areas were estimated using Autocorrelated Kernel Density Estimation (AKDE, Fleming et al., 2015) via the `ctmm` `R` package (ver. 1.1.0, Calabrese et al., 2016).

The two animals we estimated PREs for exhibited two different patterns in space use. One animal occupied a home range that was centered on the road (Fig. 3A), whereas the other occupied the roadside and surrounding area, but spent little time on the road itself (Fig. 3B). As would be expected for the animal that lived right along the roadside, the ecological effects of a road mortality were greatest near the road (Fig. 3C). For the second animal, their home range was further from the road, resulting in a weaker overall road effect, but one that peaked in probability between 1-2km from the road (Fig. 3D). In other words, although $P\{\text{Roadkilled}\}$ was greater for the first giant anteater, the road has the probability to impact the ecosystem more than 2km away from the road through the loss of the second giant anteater.

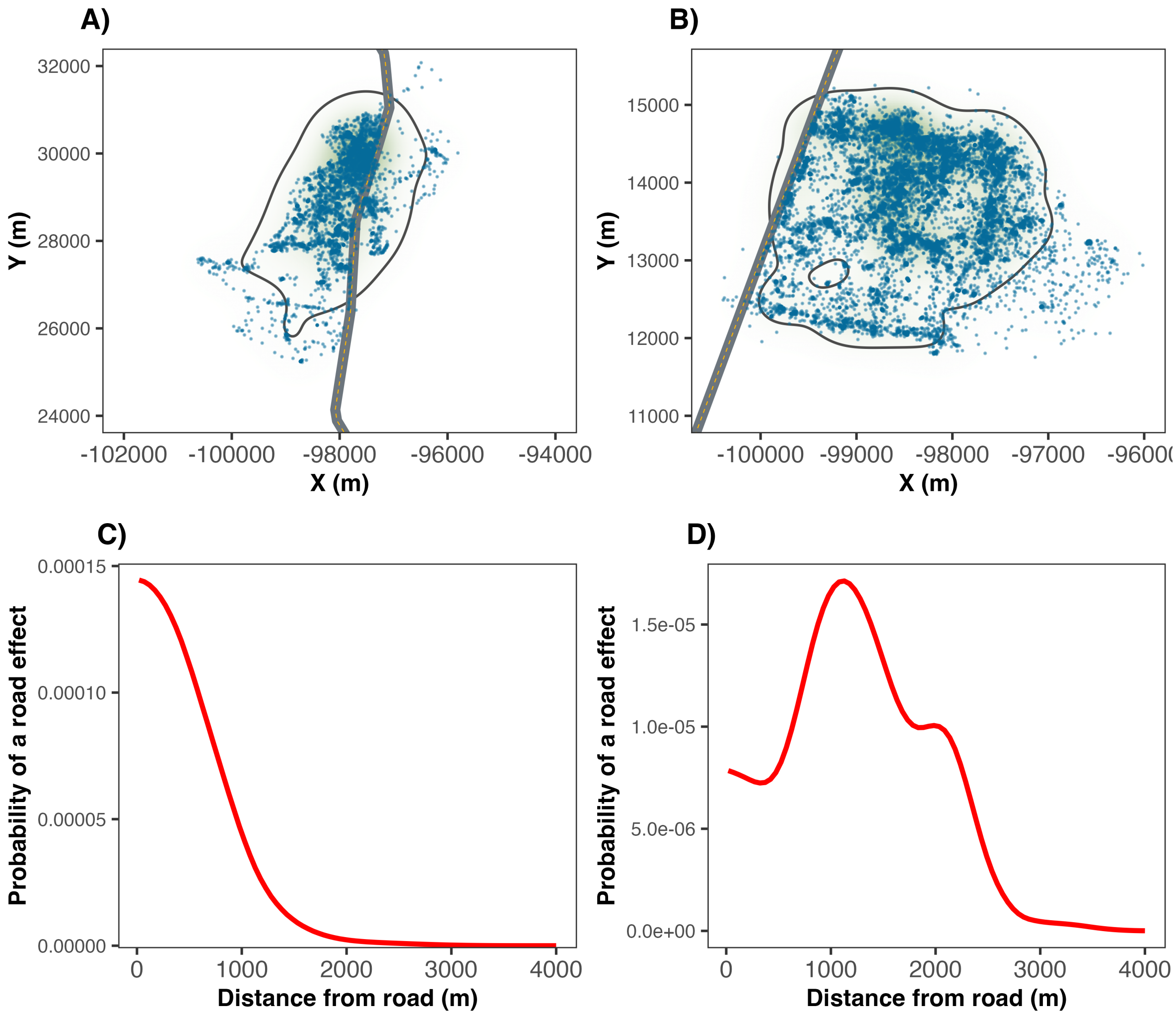

Figure 3: The relationship between space use and the road effect zone for two giant anteaters in the Brazilian Cerrado. Note how in panel A), the animal lives right along the roadside, so the ecological effects of a road mortality are greatest near the road, as shown in panel C). In Panel B), the animal's home range was further from the road and while the overall road effect was weaker, it peaked between 1-2km from the road.

Discussion

The idea that ecological conditions will be more pristine the further one moves from away from a road has been a focal point of road ecology research since Forman and Alexander (1998) first introduced the concept of the Road Effect Zone more than two decades ago (Andrasi et al., 2021; Brady and Richardson, 2017; Eigenbrod et al., 2009; Forman and Alexander, 1998; Forman and Deblinger, 2000; Peaden et al., 2015; Reijnen et al., 1996; Semlitsch et al., 2007). This conventional REZ focuses on quantifying the area over which roads alter measurable ecological impacts, typically community composition or population densities (Andrasi et al., 2021; Fahrig and Rytwinski, 2009; Reijnen et al., 1996; Truscott et al., 2005). While this concept has proven informative for understanding the ecological footprint of roads, the static nature of the REZ means that impacts related to animal movement and species interactions are not captured. For instance, consider a situation where there is a measurable reduction in the population density of a species near a road. This effect may be due to increased road-induced mortality, but it may also be due to road-avoidance and altered movement. Each of these mechanisms may reduce roadside population densities, but each would have different ecological impacts and require different mitigation strategies. Here we demonstrate how probability theory can provide a powerful tool for rethinking the road effect zone, and an individual-based framework for scaling up to population-, or community-level effects.

Of note is the fact that our PRE framework as defined here relies on the assumption that an animal's probability of being road-killed is directly proportional to the time it spends on a road. This is clearly an overly simplistic assumption as factors such as traffic volume and learning will impact mortality rates (Ascensão and Desbiez, 2022; Ford and Fahrig, 2007; Mumme et al., 2000; Noonan et al., 2022; van Langevelde and Jaarsma, 2005). Nonetheless, because our framework is based on quantifying the joint probability of independent events, incorporating additional information affecting $P\{\text{Roadkilled}\}$ is straightforward. Indeed, this flexibility is one of the strengths of this framework. For instance, if signage (e.g., altered speed limits, wildlife corridor notices, etc.) is being considered as a mortality reduction strategy, the effect should be a measureable reduction in $P\{\text{Roadkilled}\}$, and, consequently, $P\{\text{Road Effect}\}$. Similarly, if a practitioner is tasked with making recommendations on the placement of a road-crossing structure, the conventional REZ would suggest that the effects of reduced road mortality will be felt according to some decay function as shown in figure 1. In reality, however, the capacity for animals to move freely across a roadway with $P\{\text{Roadkilled}\} = 0$ (i.e., the benefit provided by the crossing structure) can have ecosystem-wide benefits over vastly larger distances than the conventional REZ might suggest, depending on the vagility and behaviour of the animals the crossing-structure would benefit. The PRE thus provides ecologists and conservation practitioners with a dynamic metric for quantifying the ecosystem-wide impacts of roads, and/or the benefits of management strategies.

In this study, we have developed a framework for estimating road effect zones from animal movement data. Using movement data from giant anteaters occupying roadside habitats in Brazil, we have demonstrated how this framework can be used in practice to understand the ecological impacts of a road, and help inform species management. Notably, this framework builds straightforwardly off of home-range estimation and requires no specialized data collection protocols, allowing researchers to easily quantify the potential ecological impacts of roads for a variety of taxa.

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Figure legends

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