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Research article

Identifying wildlife road crossing mitigation sites using a multi-data approach - A case study from southwestern Costa Rica

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ABSTRACT

Roads are one of the most widespread structures that drive habitat loss and fragmentation. But they also restrict animal movement and drive landscape-level impacts on biodiversity. The South Pacific of Costa Rica is known for its high levels of biodiversity, but little has been done to reduce road impacts upon wildlife communities. To understand these impacts and advise on possible mitigation action, we used three key data approaches: 1. Camera traps, to survey wildlife activity along two major road sections that dissect the region's protected areas and biological corridors. Seventy-eight camera traps were deployed in secondary forest patches at different distances (between 200 m and 1 km) from the roads for six months and covariates were collected to explain the patterns found. 2. Citizen science data extracted from iNaturalist to identify roadkill "hotspots" along the roads. And 3. Circuitscape analysis, to assess how landscape structure could influence animal movement. Camera traps recorded 30 terrestrial species. Ocelots and agoutis displayed a negative effect of distance from protected area, while the Apex predators displayed a positive effect toward higher forest cover and vegetation density. Circuitscape analysis showed high connectivity throughout most of the area. Only a few locations showed higher flow (bottle neck locations), which coincided with roadkill "hotspots" identified through citizen science direct observations (70 observations of 21 species). Amalgamating data from the different analyses allow us to identify four key wildlife crossing locations (one of less priority) along the Inter-American Highway. We strongly recommend the placement of under/overpasses in these locations, with the aim to ensure wildlife safe movement and connectivity of wildlife populations in the region. Culvert modifications in the area could also be considered to incorporate wildlife underpasses at a reduced cost.

1. Introduction

Land-cover change and habitat fragmentation caused by human activities are among the main drivers of global wildlife population declines (Newbold et al., 2015), shifts in community compositions, and shrinking species distributions (Ramachandran et al., 2020). One of the most widespread and pervasive processes that cause habitat loss and fragmentation is the creation of linear features for transportation and infrastructure, such as roads, railways, power lines, or seismic lines (Strevens et al., 2008; Forman et al., 2003). These features cut across natural habitats, creating landscape-scale impacts across long distances that go beyond human population centers. Roads in particular restrict animal movement (Buchanan et al., 2014), isolate populations (Andren, 1994), cause animal mortality through traffic collisions (Baskaran and Boominathan, 2010), act as ecological traps as roadside resources can also attract individuals to dangerous roadside habitats (Noonan et al., 2022), and produce air and acoustic pollution (Arévalo and Newhard, 2011; Manisalidis et al., 2020). These effects are magnified when roads are widened and paved, as it increases traffic and vehicle speeds which increase the probability of death by collision for some species

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(SmithPatten and Patten, 2008; Sur et al., 2022) while increasing road avoidance for others (Dickson et al., 2005; Patrick and Gibbs, 2010). Roads then become impermeable barriers that could lead to local extinctions if no mitigation actions are implemented to reconnect or preserve wildlife populations isolated and directly impacted by roads (Lodé, 2000).

To reduce the impacts of roads on wildlife populations, many mitigation techniques have been implemented, including speed reducers, various forms of warning signs, and the construction of wildlife-specific over and underpasses (Van der Ree et al., 2007; Rytwinski et al., 2016). These wildlife crossings in particular provide a permanent structural link between isolated habitat patches which facilitates safe movement for wildlife across roads (Clevenger and Huijser, 2011); and they have shown to be key structures in preventing animal collision with vehicles (Van der Ree et al., 2007). Additionally, when wildlife crossings are paired with wildlife fencing, studies have found an approximate 86% decrease in reported wildlife vehicle collisions (Huijser et al., 2009). The success of these structures—and other mitigation strategies in general—nevertheless hinges on proper placement and design that accounts for the ecology and behavior of target species as well as the surrounding landscape.

Wildlife crossings can vary greatly in design and size (Luell, 2003; Sołowczuk, 2020), which can majorly influence wildlife use. For example, different wildlife crossings for arboreal species (i.e., canopy bridges) designs have been used with different level of success depending on the focal species (Flatt et al., 2022; Garcia et al., 2022); while wider crossing structures (~50 m) for terrestrial species have shown to encourage the use of a broader array of taxa (Brennan et al., 2022). Location is also a key factor to consider, as mid- and large-sized mammals do not cross highways randomly, they are generally concentrated around specific areas with certain characteristics, e.g., generally the higher quality the habitat at both sides of the road the higher the rates of crossing (Barnum, 2003; Huijser et al., 2016). Subsequently, to ensure the best design and location of wildlife crossings multiple factors should be considered such as road type, vehicle use and speed, surrounding land cover, current road impacts on wildlife populations, and the species composition in the surrounding area. Therefore, to make well informed decisions regarding road mitigation (particularly wildlife crossings), multiple data sources should be utilized, such as roadkill information, surveys of wildlife distribution and activity around roads, and analyses of habitat connectivity (Araya Gamboa and Salom Pérez, 2015). Making informed decisions is even more crucial for mega-diverse tropical regions, such as rainforests, where the impacts of roads are heightened (Goosem, 2007), but where resources for building large infrastructure are usually limited.

Costa Rica has a small territorial size (51,000 km^2) and high levels of biodiversity (Maldonado and Moreno-Sánchez, 2023). At the same time, the country has one of the densest road networks in the world; it is ranked number 29 for road density (kilometer of roads per square kilometer of surface), surpassing countries such as the United States (ranked 33), China (ranked 40), Canada (ranked 85) and Russia (ranked 93) (MINAE-SINAC-CONAGEBIO-FONAFIFO. Resumen del Sexto Informe Nacional de Cotsa Rica Ante el Convenio de Diversidad Biológica, 2018; Barrantes Jiménez, 2018). Additionally, the country's rapid development associated with historical resource extraction and most recently, agriculture and ecotourism, has contributed to a further expanding road network (Arévalo et al., 2017). This development has caused a high traffic volume around and through the country's protected areas, increasing fragmentation and the risk of wildlife-vehicle collisions. For example, over the past decade, an estimated 1850 wild species were killed after being hit by vehicles (https://www.naturalist.mx, 2024). Despite the extensive risks, the impacts of roads on wildlife have been studied on only 1.3% of the road network (CC-CVVS, 2013), and very few mitigation strategies have been implemented to decrease roadkills. Only a handful of local studies have addressed the need of mitigation actions in specific areas (Araya Gamboa and Salom Pérez, 2015; Pomareda et al., 2014), and initiatives that have implemented solutions to terrestrial species roadkills along paved roads are scarce (VillalobosHoffman et al., 2022).

We performed a comprehensive study to assess the impacts of roads on wildlife in the Osa region, in the South Pacific of Costa Rica. This region is among the wildest and most ecologically intact regions of the country (Ley-López et al., 2023). The region hosts the largest contiguous lowland rainforest, and the largest mangrove wetland system, along the Pacific slope of Central America (Toft and Larsen, 2009). However, these natural habitats are disconnected by several roads which may impede the safe movement of wildlife from one area to another. Currently there are only two main paved roads, with many other gravel/dirt roads constantly under threat of a paving upgrade. Therefore, the overall impact is expected to increase as more roads are widened and paved in the near future. We conducted a survey to identify the best locations for implementing safe crossing structures for terrestrial species across this key landscape for biodiversity conservation and ecotourism. We used a multiple source approach, wildlife activity from camera traps, roadkill data from citizen scientists, and forest connectivity mapping. In addition, we explore environmental variables to explain spatial patterns of species and communities, identifying determinants of wildlife diversity and activity in tropical forest habitats fragmented by paved roads. Finally, we outline recommendations for road mitigation as a management resource for decision makers.

2. Methods

2.1. Study site

This study was conducted in the South Pacific of Costa Rica. Temperatures range between 23.4 °C and 28.8 °C (Whitworth et al., 2018), and rainfall averages 3584 mm yr^{-1} and is seasonal, with a wet season from June to November and a dry season from December to May (Taylor et al., 2015). This region is home to the biggest remaining tract of Pacific lowland wet forest in Mesoamerica (Holdridge, 1996). The region hosts four protected areas – Corcovado National Park (CNP; 424 km^2), Piedras Blancas National Park (PBNP; 140 km^2), Térraba-Sierpe National Wetland (TBNW; 330 km^2), and the Golfo Dulce Forest Reserve (GDFR; 599 km^2; MoreraBeita et al., 2021, Fig. 1), yet less than half of the original old growth area remains (Weissenhofer et al., 2001). No extractive activities are allowed in the national parks, but forest plantations (teak and gmelina) and small-scale farming are allowed in some designated areas of the Forest Reserve. Recreational hunting has been prohibited in the whole country since 2012. The region has small towns (<15,000 people) and villages, and small to medium-scale agricultural activities (cattle, palm oil, rice). The nearest large tract of forest is the high elevation protected area La Amistad International Park (PILA; 1992 km^2), in the mainland of Costa Rica which is connected to the Osa Peninsula by biological corridors (MoreraBeita et al., 2021, Fig. 1).

The wildlife community in the region, 26 wild terrestrial mammal (large and small-bodied) and ground bird species, has shown signs of recovery as species become more widely distributed across the region in comparison to being confined to the safety of CNP and in low numbers during the 1990's (Carrillo et al., 2000; Vargas Soto et al., 2022). However, apex predators like the jaguar (*Panthera onca*) and their main prey - the white-lipped peccary (*Tayassu pecari*) remain generally restricted to CNP and surrounding areas (Vargas Soto et al., 2022).

The Osa region is traversed by two major paved roads: 1) the Inter-American Highway, which stretches across the neck of the peninsula connecting the Osa region with the capital San Jose to the north and with the border in Panama to the east, and 2) the National Route 245, which branches off the Highway and connects with the peninsula along its inside edge (Fig. 1). The Inter-American Highway spans 60 km in this region, it was first established in the 1970's and was paved in the 1980's, whilst the National Route 245 is 70 km long, and was first established in 1978 and paved in 1989 (Flatt et al., 2022). The Inter-American

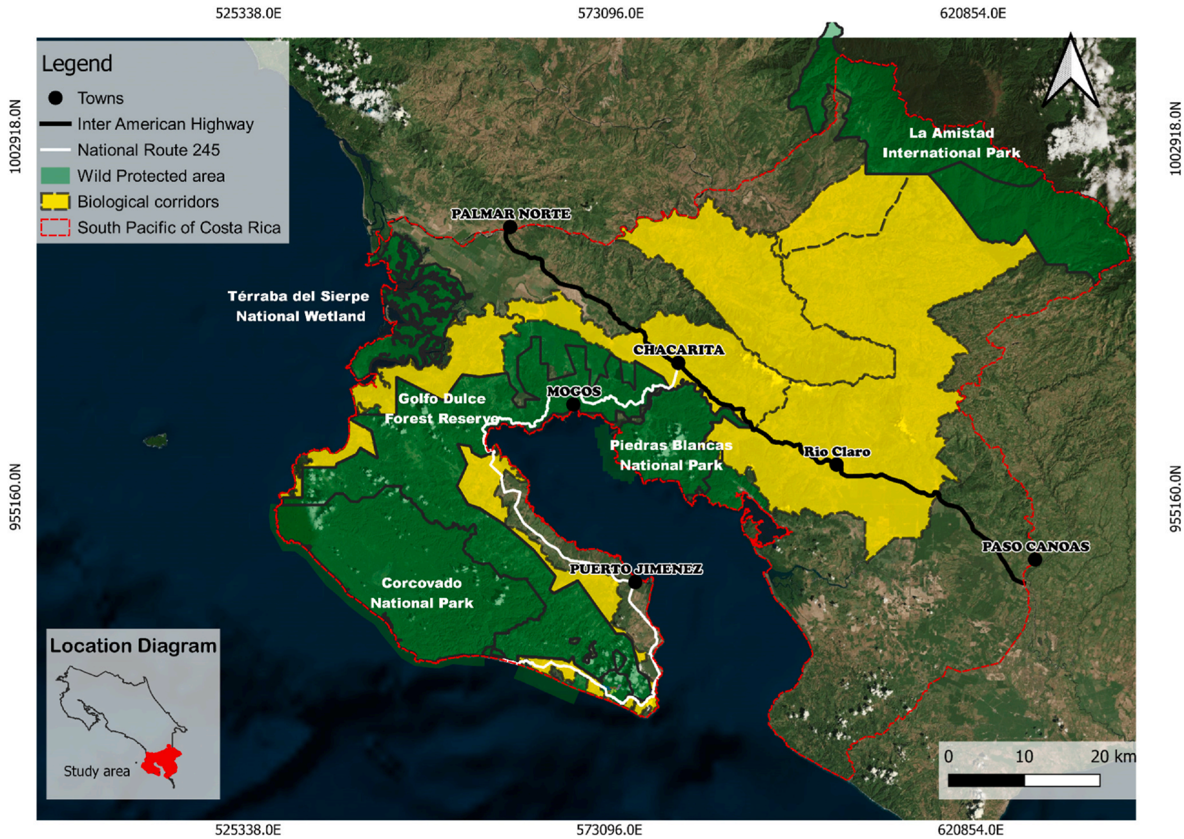

Fig. 1. The South Pacific of Costa Rica, protected areas highlighted in green, biological corridors highlighted in yellow, major roads identified by black and white lines and main towns identified by black spots. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Highway in particular has heavy traffic with mean speeds greater than 80 km/h (Vargas and Araya Villalobos, 2009) and is a potential major barrier between the Osa Peninsula and La Amistad International Park. Finally, the region comprises a network of unpaved roads that connect communities and farms across the Osa Peninsula.

2.2. Wildlife activity

Efforts were focused on the Chacarita–Río Claro section of the Inter-American Highway (19 km) and the Mogos-Chacarita section of the National Route 245 (7 km; Fig. 1). To monitor wildlife activity around the focal sections of the roads, 78 camera traps (Bushnell Trophy) were deployed in secondary forest strips and patches for 6 months (February–August 2021). We used species richness and wildlife relative abundance index (RAI) (Soto-Werschitz et al., 2023) as a proxy of wildlife activity. The RAI is calculated as the number of detections divided by the effort (trap-days) at that location. To understand the effect of the road presence on wildlife activity, camera traps were placed at different distances from the road. Every 1 km along the road, camera traps were placed 200–500 m from the road in forest habitat. Every 2 km along the road, camera traps were deployed 700 m-1km from the road in forest habitat (Fig. 2). Camera traps were installed at a height of 30–50 cm, the most effective set-up for studying terrestrial mammals and ground birds in tropical forests (Rovero et al., 2014), and configured to record 15 s videos, with 30 s resting periods. A case with a security lock was installed in areas of high probability of theft, for example close to human settlements or with evidence of frequently used human trails.

2.3. Citizen science: roadkill

To identify the roadkill levels of wildlife along the study roads, we engaged local people working and living in the area (using the roads on a frequent basis). We created a citizen science project within the iNaturalist platform, where participants could report any animals observed struck by vehicles along the road. We conducted 5 iNaturalist workshops in the communities surrounding the Piedras Blancas region training a group of 23 local people. In each workshop, we taught participants how to use the mobile application and instructed them how to create reports for the specific project. Each report has an associated date/time, GPS location, and photograph, and we asked participants to identify the species if possible. We used reports from between November 2021 and November 2022.

2.4. Data analysis

To characterize the composition of the wild vertebrate community in relation to the environmental and anthropogenic covariates at camera-trap stations, we analyzed species occurrence data from the camera-traps using a joint species distribution model. We used a model that accounts for spatial autocorrelation (Pichler and Hartig, 2021), because some of our cameras were close relative to animal movement ranges. This model also accounts for the correlation among species, revealing potentially determinant biotic relationships. We performed this analysis with the sjSDM package (Pichler and Hartig, 2021) in R 4.1 (R Core Team, 2022). We included spatial effects as a linear effect of the Moran's eigenvector map of the Euclidean distance between locations (function generateSpatialEV in package sjSDM). We included the scaled covariates also as linear effects in the model.

We included 6 explanatory covariates for each camera trap site: 1) distance to the nearest road, 2) distance to the nearest protected area, 3) surrounding forest cover (determined as the percentage of forest cover in a 100 m buffer around the station), 4) canopy cover (calculated with

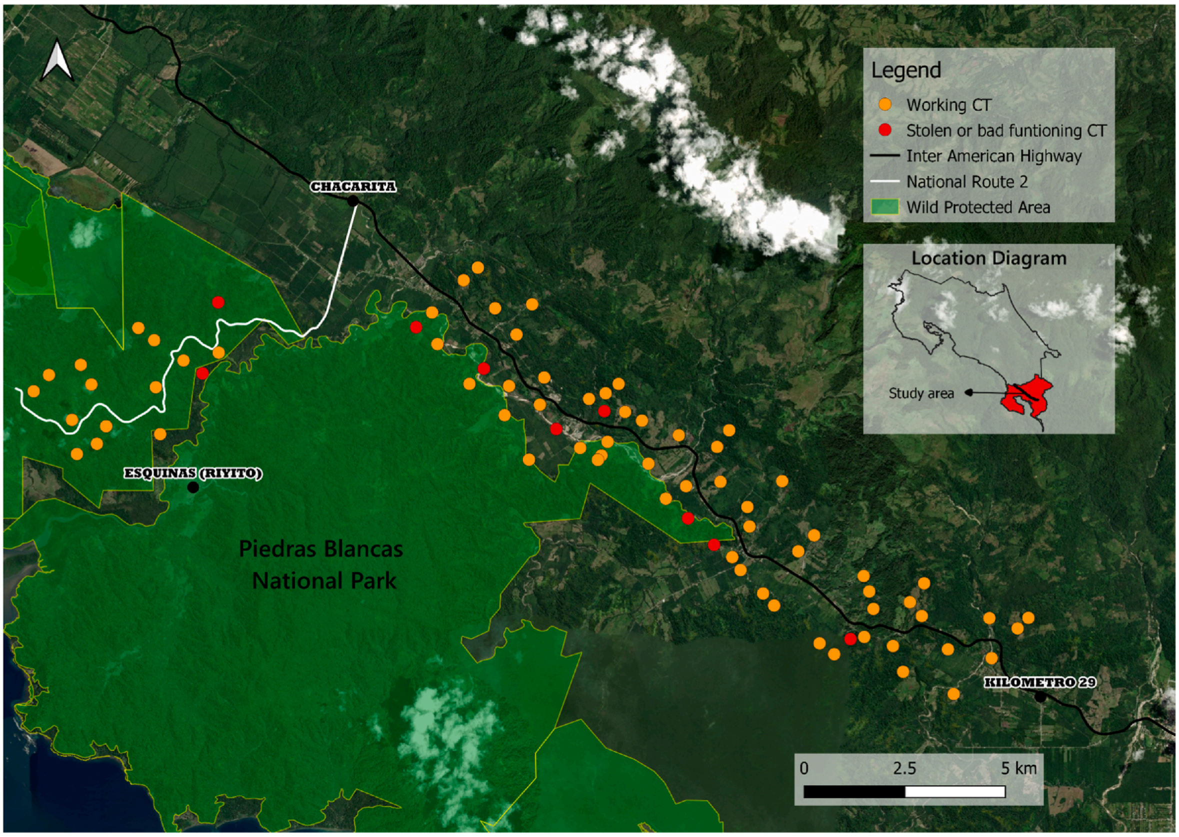

Fig. 2. Camera trap (CT) locations (orange and red dots) along the Inter-American Highway and National Route 245 in the South Pacific of Costa Rica to assess wildlife activity in forest habitat around roads. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the Canopy Capture phone app, averaged across four directions -East, West, North, South), 5) vegetation density (Enhanced Vegetation Index, calculated from satellite imagery), and 6) human disturbance (using the global Human Modification Index; Kennedy et al., 2019). The human disturbance metric includes disturbance from human settlements, agriculture, roads, and energy infrastructure, and has been shown to influence the wildlife community in the region (Vargas Soto et al., 2022). All covariates were calculated in QGIS 3.22, except for the canopy cover which was measured in the field. We evaluated the importance of covariates based on their relative effect sizes. We also explored how species functional groups (trophic guild extracted from the Elton Traits database [Wilman et al., 2014]), were related to the effect sizes.

To assess how landscape structure could be influencing animal movement through the region, we performed a circuitscape analysis (McRae et al., 2008, 2016). This method creates a map of the expected relative flow between habitat patches, based on the cost of traveling through different types of land cover. We used existing land cover maps specific to the Osa region (Shrestha et al., 2018), designated forests as source habitat, and assigned the highest relative cost to roads, intermediate cost to pastures and agriculture, and low cost to wetlands and mangroves. We performed this analysis with the Omniscape package in the Julia programming language (Landau et al., 2021). We classified locations with flow values above the 85th quantile as high flow areas, and above the 95th quantile as very high flow.

We identified sections of the roads with more frequent collisions with wildlife with a density-based clustering algorithm (DBSCAN) in QGIS. We established a minimum of three sightings within 500 m of each other to qualify as a spatial cluster. To determine how collisions with wildlife are related to the surrounding landscape, we used a linear model comparing the flow from the Omniscape analysis, between sites with observed wildlife sightings and randomly selected points on the road. We calculated the median flow in a 100 m buffer around each site.

3. Results

3.1. Wildlife activity

Overall, 25 mammal species and 5 terrestrial bird species were recorded (Table A1). Coatis (*Nasua narica,* n = 1054), agoutis (*Dasyprocta punctata,* n = 1958) and pigeons (roughly three different species, n = 1165) were the most common taxa, detected at 81.5%, 76.9% and 66.2% of camera trap stations, respectively. Mice (Cricetidae) and spiny rats (Echimyidae), anteaters (*Tamandua mexicana*), tayras (*Eira barbara*), and collared peccaries (*Pecari tajacu*) were also common, detected at more than half of the camera trap stations. The least common species were tapirs (*Tapirus bairdii*), otters (*Lontra longicauda*), and kinkajou (*Potos flavus)*, all of which were detected at a single station.

There was substantial variation across camera trap stations in the number of species detected (2–16, median = 9), and the relative abundance index (RAI), an indicator of density (0.1–52.3 day^{-1}, median = 0.7 day^{-1}). However, there was no spatial trend in either variable with respect to their distance from the road. Four areas in particular had sites with high richness (12–16 species detected) on opposite sides of the Inter-American highway (Fig. 3). One of these also corresponded to a cluster of cameras with high relative abundance indices (RAI), but the other two did not. We highlight the clusters of sites with high richness and RAI in Fig. 3.

3.2. Effect of environmental covariates on species distribution

We did not find strong systematic effects of environmental or anthropogenic covariates on the presence of wildlife species along the

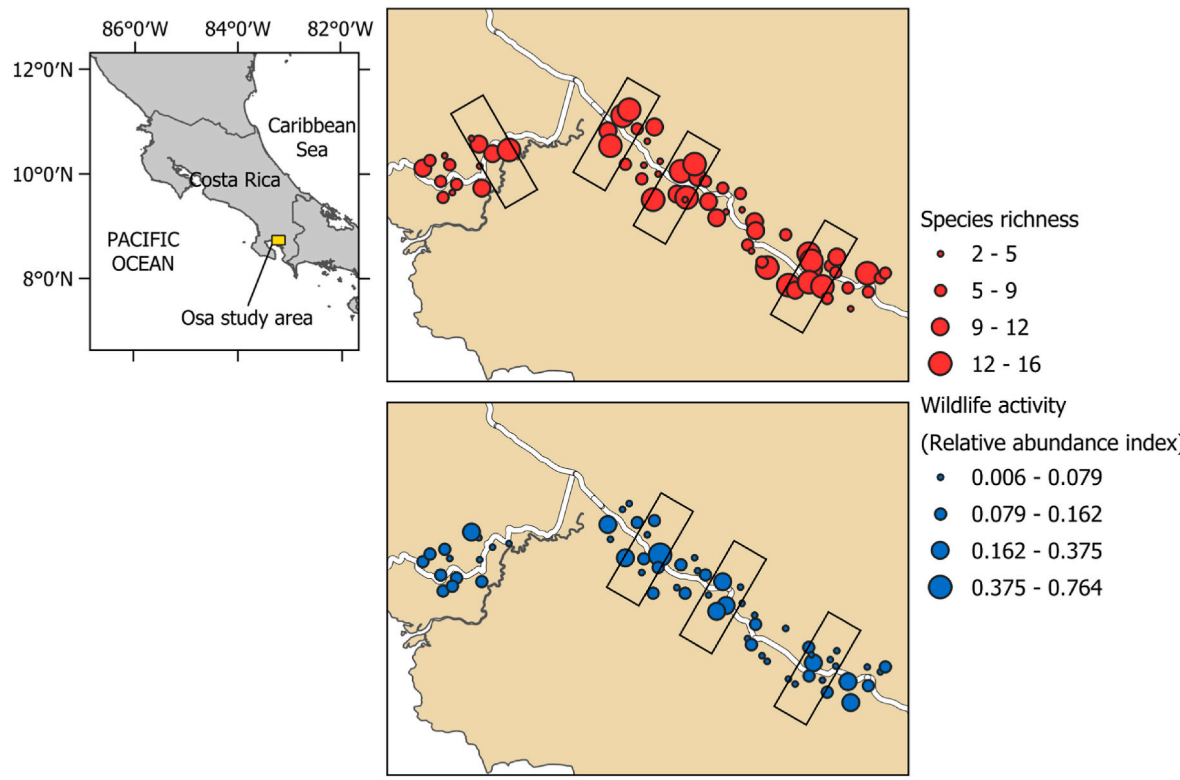

Fig. 3. Wildlife observed using motion-activated cameras located around the main roads in the Osa region. At each camera, we estimated species richness (red circles, top) and activity (blue circles, bottom). Black rectangles highlight clusters with high species richness/activity, areas where multiple cameras around the same road section had high richness or activity. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

roads in the region. The only covariate specifically related to the road (distance) had the smallest influence on the estimated probability of presence. Some of the clearest effects were a negative effect of distance to protected areas for agoutis and ocelots, meaning they are detected almost exclusively in or near protected areas (Fig. 4). Rails (family Rallidae) displayed the opposite trend, being mostly distributed outside

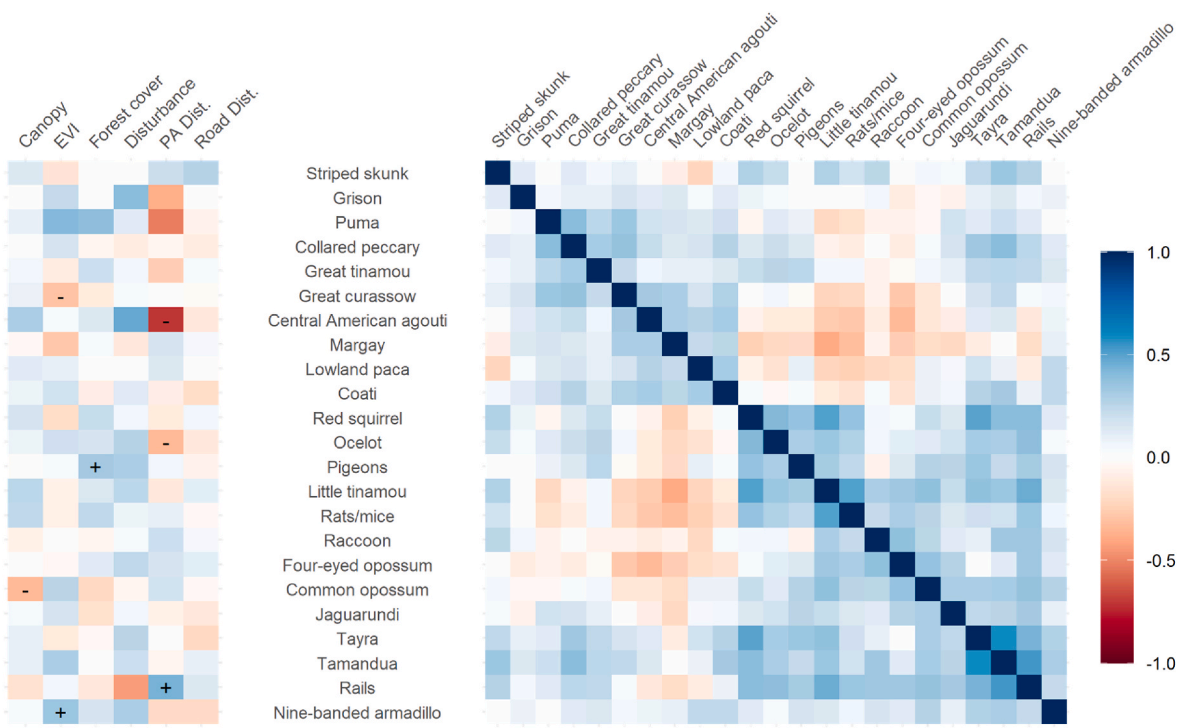

Fig. 4. Parameter coefficients and pairwise correlation between species from a joint species distribution model of terrestrial vertebrates detected with camera-traps in the Osa region, southern Costa Rica. The + and - symbols on the left signal effects with confidence intervals that do not include 0.

of protected areas. Great curassows were negatively associated with densely vegetated areas, while nine-banded armadillos were positively associated with densely vegetated habitats. Common opossums were negatively associated with higher canopy cover areas. Finally, pigeons were positively associated with higher surrounding forest cover.

Similarly, we did not find strong correlations between species (Fig. 4). The strongest negative associations were found between the Tayra (*Eira barbara*) and the Tamandua (*Tamandua mexicana*), and between Rails and Tamanduas. On the other hand, the strongest positive association was found between the Margay (*Leopardus wiedii*) and the Little Tinamou (*Crypturellus soui*), and between Agoutis (*Dasyprocta punctata)* and four-eyed opossums (*Philander opossum*).

When analyzing the coefficients by the trophic guilds, we found the strongest effects for apex predators, which in this case is represented only by puma, as no jaguars were detected during the survey period. They were associated with higher forest cover and vegetation index, close to or within protected areas (Fig. 5). Frugivores (tinamou, great curassow, red squirrel) showed an opposite response, they were negatively affected by vegetation index. There were also moderate positive effects of vegetation index and disturbance for insectivores (armadillos and tamanduas). Herbivores (agoutis, pacas, and collared peccaries) were associated with protected areas and higher canopy cover, although the latter effect was not strong.

3.3. Structural connectivity

Results from the joint species distribution model indicate that forest cover plays an important role in the distribution of some species. This analysis, however, does not explicitly incorporate connectivity, which could affect short-term movement rather than long-term distribution. In terms of connectivity, the circuitscape analysis indicated low flow, i.e., high connectivity, throughout most of the study area, which makes sense given the extensive forest cover (Fig. 6). There are nonetheless points with high flow that indicate bottleneck sites where movement of forest animals would be constrained. The areas with highest estimated flow are around the Inter-American highway where there is reduced forest cover (Fig. 6).

3.4. Roadkills

Overall, the citizen science monitoring group documented 70 observations of 21 species in total (Table A2), of which 88.4% were found dead and 11.4% alive. The most frequent species seen on the road were the northern tamandua (*Tamandua mexicana*) (25% of the observations), the raccoon (*Procyon lotor*) (12%), the white-nosed coati (*Nasua narica*)

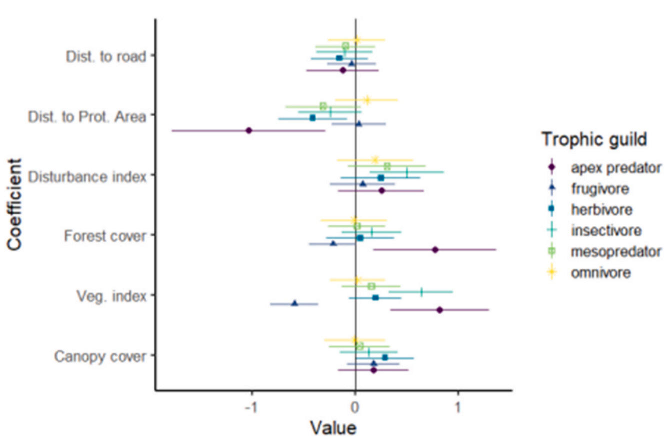

Fig. 5. Effects of environmental and anthropogenic factors on the expected presence of wild animals guilds in the Osa region, Costa Rica. The points and lines show the coefficients from a joint species distribution model, and the standard errors, averaged by guild.

(12%), and the common opossum (*Didelphis marsupialis*) (10%). Sightings were spatially aggregated around seven main clusters, three on Route 245, three on the Inter-American Highway, and one at the intersection between the two roads (Fig. 6). The expected flow—predicted from the omniscape analysis—was higher at sites where animals were sighted than at random points on the road ($\beta = 0.09$, 95% CI: 0.02–0.16, $F_{1,\,165} = 6.10$, $p = 0.015$), suggesting an association between areas with more directed movement and a higher likelihood of collisions (highlighted in Fig. 6a, b, c, and d).

3.5. Potential locations for mitigation actions

We combined the information from all our analyses to determine the best areas for potential wildlife passes or mitigation strategies. High priority areas were all located around the Inter-American Highways. Near Chacarita, where the two roads diverged, there are three roadkill clusters, likely associated with species coming from forested areas on the Northeastern side of the road (Fig. 7A). At two other sites, roadkill clusters coincided with bottleneck areas (Fig. 7B–and C), and areas where cameras determined there was high wildlife activity. These areas correspond to sites where there is forest on both sides of the road, but only over a limited stretch. One last site could also be a bottleneck site, with high species richness and activity, although it was not associated with roadkill (Fig. 7D).

4. Discussion

One of the main challenges to protect and restore natural landscapes to maintain ecological integrity is ensuring habitat connectivity so that wildlife can move safely throughout the landscape (Rudnick et al., 2012). The different methods we applied in this study complemented each other and allowed us to identify the best two locations for implementing safe wildlife crossing structures, both along the Inter-American highway. Although it is widely accepted that for wildlife safe movement sites identification, a combination of methods needs to be applied to ensure that habitat connectivity will increase (Zeller et al., 2020; Barnum, 2003), this is the first study to implement this combination of methodologies that proved to complement each other in terms of what biological information can be extracted by each of them. Wildlife activity and species richness data on opposite sides of the road gave an insight into where safe habitat connectivity might have a strong positive impact on wildlife populations, by ensuring the highest number of species that would be positively impacted by a more permeable landscape. Roadkill data showed locations with the highest current actual mortality risk for species that frequently cross the roads under study; we expect that if wildlife crossing structures were implemented, the risk would decrease considerably. In addition, the identification of sites where wildlife movements are constrained showed the location of bottlenecks, where species are likely being funneled when they need to cross the road. Finally, considering environmental variables that determine species presence along the habitats on both sides of the road showed the importance of high forest cover for wildlife species presence. These results indicate that preserving high forest cover, together with the implementation of (at least) four safe crossing structures (underpass or overpasses), could reduce road-habitat fragmentation impact for wildlife species of the Osa Peninsula.

Contrary to our expectations, in the landscape under study the distance to the roads did not impact species richness. Nonetheless, some species were found mostly close to, or inside protected areas. These results suggest that the road is not having a negative effect on the community of species present in this habitat. If these species are not avoiding roads, they might be potentially crossing, thus preventing isolated populations. However, wildlife species could be at higher risk of being hit by vehicles. On the other hand, these results could also suggest that the road impact in wildlife communities is similar across the distances that we evaluated (from 200 m to 1000 m), and the higher impact

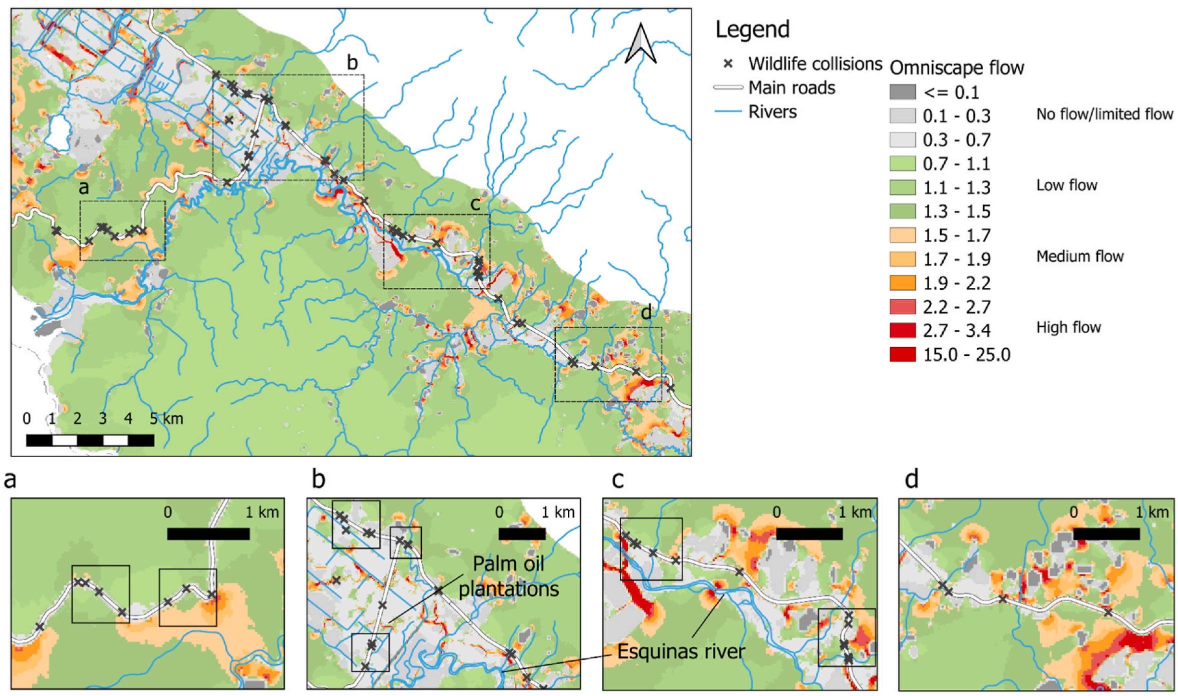

Fig. 6. Omniscape analysis based on land cover shows expected connectivity in southern Costa Rica. More intense colors (orange and red) show areas with higher expected flow, where animal movement is more restricted, that constitute bottleneck sites. These sites generally correspond with the areas where collisions with wildlife (black crosses) are clustered. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

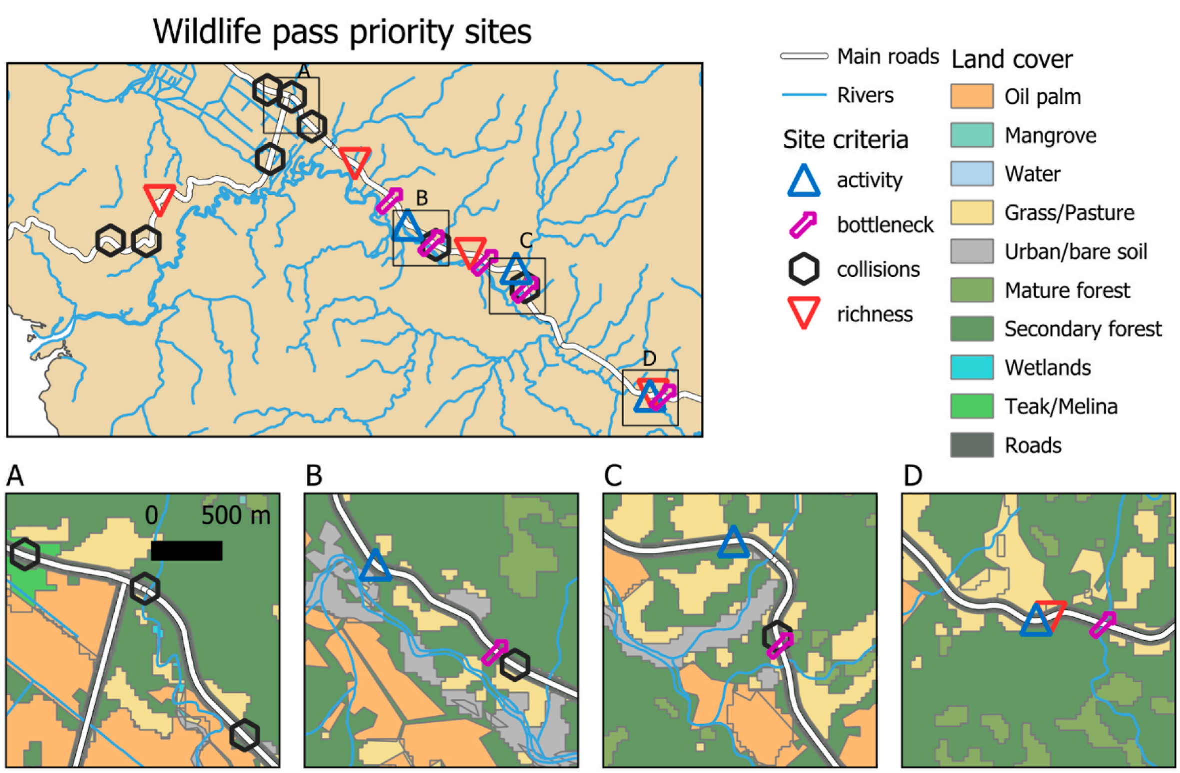

Fig. 7. We overlaid the sites prioritized according to each information source (species richness–red triangles; wildlife activity–blue triangles; bottleneck sites–purple arrows; collision clusters–black hexagons) to determine which locations would benefit the most from wildlife passes. Black squares signal priority areas for wildlife crossing structures, where multiple criteria overlap. Bottom row shows the land cover in the areas highlighted. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

of the road might occur closer to the road. To our knowledge, no study has addressed medium to large mammal species richness and activity change at both sides of the forest at different distances from the road, looking for distance to the road effect. Previous studies which analyze the effect on both sides of roads have been conducted with birds in Australia, finding species richness to start to considerably decrease at 150 m (Pocock and Lawrence, 2005) and small mammals also in Australia but with a shorter distance from the approach (up to 28 m), not reporting a considerable change along this gradient (Goosem, 2007). Overall, although it is a speculation since it is not possible to prove cause-effect relationship, our results suggested that protected areas could have a positive effect on wildlife populations in fragmented landscapes due to roads, likely reducing the negative impacts of it (i.e., wildlife species road avoidance).

Forest fragmentation due to roads has led to a decrease in habitat quality for wildlife species inhabiting these ecosystems (Harris and SilvaLopez, 1992). According to our results, apex predators (in this study represented by pumas), were the most sensitive guild to forest cover loss, vegetation density and distance to protected areas. Contrary to our expectations and previous studies conducted in the area, no effect for wildlife guilds was found for variables linked to forest fragmentation itself, such as distance to the road and human disturbance index (Vargas Soto et al., 2020; Gutierrez et al., 2019; Whitworth et al., 2018). Moreover, frugivores showed an opposite response, species found here (great curassow and tinamus) were negatively affected by vegetation density; likely due to more open forest (and therefore less complex) could raise fruit production rates and therefore benefit these species in secondary forest areas (Gonçalves da Silva, 2017). However, the lack of response to fragmentation variables could also be explained by the lack of observations of some species that used to inhabit these forest areas which are sensitive to forest cover loss and habitat fragmentation. Species such as the white lipped peccary (*Tayassu pecari*), an omnivorous species strongly linked with the presence of fruiting native species, have disappeared for over thirty years now from the area (Vargas Soto et al., 2022; Bustamante et al., 2013).

Roadkill recorded by community members who frequently use the roads under study showed clearly the need of implementing mitigation actions in specific locations to guarantee safe animal crossings. The most susceptible species to death via animal-vehicle collisions when attempting to cross were the northern tamandua, the raccoon, and the coati, coinciding with the most frequent animals found dead in other road ecology studies in Costa Rica (Artavia et al., 2015; Monge Nájera and Seas, 2018). Interestingly, all these species have been observed using under and overpass crossing structures in previous studies in the country (VillalobosHoffman et al., 2022), suggesting these species would benefit from wildlife passes in our study region. Although following a structured monitoring approach would have probably allowed us to collect more roadkill observations compared to the citizen science approach (Araya Gamboa and Salom Pérez, 2015), the data was enough to identify the locations where most accidents happen. In this research project, including community members in roadkill data collection, was part of a strategy to start a process of community sensitization to increase responsible attitudes towards nature, which is an added value of citizen science projects (Bonney et al., 2016). Citizen science projects have the limitation that volunteer scientists usually lose interest after a while, decreasing their contributions. However, Monge Nájera and Seas (2018) showed in the study they conducted analyzing worldwide roadkill data collected in citizen science projects, that Costa Rica (together with Mexico and Canada) has good output for this kind of data collection approach. In this study, roadkill clusters identification was a key variable to identify best location for wildlife safe crossing structures, and the data was mostly consistent with other methodologies applied.

The structural connectivity analyses showed that in the landscape studied the habitat next to the roads are mostly forested at both sides, generally presenting very low resistance for wildlife movement, with the exception of some bottleneck areas. Bottlenecks are areas where movement for wildlife is more restrictive due to lower forest connectivity; these sites tend to overlap with higher observations of roadkills, showing the risks of those specific locations for safe wildlife movement. These results are consistent with previous studies, for example, Meza et al. (2019) showed that the roadkill hotspots for mammals in Colombia intersect with areas where the landscape presents lower connectivity. These results could be due to mammal species being forced to leave unsuitable habitats in fragmented landscapes, increasing the risk of wildlife-vehicle collisions. While there were relatively few localized areas with very constricted flow, their location could represent significant barriers for overall movement at a regional scale as most bottleneck sites were by the Inter-American highway, which is the main barrier between the Osa Península and the mainland. Moreover, our analysis of connectivity is generous in that it does not consider factors like behavioral avoidance, which could increase impermeability even if there is structural connectivity. Paved roads are almost impermeable filters for many wildlife species such as meso-carnivores and large ungulates (Chen and Koprowski, 2019). Our results provide further evidence that the highway represents a significant barrier, between the lowlands on the west and the higher altitude habitats to the east, thus should be prioritized for wildlife crossings.

4.1. Conservation implications

The results of this study are valuable in proposing road mitigation action to ensure wildlife safe crossing through two sections of roads that disconnect the Osa Peninsula's protected areas from the mainland of Costa Rica. Underpass, culvert modifications, and canopy bridges structures have been implemented in the country before, showing success in terms of animal crossing activity and decreasing wildlife roadkills (VillalobosHoffman et al., 2022; Monge Velázquez and Sáenz, 2022). The positive impact of implementing these structures to increase the connectivity between the Osa Peninsula, a biodiversity hotspot, and the Amistad International Park in the mountains, would contribute to enhancing the permeability of biological corridors that connect the protected areas present in the South Pacific zone of Costa Rica. The safe movement of threatened megafauna such as the margay, which is now restricted to a few protected areas and surrounding buffer zones (Vargas Soto et al., 2020), would be key to ensure population recovery. To reduce road impact on these most sensitive species, safe crossing structures are needed along the Inter-American highway.

We strongly recommend that at the four locations/areas highlighted by this study, wildlife over/underpasses should be implemented with fences to reduce roadkills in the area. Rytwinski et al. (2016) meta-analysis found that the combination of fencing and crossing structures led to an 83% reduction in roadkill of large mammals. Because it is known that building these structures can be of high cost, we also advise that as a lower cost alternative (where necessary), implement modification in the big culverts (over 1×1m) that the road sections under study already have (personal inspections by the authors). Culverts can be modified by adding an elevated ledge or shelf on one or both walls of it to provide dry passage for wildlife. Moreover, modified culverts have been already tested to work as wildlife underpasses for species commonly affected by roadkills in the area such as raccoons (*Procyon lotor*) and tayras (*Eira barbara*) (Araya-Jiménez, 2019).

Finally, considering that the Osa Peninsula is a hotspot for biodiversity (Ley-López et al., 2023), we also recommend incorporating culvert modifications, when possible, in the rest of the locations where one proxy showed high species detections (e.g. higher wildlife activity in camera traps or roadkill clusters). Since, in some cases it has been shown that a great number of adapted structures (e.g., culverts) can offer better results than the construction of a single passage for fauna and might have the same total cost (Luell, 2003). We expect that the more crossing structures for wildlife are applied, the more permeable the landscape could become. We highlight the importance of implementing these measures, since similar mitigation efforts have already been tested by VillalobosHoffman et al. (2022) in the area. This study proved that fifteen mammal species were able to safely cross the highway by utilizing 29 underpasses in the ten years since they were installed (including a mixture of both culverts and 1.5 × 1.5 m square tunnels). They showed that almost all roadkill species from the area (except for the green iguanas *Iguana iguana*) used the structures. In the context of land use change and habitat fragmentation, increase in landscape permeability for wildlife movement in the South Pacific of Costa Rica will be critical as wildlife crossing structures could provide safe paths to higher quality habitats (with better environmental conditions). As such, mitigation actions will assist in immediate survival of individual animals and populations, and also for long-term adaptation and resilience of wildlife populations.

CRediT authorship contribution statement

Carolina Melisa Pinto: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Juan Sebastián Vargas Soto:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Eleanor Flatt:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Kenneth Barboza:** Visualization, Software, Formal analysis. **Andrew Whitworth:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Osa Conservation reports financial support and equipment, drugs, or supplies were provided by Disney Worldwide Conservation Fund. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix

Table A1
Number of detections of different species and species groups in the Golfito region, southern Costa Rica. Animals were detected using motion-activated cameras placed at different stations.

Group	Common name	Species	Detections	Stations (%)
Wild mammals	Central American agouti	*Dasyprocta punctata*	1958	50 (76.9)
	Coati	*Nasua narica*	1054	53 (81.5)
	Collared peccary	*Pecari tajacu*	435	35 (53.8)
	Raccoon	*Procyon* spp.	205	29 (44.6)
	Lowland paca	*Cuniculus paca*	183	23 (35.4)
	Rats and mice	*Rodentia*	198	37 (56.9)
	Nine-banded armadillo	*Dasypus novemcinctus*	152	26 (40)
	Tayra	*Eira barbara*	130	36 (55.4)
	Tamandua	*Tamandua mexicana*	91	36 (55.4)
	Ocelot	*Leopardus pardalis*	85	26 (40)
	Common opossum	*Didelphis marsupialis*	84	21 (32.3)
	Red squirrel	*Sciurus granatensis*	37	19 (29.2)
	Four-eyed opossum	*Philander opossum*	31	14 (21.5)
	Striped skunk	*Conepatus semistriatus*	30	13 (20)
	Jaguarundi	*Puma yagouaroundi*	23	16 (24.6)
	Puma	*Puma concolor*	12	8 (12.3)
	Margay	*Leopardus wiedii*	10	7 (10.8)
	Grison	*Galictis vittate*	9	9 (13.8)
	Bats	*Chiroptera*	6	6 (9.2)
	Red brocket deer	*Mazama temama*	6	2 (3.1)
	Squirrel monkey	*Saimiri oerstedii*	6	4 (6.2)
	Capuchin monkey	*Cebus imitator*	5	2 (3.1)
	Baird's tapir	*Tapirus bairdii*	3	1 (1.5)
	Kinkajou	*Potos flavus*	1	1 (1.5)
	Neotropical river otter	*Lontra longicauda*	1	1 (1.5)
Birds	Pigeons	*Columbidae*	1165	43 (66.2)
	Great tinamou	*Tinamus major*	255	30 (46.2)
	Great curassow	*Crax rubra*	131	23 (35.4)
	Rails	*Rallidae*	44	9 (13.8)
	Little tinamou	*Crypturellus soui*	40	16 (24.6)
	Crested guan	*Penelope purpurascens*	10	4 (6.2)
	Hawks	*Accipitridae*	7	2 (3.1)
	Other birds		267	41 (63.1)
Humans and domestic species	Domestic dogs	*Canis familiaris*	85	25 (38.5)
	Cow	*Bos taurus*	35	2 (3.1)
	Human	*Homo sapiens*	20	8 (12.3)

(*continued on next page*)

Table A1 (*continued*)

Pig	*Sus scrofa*	19	2 (3.1)
Domestic cat	*Felis catus*	3	2 (3.1)

Table A2
Roadkill species records collected with citizen science efforts in the Golfito region, southern Costa Rica.

Common name	Species	Nº of individuals
Tamandua	*Tamandua mexicana*	17
Coati	*Nasua narica*	8
Raccoon	*Procyon lotor*	8
Common opossum	*Didelphis marsupialis*	4
Iguana	*Iguana iguana*	6
Cane toad	*Rhinella horribilis*	4
Kinkajou	*Potos flavus*	3
Boa snake	*Boa* sp	2
Striped hog-nosed Skunk	*Conepatus semistriatus*	2
Squirrel	*Sciurus variegatoides*	2
Four-eyed opossum	*Philander opposum*	1
Squirrel monkey	*Saimiri oerstedii*	1
Tayra	*Eira barbara*	1
Brown-throated Sloth	*Bradypus variegatus*	1
Neotropical otter	*Lontra longicaudis*	1
Black-and-white Owl	*Ciccaba nigrolineata*	1
Jacana	*Jacana* sp	1
Tropical kingbird	*Tyrannus melancholicus*	1
Scarlet rumped tanager	*Ramphocelus passerinii*	1
Snake	*Clelia* sp	1
Fer-de-lance	*Bothrops asper*	1

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