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XXXVII CICLO DEL DOTTORATO DI RICERCA IN AMBIENTE E VITA

PROMOTING ECOLOGICAL CONNECTIVITY THROUGH ECOLOGICAL NETWORKS AND CORRIDORS TO FOSTER BIODIVERSITY

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ABSTRACT

Human infrastructure and activities are major drivers of habitat fragmentation and represent a significant threat to biodiversity and ecosystems. The consequences of fragmentation are particularly pronounced in developing countries, where rapid economic growth and increasing infrastructure development often caused negative impacts in areas of high biodiversity and conservation priority. Recognising the importance of maintaining ecological connectivity to support biological diversity and mitigate human-induced impacts, this thesis explores practical approaches to integrate connectivity into environmental planning and impact assessments (EIAs).

The overall aim of the thesis is to develop and apply methods to assess the impacts of different infrastructures on ecological connectivity, to propose mitigation and compensation measures, and ultimately to balance infrastructure development with biodiversity conservation. To achieve this, the thesis is structured around three related case studies conducted at different spatial scales (landscape, regional and local), providing novel tools and frameworks applicable to real-world scenarios.

At the landscape scale, Chapter 2 assesses the direct and cumulative impacts of existing and planned linear infrastructure, such as roads and transmission lines, on the structural connectivity of the landscape in two biodiversity-rich developing countries, South Sudan and Uganda (Africa). By comparing ecological networks under current conditions and a future scenario including planned infrastructures, the study identifies critical areas for connectivity conservation and highlights planned projects with potentially high impacts. This approach offers valuable insights for avoiding critical areas and reducing significant impacts on landscape connectivity in response to linear infrastructure development.

At the regional scale, Chapter 3 introduces two novel concepts in road ecology - roadkill suitability and road crossability - to assess the relationship between wildlife-vehicle collisions and habitat connectivity for forest mammals in north-eastern Italy (Friuli Venezia Giulia region). By analysing multiple mammal species with different movement abilities in natural and anthropized landscapes, the study identifies priority areas within the road network for conservation and management: Priority Areas for Barrier Effect Mitigation (PABEMs), Potential Areas for Roadkill Mitigation (PARoMs) and Potential Areas for Connectivity Preservation (PACoPs). This multi-species approach provides a method for mitigating road impacts on wildlife and preserving habitat connectivity.

At the local scale, Chapter 4 develops a method to integrate forest habitat connectivity into Environmental Impact Assessments. This method was applied to identify appropriate compensation measures for the impacts of a hydropower project in Nepal. The study assesses changes in forest connectivity before and after project implementation and prioritises reforestation areas to compensate for connectivity losses. The spatial analyses conducted allowed the identification of optimal reforestation sites to restore forest habitat connectivity for animal species with different movement abilities.

The findings of this PhD thesis highlight the urgent need to integrate ecological connectivity into environmental planning and impact assessments. The methods and approaches developed in this thesis have proven effective in providing quantitative frameworks and practical solutions to guide the evaluation and mitigation of infrastructure impacts on connectivity. Ultimately, this work contributes to advancing strategies that balance infrastructure development with biodiversity conservation, supporting global efforts to maintain ecological connectivity in an increasingly fragmented world.

RIASSUNTO

Le infrastrutture realizzate dall'uomo ed, in generale, le attività antropiche, sono tra i principali fattori responsabili della frammentazione degli habitat e rappresentano una minaccia per la biodiversità e gli ecosistemi. Le conseguenze della frammentazione sono particolarmente impattanti nei paesi in via di sviluppo, dove la rapida crescita economica e lo sviluppo delle infrastrutture spesso provocano impatti negativi in aree di elevata biodiversità e con alta priorità di conservazione. Considerando l'importanza di preservare la connettività ecologica per supportare la diversità biologica e mitigare gli impatti causati dall'uomo, questa tesi esplora approcci applicati al fine di integrare la connettività nella pianificazione ambientale e nelle valutazioni di impatto ambientale.

L'obiettivo principale della ricerca è sviluppare e applicare metodi per valutare gli impatti delle diverse infrastrutture sulla connettività ecologica, proporre misure di mitigazione e compensazione e, in definitiva, proporre un sistema per bilanciare lo sviluppo infrastrutturale con la conservazione della biodiversità. Per raggiungere questo obiettivo questo lavoro di tesi si è sviluppato attraverso tre casi studio correlati, condotti a scale spaziali differenti (paesaggio, regionale e locale), che forniscono strumenti innovativi e applicabili a scenari reali.

A scala di paesaggio, nel Capitolo 2 sono stati valutati gli impatti diretti e cumulativi delle infrastrutture lineari esistenti e pianificate, come strade e linee di trasmissione, sulla connettività strutturale del paesaggio in due paesi africani in via di sviluppo e ricchi di biodiversità: il Sud Sudan e l'Uganda. Confrontando le reti ecologiche nella situazione attuale e nello scenario futuro che include le infrastrutture pianificate, lo studio individua le aree critiche per la conservazione della connettività e identifica i progetti pianificati che avranno potenzialmente un maggiore impatto. Questo approccio fornisce indicazioni utili per evitare aree critiche e ridurre gli impatti rilevanti sulla connettività del paesaggio in risposta allo sviluppo di infrastrutture lineari.

A scala regionale, nel Capitolo 3 vengono introdotti due nuovi concetti - la *roadkill suitability* e la *road crossability* - per valutare la relazione tra gli investimenti stradali della fauna e la connettività degli habitat per i mammiferi forestali nel nord-est dell'Italia (regione Friuli Venezia Giulia). Analizzando più specie con diverse capacità di movimento in ambienti naturali e antropizzati, lo studio individua aree prioritarie nella rete stradale con differenti priorità di conservazione e gestione: Aree Prioritarie per la Mitigazione dell'Effetto Barriera (PABEMs), Aree Potenziali per la Mitigazione del Roadkill (PARoMs) e Aree Potenziali per la Conservazione della Connettività

(PACoPs). Questo approccio fornisce un metodo robusto e multi-specie per mitigare gli impatti delle strade per la fauna e preservare la connettività degli habitat.

A scala locale, nel Capitolo 4 viene sviluppato un metodo per integrare la connettività degli habitat forestali nella Valutazioni d’Impatto Ambientali. Tale metodo è stato poi applicato per identificare delle adeguate misure di compensazione per gli impatti di un progetto idroelettrico in Nepal. Questo studio valuta i cambiamenti nella connettività forestale prima e dopo l’implementazione del progetto e prioritizza le aree di riforestazione per compensare gli impatti sulla connettività. Le analisi spaziali sviluppate hanno permesso di individuare i siti da riforestare ottimali per ripristinare la connettività degli habitat forestali per specie animali con diverse capacità di movimento.

I risultati della tesi di dottorato evidenziano l'urgente necessità di integrare la connettività ecologica nella pianificazione e nelle valutazioni di impatto ambientale. I metodi e gli approcci sviluppati in questa tesi si sono resi efficaci nel fornire approcci quantitativi e soluzioni pratiche per guidare la valutazione e la mitigazione degli impatti delle infrastrutture realizzate dall’uomo sulla connettività. In conclusione, questo lavoro è risultato importante in quanto contribuisce a sviluppare strategie concrete atte a consentire uno sviluppo infrastrutturale che sia effettivamente sostenibile da un punto di vista ambientale e che sia coerente con i principi ecologici per la conservazione della biodiversità, supportando gli sforzi globali per mantenere la connettività ecologica in un mondo sempre più frammentato.

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CHAPTER 1

INTRODUCTION, OBJECTIVES AND STRUCTURE OF THE THESIS

1.1 INTRODUCTION

1.1.1 *Ecological connectivity*

“Ecological Connectivity is the unimpeded movement of species and the flow of natural processes that sustain life on Earth” (CMS 2020).

This is the most recent definition of ecological connectivity developed during a series of meetings organised by the Convention on the Conservation of Migratory Species and Wild Animals (CMS) to identify priorities for the post-2020 Global Biodiversity Framework. These meetings included members of the CMS Working Group, the Connectivity Conservation Specialist Group of the IUCN World Commission on Protected Areas, and other experts. This definition was endorsed in 2020 at the 13th meeting of the Conference of the Parties, held in Gandhinagar (India), and is now the latest globally accepted way of describing ecological connectivity.

Despite being a current focus in conservation science, the concept of ecological connectivity is not new. It has been developed over the past century and is deeply rooted in fundamental ecological theory and research, such as the theory of island biogeography (MacArthur and Wilson, 1967) and metapopulation theory (Levins, 1969). These theories emphasised the critical role of connectivity in maintaining biodiversity, supporting species survival and ecosystems functioning, in a world increasingly dominated and transformed by human activities. For example, island biogeography explains how the isolation and size of habitat patches affect the colonization, extinction rates and diversity of the species they support, while metapopulation theory highlights the importance of connectivity to ensure gene flow and the survival of viable populations (Hanski, 1999; MacArthur and Wilson, 1967, 1963; McCullough, 1996).

Ecological connectivity is fundamental to ensuring the long-term conservation of nature by ensuring ecosystem functionality, species survival, genetic diversity and adaptation to global change (Crooks and Sanjayan, 2006; Hilty et al., 2020, 2019; Pulsford et al., 2015). It supports key processes such as dispersal, emigration, immigration and gene flow, which are essential for maintaining population viability. These processes enhance genetic exchange, counteracting the negative effects of genetic drift, increasing genetic variability and reducing inbreeding depression. Connectivity also supports demographic and genetic rescue effects, increasing the resilience of populations to environmental and demographic stochasticity. By facilitating the movement of individuals and genetic material among populations, connectivity reduces the risk of extinction and enhances the long-term persistence of species, making it a critical component of biodiversity conservation. Given its importance, it is increasingly recognised as an essential element of global conservation efforts, and increasing

attention is being devoted to developing guidelines, tools and best practices to protect ecological connectivity and reduce fragmentation (Hilty et al., 2020).

In recent years, numerous efforts have been made to include the evaluation of ecological connectivity in decision-making processes, land-use planning and conservation initiatives. At the international level, the recognition of the need to maintain well-connected systems of protected areas was behind the adoption of Aichi Target 11 of the Convention on Biological Diversity (CBD) in 2010. In December 2022, the 15th Conference of the Parties to the CBD adopted the Kunming-Montreal Global Biodiversity Framework (CBD, 2022), which posed greater emphasis on ecological connectivity. This important agreement serves as a strategic plan for global biodiversity conservation from 2022 to 2030, introduces indicators for ecological connectivity and highlights its critical role in maintaining healthy ecosystems. In addition, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) released the Global Assessment on Biodiversity and Ecosystem Services which highlight the requirement to include connectivity into economic growth and development to achieve the 2030 Agenda (IPBES, 2019). Therefore, as mentioned before, the CMS reaffirmed its commitment to maintain ecological connectivity as a top priority.

During the World Conservation Congress in 2021, the International Union for the Conservation of Nature (IUCN) adopted the Policy Resolution 073 titled “Ecological connectivity conservation in the post-2020 global biodiversity framework: from local to international levels” and Resolution 071 “Wildlife-friendly linear infrastructure”, to conserve connectivity and mitigate the fragmentation caused by human infrastructure. Previously, by adopting the policy resolutions 087 and 102, “Awareness of connectivity conservation definition and guidelines” and “Protected areas and other areas important for biodiversity in relation to environmentally damaging industrial activities and infrastructure development” respectively, IUCN published the first Guidelines for conserving connectivity (Hilty et al., 2020).

1.1.1.1 Different approaches to connectivity

The inherent complexity of the ecological connectivity concept lies in the difficulty of effectively translating and quantifying it for scientific research and realistic, useful applications (Crooks and Sanjayan, 2006). Connectivity definitions, metrics, functions, conservation strategies and indicators depend on the taxa or processes under consideration, as well as the spatial and temporal scale at which they occur (Crooks and Sanjayan, 2006; Hilty et al., 2019).

In landscape ecology, connectivity is “*the degree to which the landscape facilitates or impedes movement among resource patches*” (Taylor et al., 1993). There are two main approaches associated with connectivity: structural and functional (Hilty et al., 2020). Structural connectivity refers to the

degree of habitat permeability, which is determined by the physical characteristics and spatial arrangement of habitat patches, disturbances, and other landscape features that influence organism movement (Hilty et al., 2019). Often, structural connectivity aims to identify potential pathways or areas that could facilitate the movement of different species through their environment. Functional connectivity, on the other hand, refers to how well genes, gametes, propagules or individuals move through the landscape (Hilty et al., 2020). This can be more difficult to assess, in part because it involves not only the relationship with landscape features, but also other aspects such as species behaviour. In some cases, these two approaches - structural and functional connectivity - may overlap, while in others habitat patches may be structurally connected but not functionally connected.

1.1.1.2 Ecological network for conservation

Ecological network (*sensu* Hilty et al. 2020) generally refers to a network of areas (nodes or core areas) that are connected by corridors or edges to enhance biodiversity conservation (Figure 1.1; Boitani et al. 2007).



Figure 1.1 - Example of ecological network for conservation. The core areas (or nodes) are outlined in darker colors and the different type of corridors are represented with dashed lines. Source: “Guidelines for conserving connectivity through ecological networks and corridors” (Hilty et al., 2020).

Ecological networks serve as a management tool in fragmented landscapes to maintain ecosystem processes, connect populations and ensure genetic exchange (Hilty et al., 2019). Proposed by Forman

(1995) and subsequently developed, ecological networks include high quality habitats, core areas that may or may not be protected, and corridors that act as pathways for organisms to move between core areas. Surrounding these elements is a matrix, a landscape dominated by human activities that impede the movement of organisms to varying degrees. The main objective of these networks is to mitigate the negative impacts of habitat fragmentation, and by promoting connectivity, they reduce the risk of population isolation and extinction. Ecological networks, and more broadly connectivity, are therefore essential for biological conservation in increasingly fragmented environments.

1.1.2 *Impacts on connectivity*

1.1.2.1 *Habitat fragmentation and infrastructure development*

Habitat fragmentation caused by human activities is one of the major threats to biodiversity and ecosystems worldwide (Fischer and Lindenmayer, 2007; Vitousek et al., 1997). Large, continuous habitats are fragmented into smaller, isolated patches due to human activities such as urbanization, agriculture and infrastructure development, resulting in serious ecological consequences (Fischer and Lindenmayer, 2007). Fragmentation leads to habitat loss, reduced patch size, and increases isolation of remaining habitat patches (Andren, 1994). These changes disrupt or alter connectivity, affecting organisms movements, ecological processes and genetic flow (Forman, 1995). A key concept in understanding these impacts is landscape permeability, which describes the ease with which organisms and ecological processes can move through a landscape. High permeability allows for effective dispersal, gene flow, and ecological interactions, whereas landscape resistance refers to physical and environmental barriers that restrict movement and reduce connectivity. Anthropogenic activities, particularly infrastructure development, significantly increase landscape resistance by creating both direct and indirect barriers to movement, thereby increasing fragmentation. Fragmentation caused by human activities and infrastructure development occurs across different spatial scales, from local to global. Addressing its consequences and long-term impacts requires not only the protection of important areas, but also the maintenance of their connectivity, thereby promoting natural flows and the movement of species between habitat patches (Hilty et al., 2020).

The proliferation of infrastructure projects, including roads, transmission and power lines, dams and urban development, significantly alters landscapes and intensifies fragmentation. Linear infrastructure, such as roads and transmission lines, are particularly impactful, as they fragment habitats, create direct barriers to animal movement, increase wildlife mortality, and facilitate the spread of invasive alien species (Figure 1.2). Other types of infrastructure that require significant land

use, such as reservoir-based hydropower projects, also have relevant negative effects on connectivity which, however, are often underestimated (Figure 1.3).

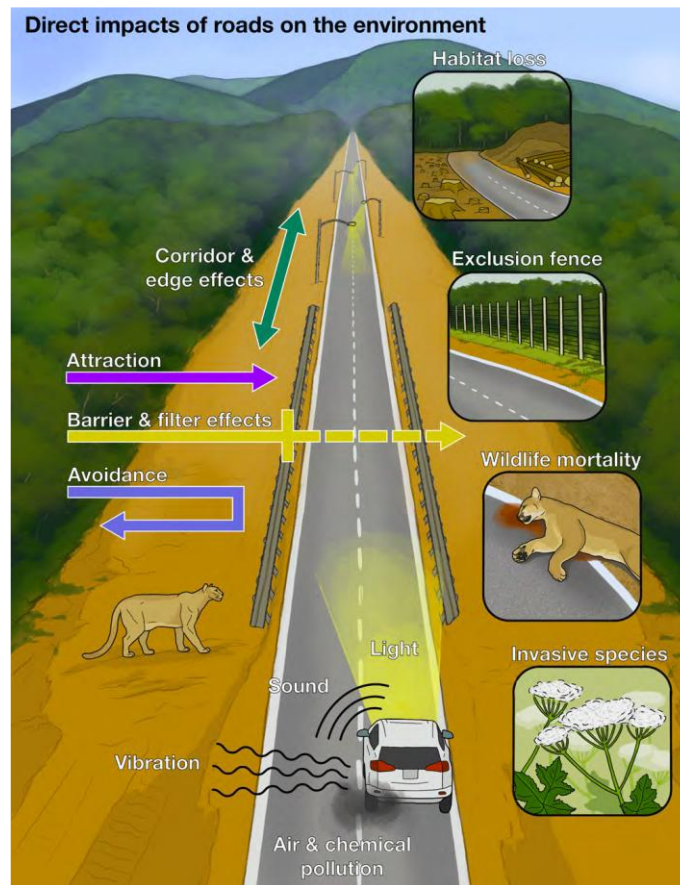


Figure 1.2 - Different type of road impacts on the environment. Source: (Ament et al., 2023).



Figure 1.3 - Example of how a large land-consuming hydropower project could affect the landscape, with consequent negative impacts on habitat connectivity. On the left is the landscape before construction of the dam, while on the right is the landscape during the operational phase of the hydropower project. Source: <https://earthobservatory.nasa.gov/images/91761/a-new-reservoir-in-cambodia>.

Globally, rapid population growth, urbanisation and industrialisation continue to increase the demand for infrastructure at an alarming rate. Particularly in regions where biodiversity is already under threat, this increase in infrastructure development is exacerbating the challenges of maintaining ecological connectivity. The situation is particularly critical in developing countries, where achieving economic growth while safeguarding their rich biodiversity represent a significant challenge. Indeed, these countries are often home to a significant proportion of the world's most threatened and diverse ecosystems and endangered species (Mittermeier et al., 2011). Balancing economic development with conservation goals in these regions is complex, as the pressure to improve infrastructure growth can conflict with the need to conserve biodiversity and connectivity. This requires that infrastructure development, particularly in developing countries, is carefully planned and implemented in a sustainable manner. To ensure that critical habitats are preserved and connectivity maintained, strategic planning should integrate conservation objectives alongside development objectives.

1.1.2.2 Mitigation of the impacts - the Environmental Impact Assessment

The Environmental Impact Assessment (EIA) is a general process regulated under international legislations aiming at assessing the potential environmental impacts and feasibility of a proposed project before its implementation. The main objectives of EIAs are to identify, predict and evaluate impacts of the proposed project on all aspects of the environment, both physical and biological. The goal is to mitigate and/or compensate for negative impacts by planning and proposing measures to enhance positive environmental outcomes, thus balancing infrastructure development and environmental protection. EIAs are designed to identify all potential direct, indirect and cumulative impacts of the proposed project. This means not only those impacts that result in immediate changes, but also those that result from the combined effects of the project and other infrastructure or activities, leading to wider degradation.

After the identification and quantification of the impacts, EIAs include the Environmental Management Plan (EMP), that aim at proposed the mitigation and/or compensation measures for the potential impacts. The purpose of the EMP is to describe in detail the possible actions to be taken to ensure that identified impacts are mitigated as far as possible or, in some cases, compensated (Figure 1.4). The difference between mitigation and compensation relates to their different approaches to managing environmental impacts. Mitigation measures are actions taken to minimise or avoid negative impacts, while compensation measures come into play when residual impacts cannot be fully mitigated (Offsets; IFC 2019). To manage the identified environmental impacts, the EIAs and EMP follow the common framework of the mitigation hierarchy, which consists in four sequential steps (Figure 1.4; Bennun et al. 2021):

1. **Avoidance:** prevent impacts by early planning, site selection and design adjustments to avoid sensitive areas.
2. **Minimisation:** reduce the severity of unavoidable impacts during project design, construction and operation.
3. **Restoration:** restore ecosystems or biodiversity features affected by impacts that could not be avoided or minimised.
4. **Offsets:** compensation for residual impacts that cannot be avoided, minimised or restored. Offsets aim to achieve a measurable conservation outcome for the biodiversity features.

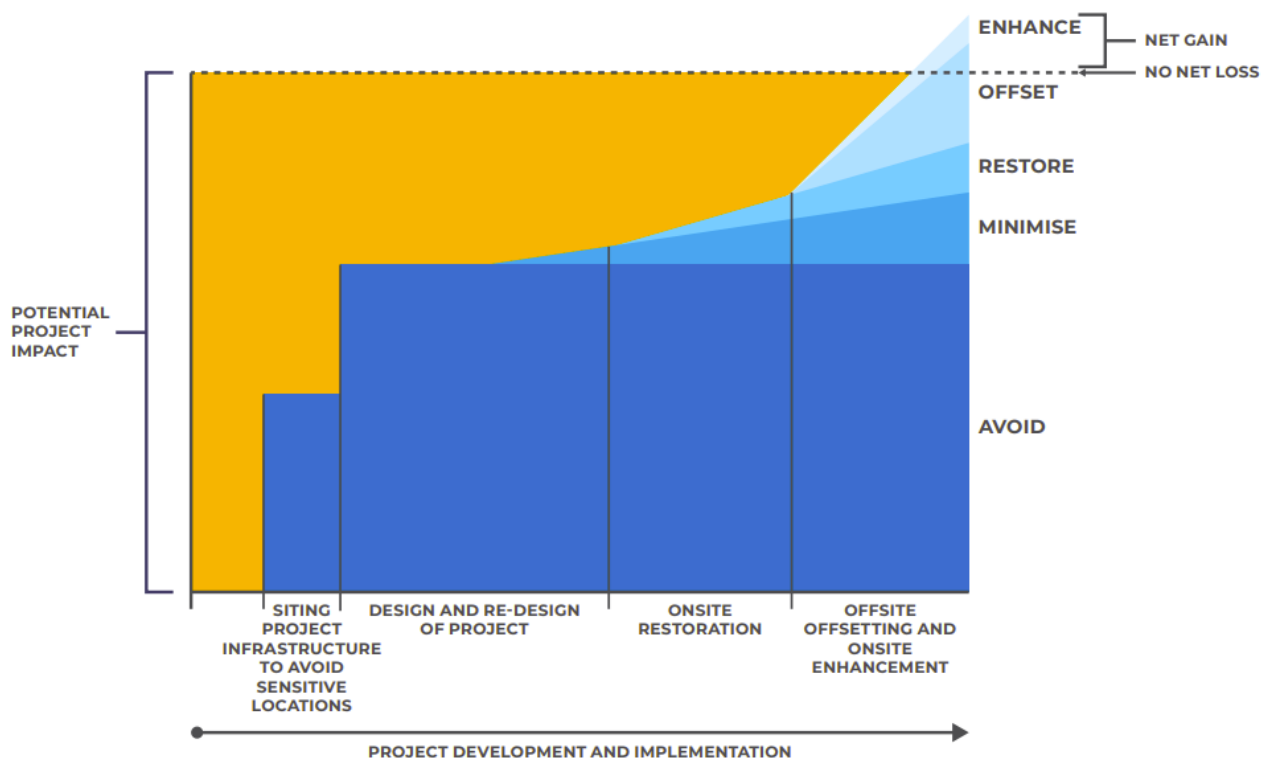


Figure 1.4 - Mitigation hierarchy to follow during project development and implementation. Sources: Bennun et al. (2021).

Despite EIAs remain one of the most important tools for environmental protection in infrastructure and project developments, the ecological connectivity is often overlooked or underestimated (Torres et al., 2022). Many EIAs focused on direct impacts, neglecting the wider consequences of habitat fragmentation, leading to long-term ecological degradation. The inclusion of ecological connectivity in EIAs, and more generally in environmental planning, is therefore essential and critical to protect biodiversity and maintain ecosystem resilience. Planning including connectivity could ensure sustainable development and biological conservation at local and landscape scales.

1.2 THESIS OBJECTIVES

The main aim of my PhD thesis is to explore how ecological connectivity can be effectively incorporated into environmental planning and impact assessment processes. This research aims to propose practical solutions and strategies to promote and enhance connectivity by mitigating or compensating for the negative impacts of human infrastructure.

Specifically, this overarching goal is pursued through three interrelated research objectives:

- To assess the direct and cumulative impacts of planned linear infrastructure on landscape connectivity in two African developing countries, South Sudan and Uganda, where biodiversity is rich and infrastructure development is accelerating.
- To study the relationship between road mortality and habitat connectivity for forest mammals at a regional scale. This includes zoning plan based on different levels of conservation and mitigation priorities, providing a novel approach to minimise impacts and promote species conservation.
- To provide a framework for assessing changes in forest habitat connectivity resulting from the construction of a proposed hydropower project. This framework will also guide the planning of mitigation measures to improve connectivity in affected areas.

These research objectives share common need to address the impacts of human infrastructure on connectivity and to propose solutions that balance development and biodiversity conservation.

1.3 THESIS STRUCTURE

The core of the thesis (Chapters 2-4) is organised around three case studies conducted at different spatial scale (Figure 1.5), two of which (Chapters 2 and 4) were developed during an applied research period in collaboration with Electroconsult S.p.A., an engineering consultancy specializing in Environmental and Social Impact Assessments (ESIAs) for development projects in various developing countries. During this period, I worked on the practical application of scientific principles underpinning the development of ESIAs and management plans. I applied the methods and frameworks developed in my PhD to assess connectivity impacts and propose measures to avoid, minimise or compensate for these impacts in real proposed projects. The three studies address the main objective of my thesis at different spatial scale - landscape, regional and local - and follow the incremental steps of management and mitigation hierarchy.

Specifically, Chapter 2 presents a study conducted at landscape level to evaluate the impacts of planned linear infrastructure on the structural connectivity of the landscape in two biodiversity-rich,

developing countries, South Sudan and Uganda. By comparing the macro-regional ecological networks before and after the implementation of proposed infrastructure, I examined how individual projects and the cumulative effects of multiple infrastructure developments may affect the landscape connectivity. This study provides valuable insights for assessing direct, indirect and cumulative impacts, and can guide future infrastructure development planning by identifying and avoiding critical areas important for connectivity conservation.

Chapter 3, focusing on regional scale, examines the relationship between wildlife-vehicle collisions and habitat connectivity for forest mammals with different movement abilities and across natural and fragmented environments. By introducing two novel concepts in road ecology - *roadkill suitability* and *road crossability* - and studying their relationship, I proposed a road zoning plan with different zones, each characterised by conservation and mitigation priorities: Priority Areas for Barrier Effect Mitigation (PABEM), Potential Areas for Roadkill Mitigation (PARoM) and Potential Areas for Connectivity Preservation (PACoP). The novelty of this study could contribute to support species conservation and road impact mitigation efforts.

In Chapter 4, I develop a framework for explicitly incorporating the impact of a proposed hydropower project on forest habitat connectivity into Environmental Impact Assessments (EIAs). The framework includes an assessment of forest habitat connectivity before and after project implementation, and the prioritisation of potential reforestation areas to improve connectivity as compensatory measure. To demonstrate its practical application, the framework is applied to a proposed reservoir-based hydropower project on the Dudh Koshi River in Nepal, providing a tool for impact assessment and support for compensation measures.

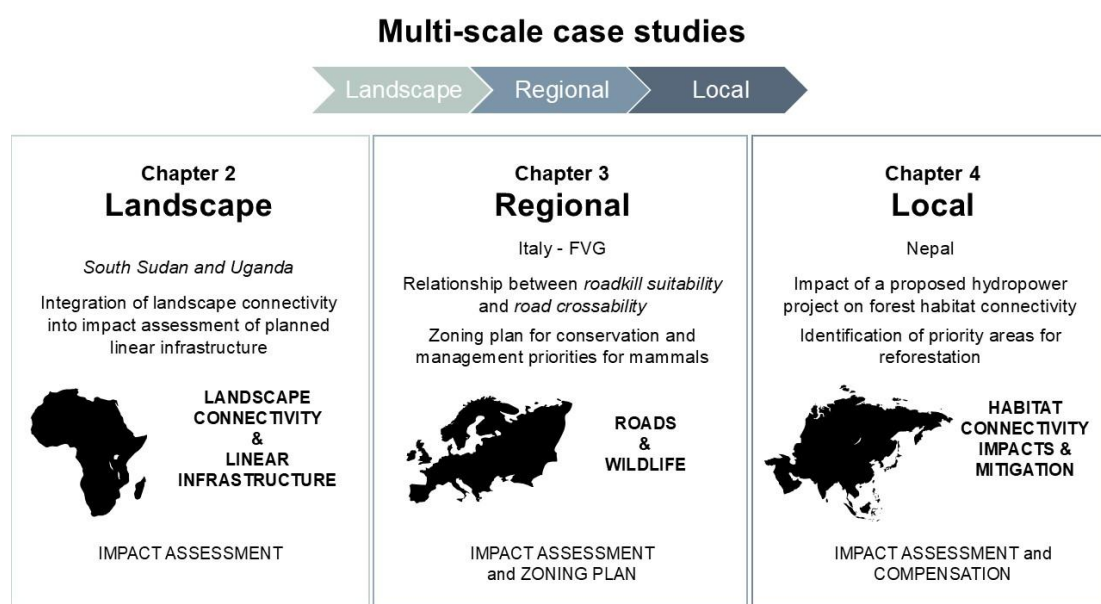


Figure 1.5 - Overview of the thesis chapters highlighting the key case studies and their spatial scales.

CHAPTER 2

ASSESSING THE IMPACT OF LINEAR INFRASTRUCTURE ON LANDSCAPE CONNECTIVITY: A WORKED EXAMPLE FROM SOUTH SUDAN AND UGANDA

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ABSTRACT

Human infrastructure development is a major cause of environmental fragmentation, which threatens biodiversity globally. Fragmentation and its consequences are particularly pronounced in developing countries, where rapid economic growth and infrastructure development often have devastating impacts on biodiversity and ecosystems. Strategies to halt biodiversity loss require the protection of ecological connectivity between areas of high conservation importance, but this is often overlooked in environmental planning and infrastructure impact assessment. In this study, we provided a worked example demonstrating how structural landscape connectivity can be integrated into the impact assessment of new linear infrastructure projects in two developing countries: South Sudan and Uganda. To achieve this aim, we (i) created macro-regional ecological networks under two scenarios, i.e. the present landscape and a future scenario that also includes the planned linear infrastructure, (ii) assessed future changes in landscape connectivity due to their implementation, and (iii) identified which linear infrastructure will pose the greater threat to ecological corridors and will impact the integrity of the ecological network. Specifically, we prioritized conservation areas with high biodiversity, threatened species and minimal human disturbance and identified the corridors connecting them. The impact of the planned linear infrastructure on corridors was assessed by quantifying the changes in connectivity between the two scenarios, both at the landscape level and in proximity of each linear infrastructure. The proposed approach could provide a basis for informing conservationists, policy makers and environmental planners in prioritising actions to maintain and restore ecological connectivity and promoting its inclusion in environmental planning and impact assessments.

KEYWORDS

Circuitscape, developing countries, infrastructure development, least cost path, structural connectivity.

2.1 INTRODUCTION

In an increasingly interconnected world where human activities and infrastructure development continuously reshape landscapes, habitat fragmentation is one of the main threats to biodiversity and ecosystems (Fischer and Lindenmayer, 2007; Vitousek et al., 1997). Human activities have reduced and fragmented habitats into smaller patches, leading to a global loss of biodiversity and the ecosystem functions and services it provides (Western, 2001). The impacts of habitat fragmentation are especially pronounced in developing countries, where the drive for economic growth and rapid infrastructure development often results in devastating effects on habitats and species (Tilman et al., 2017). Worsening the situation, many of these countries have limited resources and lack comprehensive conservation initiatives and regulations (Chandra and Idrisova, 2011). Together, these conditions pose a serious threat to the integrity of fragile and often threatened ecosystems and species. To achieve effective conservation goals, long-term strategies to halt biodiversity loss and avoid habitat fragmentation should include not only the protection of some important areas, but also the connectivity between them (Hilty et al., 2019). Maintaining, restoring and promoting ecological connectivity is therefore essential for sustainable development and responsible use of natural resources (Hilty et al., 2020). Nowadays, however, ecological connectivity remains insufficiently considered in environmental planning and infrastructure development projects (Hilty et al., 2020). For instance, Environmental Impact Assessments (EIAs), the most commonly used tool to evaluate the environmental impacts of proposed projects, often overlook the assessment of loss and changes in ecological connectivity, primarily due to the challenges involved and the lack of clear guidelines, best practices and standards (Torres et al., 2022). Indeed, assessing ecological connectivity, defined as “the unimpeded movement of species and the flow of natural processes that sustain life on Earth” (Convention on Migratory Species (CMS), 2020), is inherently complex. It requires consideration of species movement, genetic and ecological processes across diverse landscapes and at multiple spatial scales, along with a range of biotic and abiotic factors. Several elements determine which aspect of ecological connectivity should be prioritized in a project's impact assessment, including the project itself, the area of interest, species or habitats of conservation concern, and relevant legislation (Ament et al., 2023). For example, Leskova et al. (2022) selected the Florida panther *Puma concolor coryi*, an endangered umbrella species, to assess impacts on habitat connectivity before and after the construction of 45 utility-scale solar energy facilities. Kor et al. (2022) chose a multi-species approach based on legally protected species to estimate impacts on connectivity for the Heathrow Third Runway Expansion Project in England. Botting et al. (2023) evaluated the effects of various types of linear infrastructure on landscape connectivity for red deer *Cervus elaphus* and wild boar *Sus scrofa* in Spain.

Habitat fragmentation from human infrastructure construction can also have landscape-scale effects (Torres et al., 2022). The presence of multiple infrastructure projects within an area can significantly intensify habitat fragmentation, leading to cumulative negative impacts on biodiversity at a larger scale (Dorber et al., 2023). Cumulative impacts of a project referred those impacts that result from the combined effects of the project and other infrastructure or activities, leading to wider degradation. However, these issues are often inadequately addressed in the environmental planning and impact assessment of individual projects, with serious consequences for biodiversity and ecosystems (Harker et al., 2021; Niebuhr et al., 2022). While assessing impacts on connectivity is undeniably complex, global attention to this issues is growing, and numerous efforts are advising our understanding of how to measure and mitigate impacts on ecological connectivity (Ament et al., 2023; Patterson et al., 2022; Torres et al., 2022).

In this context, we present a working example demonstrating how landscape connectivity analysis can inform the design of new linear infrastructure projects. Using pre- and post- intervention assessments, this approach contributes to decision-making aimed at maintaining or enhancing landscape connectivity. Our focus is on the landscape structural connectivity, defined as a measure of landscape permeability based on the characteristics and arrangement of habitats, barriers and other landscape elements considered important for the movement of organisms (Girardet et al., 2013; Hilty et al., 2019). We specifically examine linear infrastructure, such as roads, railways and power lines, which are globally recognised as key drivers of landscape fragmentation, disrupting ecological connectivity (Biasotto and Kindel, 2018; van der Ree et al., 2015). In this study, we selected two African developing countries, South Sudan and Uganda, both known for their rich biodiversity and ongoing plans to expand and develop new linear infrastructure (AfDB 2013, 2022). Especially South Sudan, as the world's newest country, faces particular challenges due to limited information, previous scientific literature and baseline data available - issues that complicate impact assessments, environmental planning and conservation projects in under-studied regions of the world (Christie et al., 2020; Patterson et al., 2022). To address these challenges, we used freely available data, providing a valuable, replicable example for assessing the impact of planned linear infrastructure on landscape connectivity in resource- or data-limited regions. In particular, we (i) created macro-regional ecological networks based on the structural connectivity of the landscape under two scenarios: the present landscape and a simulated future landscape that includes the development of the already planned linear infrastructure, (ii) assessed future changes in landscape connectivity resulting from this development, and (iii) identified which linear infrastructure will have a greater impact on ecological network and corridors.

2.2 MATERIALS AND METHODS

2.2.1 Study area

The study area encompasses South Sudan and Uganda, two neighbouring countries in central and eastern Africa, with a combined area of 876,080 km² (South Sudan: 634,608 km², Uganda: 241,472 km²; Figure 2.1). Despite their geographical proximity, South Sudan and Uganda exhibit distinct socio-cultural, historical and infrastructural development pathways, each of which has significantly shaped their respective landscapes. As developing countries, both countries have an urgent need for infrastructure development to support economic growth and social progress (AfDB 2013, 2022). South Sudan, the world's youngest nation, gained independence from Sudan in 2011 after decades of civil war. The country continues to face significant challenges, including political instability, ethnic tensions and ongoing conflict, which have hindered both infrastructure development and environmental protection efforts. In contrast, Uganda has a more developed infrastructure than South Sudan, with a growing economy driven by agriculture, tourism and recently discovered oil reserves (FAO, 2014). Uganda has also made progress in environmental protection, including the establishment of a network of protected areas (Howard et al., 2000).

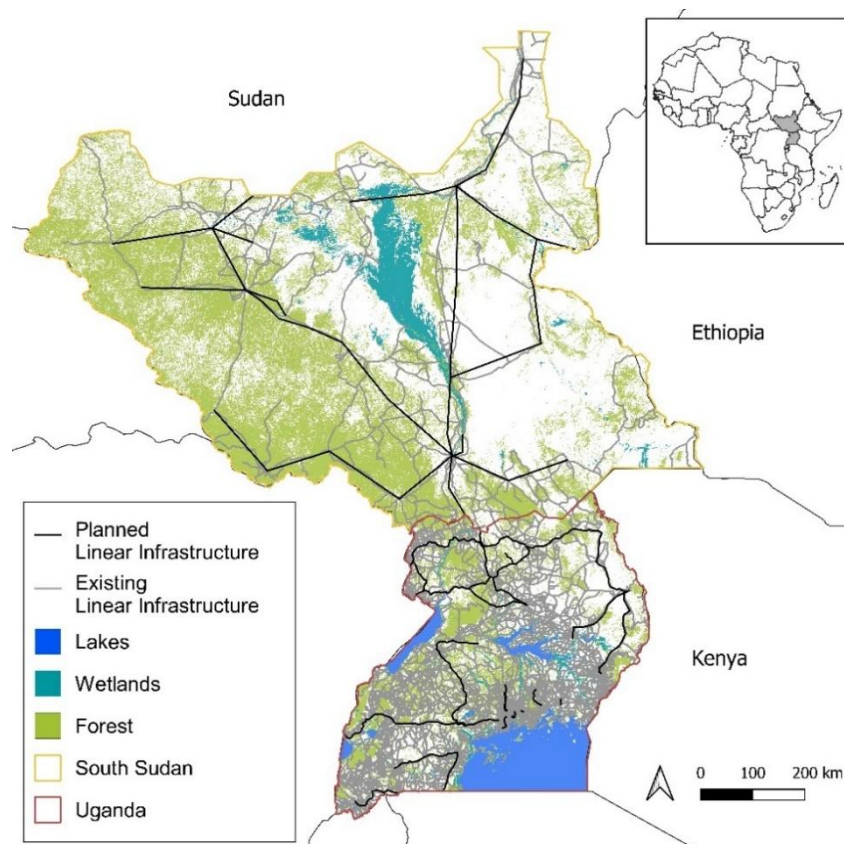


Figure 2.1 - Study area location and distribution of existing and planned linear infrastructure, such as roads, power lines and railways. Lakes, wetlands and forests were derived from Copernicus landcover 2019 (Buchhorn et al., 2020).

The average population density in South Sudan is 16.93 inhabitants/km², while Uganda's is 189.93 inhabitants/km². South Sudan has a high level of biodiversity, with forests covering about one-third of its total area, shrublands about 39% and herbaceous vegetation about 22% (FAO, 2015). Uganda is characterised by 59% agricultural land, 17.3% inland water, 10.9% swamps and 12% forests, with the remaining land mostly covered by grasslands (FAO, 2014). South Sudan has a road network estimated to be around 16,882 km in total length, but only few roads are paved; it has also a limited railway network along its border with Sudan. Uganda's linear infrastructure includes over 37,579 km of roads and a limited railway network. South Sudan has a sub-humid climate with average temperatures above 25 °C, peaking at over 35 °C in the dry season (FAO, 2015), while Uganda has an equatorial climate with average annual temperatures ranging from 18 °C to 35 °C (FAO, 2014).

2.2.2 Methodological workflow

This study was conducted in a series of sequential steps according to the workflow presented in Figure 2.2, integrating freely available global databases (World Bank Group 2017, 2018; CIESIN 2018; Buchhorn et al. 2020; NASA 2021; IUCN 2023; IUCN and UNEP-WCMC 2024, www.openstreetmap.org) and using QGIS v3.28.4, R v4.3.1 (R Core Team, 2023) with *terra* packages (Hijmans et al., 2022) and ArcGIS Pro v3.2.0 with the Linkage Mapper program (McRae and Kavanagh, 2011). In the following, we described in detail the three-step methodological workflow for assessing the impact of planned linear infrastructure development on structural landscape connectivity. In Step 1, input data on human disturbance, land cover, topography and conservation were used to calculate a modified Continuum Suitability Index (CSI, Favilli et al. 2023), allowing us to create resistance surfaces and identify priority conservation areas. In Step 2, structural connectivity models were developed for both present and future scenarios. Finally, in Step 3, we quantified the impact of the planned linear infrastructure at both landscape and local scales.

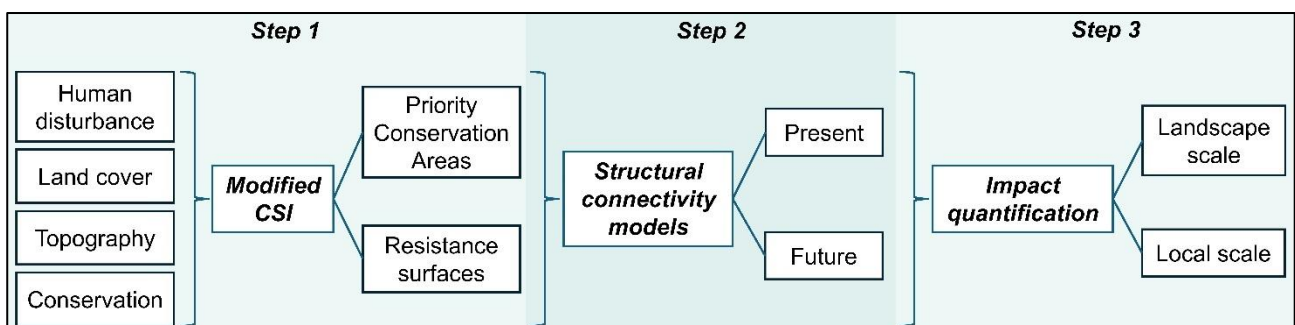


Figure 2.2 - Three-step workflow for assessing the impact of linear infrastructure on landscape connectivity. CSI: Continuum Suitability Index.

2.2.3 Step 1: Definition of resistance surfaces and priority conservation areas

Landscape resistance describes the degree to which an organism is willing, physically able or successful in moving across the landscape (Zeller et al., 2012) and underlies most ecological connectivity models (Dutta et al., 2022). This concept is typically represented as a resistance surface, where a resistance value is assigned to each element of the landscape (Dutta et al., 2022). In our study, we used the framework proposed by Favilli et al. (2023) to first generate the landscape permeability map, which was then converted into a resistance surface for developing the macro-regional ecological network. According to Favilli et al. (2023) and Laner et al. (2024), landscape permeability is quantified using the Continuum Suitability Index (CSI), calculated based on human disturbance, biotic and physical factors (Affolter et al., 2011; Favilli et al., 2023; Haller, 2016). In our adaptation of the CSI, we included additional variables tailored to our study area and specific objectives. In particular, we introduced a species conservation variable (CONS) to account for species distribution and prioritise areas with species of conservation concern. In addition, differently from Favilli et al. (2023), we replaced the fragmentation variable (FRA) with linear infrastructure variable (LI) to emphasise the impact of linear infrastructure projects, which are central to this study. We integrated spatially explicit data derived from global open-access datasets, encompassing information on species spatial distribution and conservation status, protected areas, land cover, topography, human population, and linear infrastructure density to obtain the modified CSI. This index was calculated as follows:

$$\text{ModifiedCSI} = \frac{\text{CONS} + 2 * \text{LAN} + \text{ENV} + \text{TOP} + \text{LI} + 2 * \text{POP}}{8}$$

where,

- *Species conservation (CONS)* represents the distribution of various species, weighted by their conservation status (Ascensão et al., 2022). It is calculated by integrating information on threatened species with total species richness. Areas that contain a high number of threatened species alongside high species richness contribute positively to ecosystem integrity. Data for this variable were retrieved from the IUCN Red List of Threatened Species (Appendix 2.I; IUCN 2023; <https://www.iucnredlist.org/>).
- *Land cover (LAN)* represents landscape permeability based on different land cover types. The land cover map was obtained from the Copernicus Global Land Service (Buchhorn et al., 2020). The landscape permeability values were assigned to each land cover classes according to the habitat suitability for each threatened species in the study area, as retrieved from IUCN spatial data.

Higher permeability values are assigned to land cover classes which are suitable for the higher the number of species (Appendix 2.I).

- *Environmental protection (ENV)* defines the level of environmental protection (Favilli et al., 2023). Data on the location and level of protection of protected areas were obtained from the World Database on Protected Areas (IUCN and UNEP-WCMC, 2024). Permeability values were assigned to protected areas based on their IUCN management category and strategy (Appendix 2.I).
- *Topography (TOP)* represents the elevation and slope of the study area. As elevation and slope increase, it is generally assumed that movement decrease, resulting in lower landscape permeability (Appendix 2.I). Elevation and slope were calculated using the Digital Elevation Model distributed by NASA (NASADEM; NASA 2021).
- *Linear infrastructure (LI)* refers to the density of linear infrastructure – such as roads, railways and power lines - that prevents or hampers movement in a given area (Ascensão et al., 2022). Higher linear infrastructure density corresponds to lower permeability (Appendix 2.I). Spatial data for roads and railways were obtained from Open Street Map (www.openstreetmap.org), while existing and planned transmission lines were obtained from Energydata.info (World Bank Group, 2018, 2017). Data on planned roads and railways were not available.
- *Human population (POP)* represents human disturbance in and around settlements, with higher human pressure reducing landscape permeability. We combined population density from NASA (CIESIN 2018) with kernel density estimates of buildings obtained from Open Street Map (www.openstreetmap.org) to assess human pressure (Appendix 2.I).

All these variables were calculated at a spatial resolution of 1 km by assigning a permeability value (see Appendix 2.I for more information) that range from 0 (minimum permeability) to 10 (maximum permeability). This method produced a map using the modified CSI that represented the landscape permeability of our study area, with higher CSI values representing higher permeability. We then calculated the resistance surface by converting the modified CSI values into resistance values, where the minimum resistance (1) corresponded to the maximum permeability (i.e. the highest modified CSI value), and the maximum resistance (100) corresponded to the lowest permeability (i.e. lowest modified CSI value) (Appendix 2.I Table S2.I.10; Bowman et al. 2020; Favilli et al. 2023). Consequently, we identified priority conservation areas defined as those with a modified CSI ≥ 8 , indicating higher permeability.

To assess the impact of new linear infrastructure on landscape connectivity, we calculated the modified CSI, the resistance surface, and the corresponding priority conservation areas in the two scenarios: (i) the present landscape, which includes only the existing linear infrastructure, and (ii) the

future landscape, which also considers all planned linear infrastructure. Specifically, the modified CSI in the future scenario was derived by adjusting the LI indicator to account for both the new and the existing infrastructure.

2.2.4 Step 2: Structural connectivity modelling

Following Favilli et al. (2023), we used the priority conservation areas as cores (or nodes; Hilty et al. 2019) to model the ecological network, restricting the selection to those with an area $\geq 10 \text{ km}^2$ due to time and computational constraints. Corridors identification was carried out using the Linkage Mapper program (McRae and Kavanagh, 2011) in ArcGIS Pro v3.2.0, integrating both the Least-Cost Path (LCP) and circuit theory approaches. We used the Linkage Pathways Tool to identify the LCPs, which represent the single path associated with the minimum cost-weighted distance between two core areas (Adriaensen et al., 2003), and to calculate the width of the corridors, defined as the deviation from the LCP in terms of cost-weighted distance. The Linkage Pathways tool was configured with a maximum Euclidean corridor distance of 250 km, a bounding circle buffer distance of 60 km, and a truncated cost-weighted distance threshold (corridors width) of 100 km. Then, we used the Centrality Mapper (McRae, 2012a) and Pinchpoint Mapper (McRae, 2012b) tools in ArcGIS Pro, which rely on Circuitscape software (McRae et al., 2013), to calculate the current density and flow centrality, as well as to identify pinch points within the network, setting the cost-weighted distance cut-off at 100 km. These tools consider the least-cost corridors as a surface, where current density between priority conservation areas depends on the resistance of each cell within the least-cost corridor (Dutta et al., 2016). This analysis enabled us to prioritise corridors based on their importance in maintaining overall landscape connectivity (centrality) and to identify corridors that act as movement bottlenecks (pinch points), where their loss could excessively affect overall connectivity. In our study, all areas with current densities above the 95th quantile were identified as 'pinch points', while the centrality of each corridor was classified as high, medium and low based on its tercile. This process was repeated for the present and future scenarios, considering the differing resistance surfaces and priority conservation areas.

2.2.5 Step 3: Impact quantification

The impact assessment of planned linear infrastructure on landscape connectivity was estimated at both broader, i.e. on the entire ecological network, and finer scales, i.e. considering a 5 km radius buffer around each proposed linear infrastructure, as in Leskova et al. (2022). For this assessment, we compared the present and future ecological networks based on the following criteria: (i) the variation in the number and size of core areas (i.e. priority conservation areas); (ii) the number and

length of LCPs; (iii) the relative change in current density, calculated by subtracting present current density from the future current density, giving positive values if current density increases and negative values if it decreases (Leskova et al., 2022), and (iv) the change in LCPs centrality and the extent of pinch points.

2.3 RESULTS

2.3.1 Macro-regional ecological networks in the present and future scenarios

The two countries exhibit notably differences in existing infrastructure development and human pressure, which is reflected in the resistance surfaces; Uganda shows higher resistance values than in South Sudan (Appendix 2.II and Figure S2.II.1). When comparing the present and future resistance surfaces, marked differences are observed along the planned linear infrastructures (Appendix 2.II Figure S2.II.2 and S2.II.3). Areas with a high number of species of conservation concern are predominantly located in the northern and eastern regions of South Sudan and the southern and western regions of Uganda (Appendix 2.II Figure S2.II.4). The permeability values associated with land cover and human pressure indicators are lower in Uganda, which is more densely populated and cultivated than South Sudan (Appendix 2.II Figure S2.II.5 and S2.II.6). Although the number of protected areas is higher in Uganda, their relative extent is greater in South Sudan (Appendix 2.II Figure S2.II.7). The topography indicator shows no clear difference between the two countries, as permeability values is generally very high (Appendix 2.II Figure S2.II.8).

In the present scenario, there are 232 priority conservation areas (186 in South Sudan and 46 in Uganda), which increase to 241 (193 in South Sudan and 48 in Uganda) in the future scenario. The total area of these priority conservation areas is 114,647 km² (106,202 km² in South Sudan and 8,445 km² in Uganda) in the present scenario, and 114,218 km² (105,816 km² in South Sudan and 8,402 km² in Uganda) in the future scenario (Appendix 2.II Table S2.II.1). Among the 232 priority conservation areas identified in the present scenario, 25 are impacted by the planned linear infrastructure (Appendix 2.II Table S2.II.1), resulting in the complete loss of one protected area, fragmentation into smaller, more isolated areas, and a total loss of 429 km² of priority conservation areas (Appendix 2.II Table S2.II.1). In Uganda, 88.4% of priority conservation areas are already located within protected zones, whereas only 45.3% of those in South Sudan fall within protected areas.

The connectivity models identify 495 and 515 LCPs with a total length of 18,962 km and 19,421 km in the present and future scenarios, respectively (Appendix 2.II Fig. S2.II.9). Changes in current density were observed both along each planned linear infrastructure and within the ecological

network. Overall, current density increased in the future scenarios due to the presence of new corridors connecting newly designed priority conservation areas and the adjustment of current density to find alternative routes around the planned linear infrastructure (Figure 2.3). However, in some areas, we noted a 100% decrease in current density, resulting in the disappearance of some corridors in the future scenario (Figure 2.3).

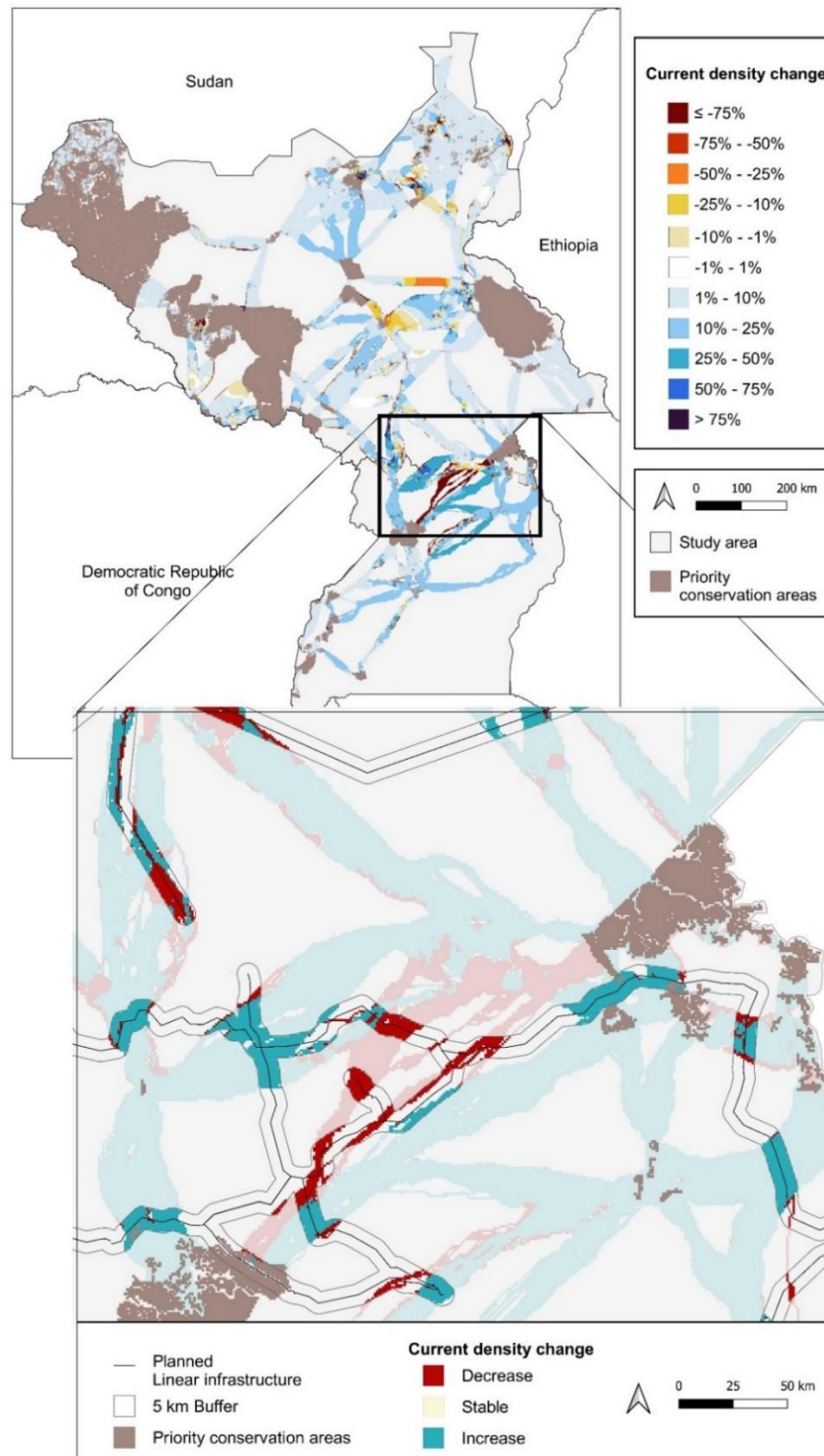


Figure 2.3 - Location of priority conservation areas and amount of change in percentage of current density between present and future scenarios, with a zoom in on the area where corridors were most impacted.

2.3.2 Local impacts of planned linear infrastructure

In both countries, 54 transmission lines are planned, with voltage ranging from 132 to 400 kV (Figure 2.4, Appendix 2.II Figure S2.II.10, S2.II.11 and Table S2.II.2). Of these, 34 transmission lines intersect ecological corridors, 14 in South Sudan and 20 in Uganda (Figure 2.4 and Appendix 2.II Table S2.II.2). When assessing the local impact within a 5 km buffer from the Right of Way, we observed the complete loss of LCPs in 3 planned linear infrastructures (ID3, 18 and 26). In addition, the number of LCPs decreased in two planned linear infrastructures (ID11 and 31) and remained unchanged for 17 planned linear infrastructures (Figure 2.4 and Appendix 2.II Table S2.II.2). The increase in priority conservation areas (i.e. cores of our ecological network) in the future scenario led to an increase in the number of LCPs around the planned linear infrastructure (Appendix 2.II Table S2.II.2). We found that within the 5 km buffer, current density decreased around 11 planned linear infrastructures in the future scenario, with the largest declines (100-97%) observed for IDs 3, 18 and 26 (Appendix 2.II Table S2.II.2).

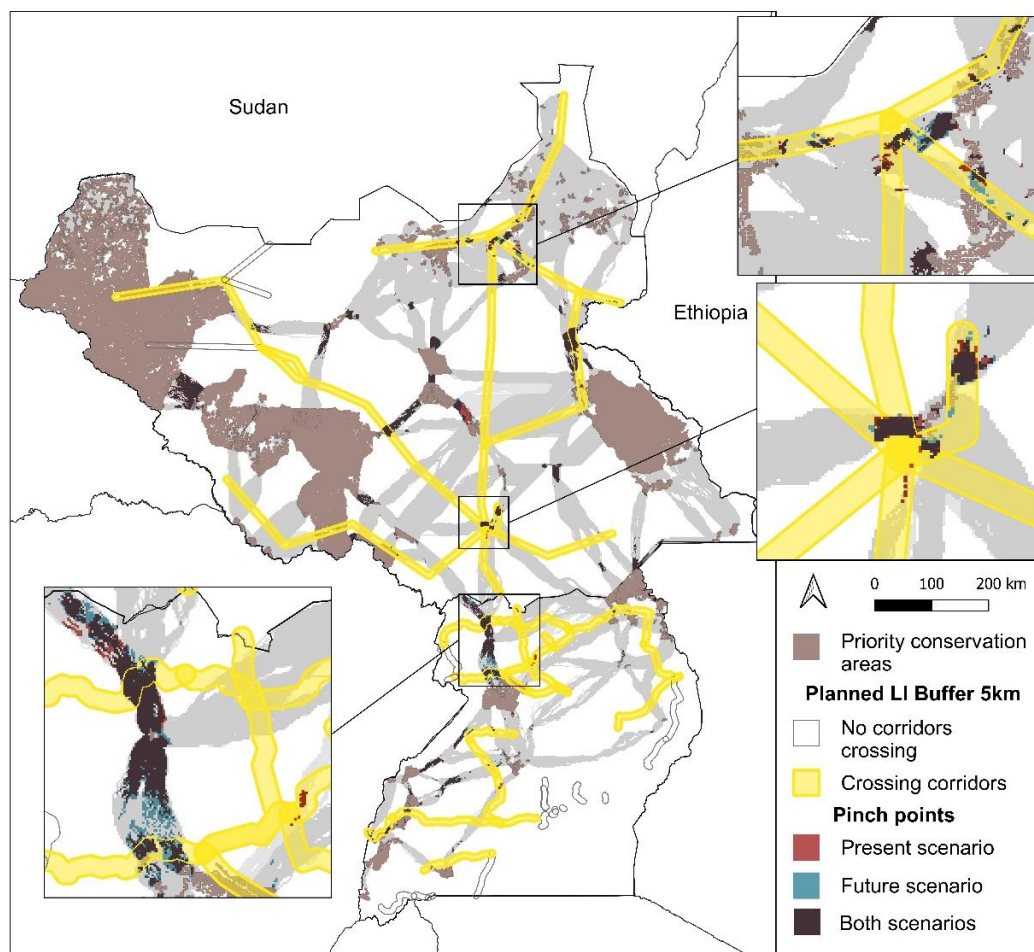


Figure 2.4 - The map highlights the planned linear infrastructure (LI) that will directly cross corridors and priority conservation areas and the locations and extent of pinch points in the present and future scenarios.

Interestingly, in most buffers around planned linear infrastructure - excluding those where corridors were completely lost - the extent of pinch points increased from the present to the future scenario (Figure 2.4 and Appendix 2.II Table S2.II.2). In contrast, no relevant changes were observed in the centrality of corridors around the planned linear infrastructure. In total, we identified eight corridors with decreased centrality (planned linear infrastructure ID 43, 44, 47 and 48, all in South Sudan) and five corridors with increased centrality (planned linear infrastructure ID 11, 29, 44 and 48) (Appendix 2.II Table S2.II.3).

2.4 DISCUSSION

In our study, we assessed both direct and cumulative impacts of linear infrastructure on landscape connectivity, providing insights to support environmental planning, impact assessment and conservation strategies. Specifically, we quantified impacts at the scale of individual planned linear infrastructure projects and across the entire ecological network. By comparing ecological networks in present and future scenarios, we observed that landscape connectivity would be altered along 34 of the 54 planned transmission lines. Additionally, we identified critical zones where connectivity could be substantially reduced due to the cumulative effects of multiple linear infrastructure projects.

2.4.1 Macro-regional ecological networks design

We developed the ecological network by integrating multiple factors known to affect landscape permeability and organism movements, including land cover (Pither et al., 2023), human population (Correa Ayram et al., 2017), linear infrastructure density and distribution (Ament et al., 2023; Ascensão et al., 2022), protected areas (Saura et al., 2018) and species distribution ranges (Ascensão et al., 2022). By adapting the CSI methodology, a robust tool for assessing landscape permeability, our study provides a nuanced view of structural connectivity at macro-regional scale (Laner et al., 2024). While CSI approach has been widely adopted in conservation projects across Europe (Favilli et al., 2023; Haller, 2016; Plassmann et al., 2019), this study represents the first application of the method outside Europe and within developing countries to assess the impacts of new infrastructures on ecological network. Following the workflow of Favilli et al. (2023) to develop the macro-regional ecological network, we slightly modified specific variables within the CSI calculation to better align with our study objectives and regional context. Given our focus on the impacts of linear infrastructure, we included the LI variable, representing the density and spatial distribution of linear infrastructure. This addition is fundamental to emphasise the role of linear infrastructure in our analysis and aligns with previous studies examining infrastructure impacts on ecological connectivity (Ascensão et al., 2022; Grilo et al., 2021; Medrano-Vizcaíno et al., 2023). We also included the CONS variable, which

summarises data on species distribution and conservation status. This inclusion was essential for refining the landscape permeability index by highlighting critical areas that support a high number of species of conservation concern. When combined with the ENV variable, i.e. the distribution of protected areas, the CONS variable enables a comprehensive, conservation-oriented characterisation of the landscape. This approach is consistent with previous research on infrastructure impacts, such as the study by Ascensão et al. (2022), which highlights the relevance of such variable in identifying conservation and management priorities. All data used in this study were obtained from open-access databases, enhancing the reproducibility of our research and supporting its application in understudied regions (Rocchini and Neteler, 2012). These open sources provided critical landscape level data, contributing to filling the knowledge gaps in these regions. However, the quality and detail of data from these open-access sources may limit our findings. For instance, although we successfully acquired information on planned transmission lines in both countries, data on other linear infrastructures, such as planned roads and railways, were unavailable. This lack of comprehensive data highlights a significant source of uncertainty for environmental planning and impact assessment, emphasising the need for accessible and verifiable regional or national databases (Hodgson et al., 2019; Leblanc-Rochette, 2023).

In implementing the ecological network, we used a structural connectivity approach, which is generally considered easier to assess than functional connectivity (Taylor et al., 2006). The structural connectivity of the landscape provided a clear, easily interpretable measure of how different priority conservation areas are structurally connected across the landscape. However, it did not fully capture the effectiveness of these connections in supporting the movement of genes, gametes, propagules or individuals movement, which are key elements of functional connectivity (Hilty et al., 2020; Rudnick et al., 2012; Tischendorf and Fahrig, 2000). It is important to acknowledge that our analysis does not determine whether the identified, impacted and new corridors potentially created by planned infrastructure development are functionally connected. This consideration is crucial when interpreting our findings, as they offer a landscape-level assessment of potential changes in structural connectivity due to infrastructure, rather than a conclusive assessment of functional connectivity impacts.

2.4.2 Impacts on landscape connectivity

Our research focuses on the potential impacts of planned linear infrastructure projects on landscape connectivity in two African developing countries, Uganda and South Sudan, which differ in socio-economic statuses and environmental protection regimes. These distinctions are reflected in their landscape configurations, especially in landscape permeability. Uganda, with higher infrastructure

density and human population, shows smaller and fewer priority conservation areas compared to South Sudan, where such areas are more extensive and numerous.

Priority conservation areas are generally within nationally and internationally recognized protected areas (IUCN and UNEP-WCMC, 2024), with some differences among the two countries. In Uganda, priority conservation areas aligned more closely with existing protected areas, indicating effective management within these areas but higher disturbance outside them. This contrast implies that South Sudan may face more fragmentation and isolation of priority areas with future infrastructure development. Additionally, we observed substantial changes in the configuration and characteristics of corridors between present and future scenarios, indicating that the implementation of the planned infrastructure will impact the entire macro-regional ecological network. Although new infrastructure can impede movement (Beyer et al., 2016), we observed an increase in the number and length of LCPs and in current density, consistent with findings from similar studies on infrastructure impacts (Fullman et al., 2021; Leskova et al., 2022). However, this increase should not be interpreted as an improvement; rather, it results from the higher number of priority conservation areas in the future scenario and the need to adjust current density to find alternative routes around the new infrastructures. Indeed, priority conservation areas identified in the present scenario are likely to become more fragmented in future, increasing from 232 to 241 areas, and requiring a higher number of corridors will be needed to connect them. Furthermore, the planned linear infrastructure will lead to higher current density within corridors close to those that expected be lost.

Our analyses identified regions where corridors are most susceptible to be impacted by the construction of planned linear infrastructure (Figure 2.2). The most affected area is in northern Uganda, along the South Sudan border, where infrastructure construction could disrupt landscape connectivity between Kidepo Valley and Murchison Falls National Parks in Uganda and Kidepo Game Reserve and Imatong Forest Reserve in South Sudan. These protected areas are important global biodiversity hotspots, hosting unique and threatened species and ecosystems (Mittermeier et al., 2011). Among them, Kidepo Valley, Kidepo Game Reserve, and Imatong Forest Reserve are part of transboundary conservation areas recognized by international institutions such as the IUCN (IUCN ESARO, 2020). Historical records report animal movement, such as elephants, between these reserves (Ross et al., 1976), although ongoing armed conflict in the region poses significant challenges for conservation efforts (Aleper and Moe, 2006). Our findings suggest that the loss of corridors in this region, exacerbated multiple linear infrastructure projects (ID 3, 8, 11, 18 and 26; Figure S2.II.11), could have serious implication for landscape connectivity. Therefore, we emphasise that careful consideration of the cumulative impacts of multiple infrastructures projects is both urgent and critical when assessing the environmental impacts of new infrastructure (Dorber et al., 2023).

Despite this urgency, inadequate assessment of cumulative impacts remains a systemic problem in environmental impact assessment. When cumulative impacts are evaluated, they often focus on the project-specific scale (Blakley and Franks, 2021; Patterson et al., 2022), making it challenging to identify broader effects, including impacts on transboundary corridors, as our study demonstrates.

In examining the local impact of each infrastructure, we found that the higher infrastructure density in Uganda is likely to lead to a more pronounced reduction in structural connectivity than in South Sudan (Appendix 2.II Table S2.II.2). This difference is likely due to Uganda's inherently lower landscape permeability, which results in narrower corridors. Conversely, South Sudan's generally higher landscape permeability allows for wider corridors and alternative areas for connectivity with minimal resistance. However, the future scenario indicates notably changes in corridors widths, especially in pinch points areas (i.e., movement bottlenecks). The infrastructures causing corridor losses also led to the loss of pinch points (IDs 3, 11, 18 and 38), while pinch points near other infrastructures expanded, increasing the concentration of critical areas within corridors and their vulnerability (Beier, 2019; Clevenger, 2012; McClure et al., 2017). As discussed above, the locations of planned infrastructure appear to be biased towards areas that are important for connectivity and animal movement, and the results of this research suggest that landscape connectivity is not being adequately considered in the placement of proposed infrastructure, particularly in transboundary areas, which could have negative consequences for biodiversity. For instance, the infrastructures IDs 44 and 45 (Appendix 2.II Figure S2.II.10) are located in eastern South Sudan near the Ethiopian border, overlapping an area known for hosting the world's largest land mammal migration (African Parks, 2024).

2.5 CONCLUSION

In this study, we demonstrated how the structural landscape connectivity can be effectively integrated into environmental planning and impact assessments for linear infrastructure projects. Our approach provides an initial evaluation of potential impacts and could serve as a useful tool for conservationists, policymakers, and environmental planners in prioritising actions to maintain and restore landscape connectivity. This example offers a decision-support system for planning and guiding mitigation measures for the impacts of new infrastructure. However, a comprehensive understanding of these impacts requires validation through field data, such as animal movement studies, which would increase the robustness of our findings and better guide conservation efforts.

With this study we provide insights that could address gaps in current environmental planning and impact assessments. Specifically, this study enables the identification of potential modifications to priority conservation areas, highlighting how these might be impacted by infrastructure growth.

Additionally, it allows for the detailed detection of changes within landscape connectivity, considering also the cumulative effects of multiple planned linear infrastructures.

The relevance of this approach is particularly pronounced in developing countries, where ongoing infrastructure development is encroaching upon previously intact landscapes and regions of high biodiversity. Particularly in under-studied regions, future research should extend this initial assessment and incorporate additional data to refine and support mitigation strategies for new infrastructure projects. Integrating ecological connectivity considerations into infrastructure planning and decision-making processes is essential to promote environmentally sustainable development and connectivity conservation (Hilty et al., 2020; Tilman et al., 2017).

APPENDIX 2.I - METHODS

Indicators used to calculate the modified CSI:

- *Species conservation (CONS):*

The distribution range and IUCN category of species including mammals, birds, herptiles, arthropods and vascular plants in our study area were obtained from the IUCN Red List of Threatened Species (IUCN, 2023). These spatial data are generally provided in the form of a distribution map, which aims to represent the known and possible presence and historical distribution of a taxon within its native and introduced range. A weight from 1 to 10 was assigned to each species distribution range according to its IUCN category: 10 for Critically Endangered (CR), 8 for Endangered (EN), 6 for Vulnerable (VU), 4 for Near Threatened (NT) and 1 for Least Concern (LC). After weighting, the distribution areas of each taxon were converted into a raster format with a resolution of 1 x 1 km. This conversion was done by summing the weights of the species present in each cell, thereby assigning conservation values. We created two layers (raster) by separately summing (i) one including all species (TOTsp) and (ii) one considering only threatened species (THRsp), i.e. VU, EN and CR. Both obtained layers were reclassified by assigning permeability values as shown in Table S2.I.1 and Table S2.I.2.

Table S2.I.1 - Scheme for the conversion of the conservation values to the permeability values for the layer including all species (TOTsp).

Conservation values	Permeability value
0 - 0	0
513 - 671	6
672 - 740	7
741 - 809	8
810 - 1001	9
1002 - 1600	10

Table S2.I.2 - Scheme for the conversion of the conservation values to the permeability values for the layer including only threatened species (THRsp).

Conservation values	Permeability value
0 - 0	0
27 - 112	6
113 - 128	7
129 - 150	8
151 - 168	9

Conservation values	Permeability value
169 - 320	10

The final permeability values for the conservation indicator were calculated as the weighted average of the two layers, TOTsp and THRsp, with the highest weight given to threatened species according to the following formula:

$$CONS = 0.75 * THR_{sp} + 0.25 * TOT_{sp}$$

- *Land cover (LAN):*

Defines the permeability of the landscape according to land cover classes. Land cover data were obtained from the Copernicus Global Land Service at a resolution of 100x100 m (Buchhorn et al., 2020). Landscape permeability values were assigned to land cover classes based on the habitat suitability of each threatened species considered to be present in the study area according to the IUCN spatial data. Habitat suitability information for each species was collected from the IUCN Red List. First, for each species, a value of 1 (suitable) or 0 (not suitable) was assigned to each land cover class. The suitability values were summed to give the total number of species for which each land cover class was suitable. Secondly, the total suitability values were divided by the total number of species and then multiplied by 10 to obtain the permeability values. This step ensured that the resulting permeability values were scaled proportionally to the suitability of each land cover type relative to the total number of species. Third, the permeability values were further adjusted to a range of 0 to 10 by assigning the highest permeability value (10) to the most suitable land cover class (forest) (Table S2.I.3).

Table S2.I.3 - Scheme for the classification of the land cover classes to the permeability values.

Land cover class	Permeability value
Forest	10
Herbaceous wetland	6.08
Herbaceous vegetation	6.23
Shrubs	5.79
Bare/sparse vegetation	2.75
Urban/Built up	0.58
Permanent water bodies	0.29
Snow and ice	0
Cultivate and managed vegetation/agriculture (cropland)	3.33

- *Environmental protection (ENV):*

Defines the degree of environmental protection. Spatial data on protected areas were obtained from the World Database on Protected Areas (IUCN and UNEP-WCMC, 2024). Permeability values were assigned to protected areas according to their IUCN management category as shown in Table S2.I.4. The entire surface of the study area outside protected areas has a permeability value of 0. In areas with multiple levels of protection, the highest indicator value was used.

Table S2.I.4 - Scheme for the classification of the protected areas to the permeability values.

Protected areas	Permeability value
National Park	10
World Heritage Site	10
UNESCO-MAP Biosphere Reserve	10
Ramsar Site	7
Wildlife Reserve	7
Wildlife Sanctuary	5
Community Wildlife Management Area	5
Forest Reserve	5
Game Reserve	5
No protection	0

There are some exceptions to this general pattern of classification:

- The Sudd wetland in South Sudan is one of the largest freshwater ecosystems in the world and its area partially overlaps with other protected areas, so it was given a weight of 8.
- The Otze Forest Wildlife Sanctuary in Uganda was given a weight of 6 as it falls under IUCN Management Category IV.
- The Lomunga Wildlife Reserve in Uganda was given a weight of 5 as it falls into IUCN Management Category VI.

- *Topography (TOP):*

Describes the permeability of the landscape based on the elevation and slope of the study area. As elevation and slope increase, general movement is assumed to decrease. The elevation grid was obtained from NASADEM (NASA 2021) using the OpenTopography DEM Downloader plugin for QGIS with a resolution of 30 x 30 m. Slope was calculated using QGIS *Raster Analysis* and both elevation and slope rasters were reclassified according to the classification scheme in Table S2.I.5 and Table S2.I.6. The final TOP indicator was calculated as the average of elevation and slope.

Table S2.I.5 - Scheme for the classification of the elevation range to the permeability values.

Elevation range (m a.s.l.)	Permeability value
0 - 1500	10
1500 - 1675	9
1675 - 1850	8
1850 - 2025	7
2025 - 2200	6
2200 - 2375	5
2375 - 2550	4
2550 - 2725	3
2725 - 2900	2
> 2900	1

Table S2.I.6 - Scheme for the classification of the slope range to the permeability values.

Slope range (°)	Permeability value
0 - 30	10
30 - 40	7
40 - 45	5
45 - 90	3

- *Linear infrastructure density (LI):*

Quantifies the disturbance caused by the presence of linear infrastructure in a given area that prevents or hampers movement. The linear infrastructures considered are roads, railways and power lines. Spatial data for roads and railways were obtained from Open Street Map (OSM; www.openstreetmap.org) through the Geofabrik download service, while spatial data for existing and planned power lines were obtained from Energydata.info (World Bank Group, 2018, 2017). Despite the availability of spatial information for power lines below 132 kW in Uganda, we only considered those above 132 kW. This choice was due to the lack of information on power lines below 132 kW in South Sudan. Information on planned roads was not available. Roads were classified based on documentation available on OpenStreetMap Wiki (<https://wiki.openstreetmap.org/>). Only roads of medium and major importance were considered and reclassified as follows: primary roads (including motorways, trunk, and primary roads *s.s.*), secondary roads, and tertiary roads. The density of linear infrastructure was calculated and rasterised at a resolution of 1x1 km. The raster was then reclassified according to the permeability values shown in Table S2.I.7. In particular, areas with high landscape

permeability were defined as those where the density of linear infrastructure was either absent or extremely low (0.0001 km²). Conversely, as linear infrastructure density increases, permeability values were assigned progressively lower scores to reflect the growing impact of fragmentation and movement barriers. Intermediate values of permeability were excluded to provide a clearer distinction between areas without linear infrastructure and those with such structures. This approach was intended to emphasise the stark contrast between highly permeable landscapes, where movement is largely unhindered, and highly resistant landscapes, where infrastructure significantly disrupts connectivity.

Table S2.I.7 - Scheme for the classification of the linear infrastructure density to the permeability values.

Linear infrastructure density	Permeability value
0 - 0.0001	10
0.0001 - 0.0005	3
0.0005 - 0.001	2
0.001 - 1	1

- *Human population (POP):*

Describes human pressure in and around settlements, with higher human populations reducing landscape permeability. The population density grid was obtained from NASA (Center for International Earth Science Information Network - CIESIN - Columbia University, 2018) at 30 arc-second resolution (~ 1 km), and resampled to 1x1 km resolution. Population densities were reclassified as shown in Table S2.I.8. In addition, to obtain a more detailed distribution of human population, buildings spatial data was used as a proxy for human population, i.e. more buildings indicate more inhabitants. The location of buildings was obtained from Open Street Map (www.openstreetmap.org) via the Geofabrik downloads service as a point layer, and the kernel density estimation (Worton, 1989) was calculated to take into account that the effect of human population density is not limited to settlements, but also the surrounding areas. The permeability values of the building densities were assigned as shown in Table S2.I.9. The final permeability values of POP were obtained by selecting the minimum values of both building density and population density.

Table S2.I.8 - Scheme for the classification of the human population density to the permeability values.

Human population density (inhabitants/km²)	Permeability value
0 - 1.22	10

Human population density (inhabitants/km²)	Permeability value
1.22 - 6.77	9
6.77 - 12.09	8
12.09 - 15.82	7
15.82 - 21.83	6
21.83 - 27.51	5
27.51 - 44.52	4
44.52 - 65.13	3
65.13 - 181.59	2
181.59 - Inf	1

Table S2.I.9 - Scheme for the classification of the buildings density to the permeability values.

Building density (buildings/km²)	Permeability value
0	10
0 - 86.15	8
86.15 - 156.49	4
156.49 - 356.49	3
356.49 - 856.49	2
> 856.49	1

Table S2.I.10 - The conversion of the modified CSI values into resistance values for the creation of the resistance surface.

Modified CSI value	Resistance value
1	100
2	95
3	80
4	65
5	50
6	40
7	30
8	20
9	10
10	1

APPENDIX 2.II - RESULTS

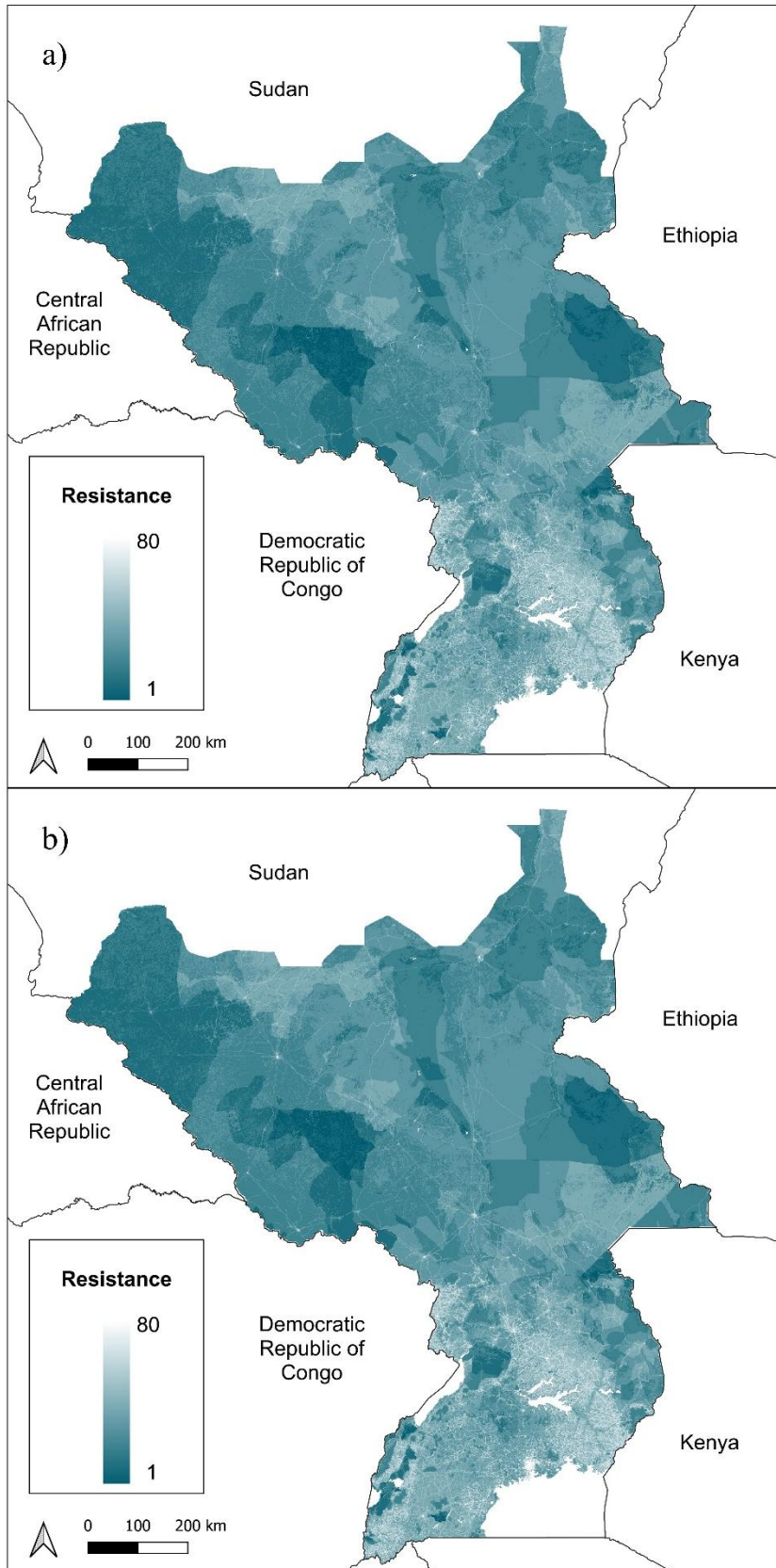


Figure S2.II.1 – Resistance surfaces of the present scenario (a) and future scenario (b).

Indicator used to create resistance surfaces:

- *Linear infrastructure density (LI)*: values are 10 for 92.60% of the study area (Figure S2.II.2), reflecting the differences between the two countries. The distribution of values across the study area shows greater environmental permeability in South Sudan, which has a lower density of linear infrastructure than Uganda. Only spatial data on planned power lines were available in the open access database, while data on roads, railways and other linear infrastructure were not freely available. The total length of planned power lines is 6865 km, of which 2885 km in South Sudan and 3980 km in Uganda (Figure S2.II.3).

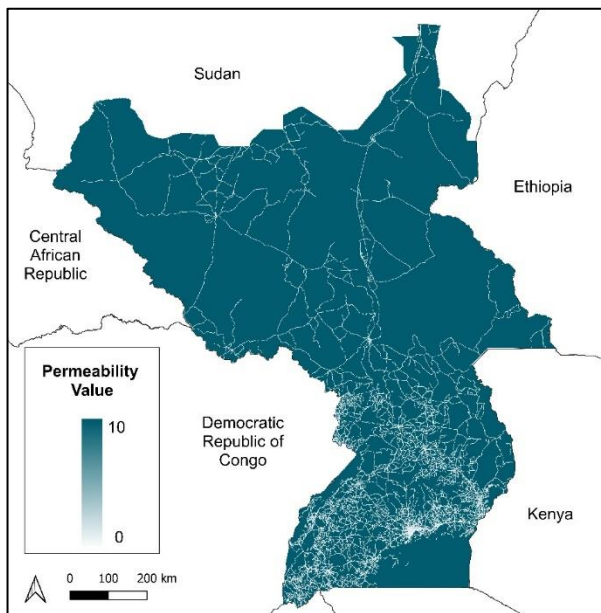


Figure S2.II.2 - Values of permeability obtained for the linear infrastructure density (LI) indicator used in the present scenario.

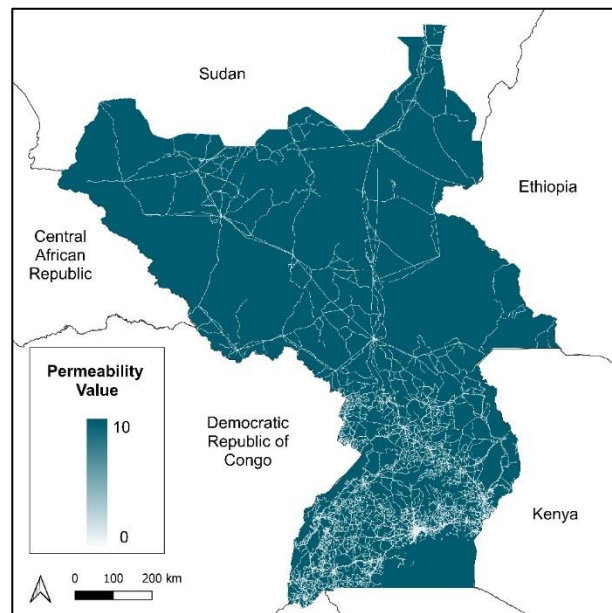


Figure S2.II.3 - Values of permeability obtained for the linear infrastructure density (LI) indicator used in the future scenario.

- *Species conservation (CONS)*: The distribution ranges used to calculate the CONS indicator (Figure S2.II.4) included a total of 2,177 species, of which 1,068 were birds (49.06% of the total), 353 mammals (16.21%), 198 reptiles (9.09%), 84 amphibians (3.86%), 292 arthropods (13.41%) and 182 plants (8.36%). The number of threatened species was 103 (4.73% of total species), of which 53 (51.46%) were vulnerable (VU), 42 (40.78%) endangered (EN) and 9 (8.74%) critically endangered (CR). 38 birds (36.89%), 35 mammals (33.98%), 11 reptiles (10.68%), 2 amphibians (1.94%), 7 arthropods (6.79%) and 10 plants (9.71%).

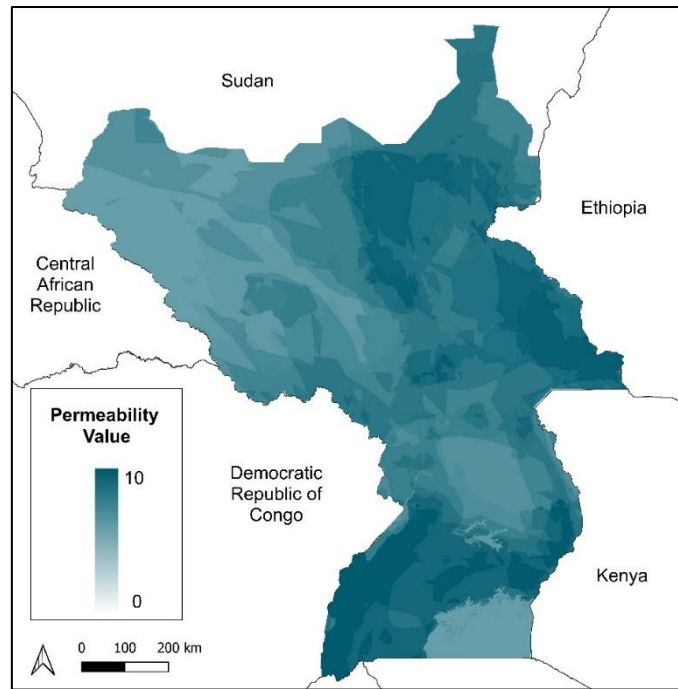


Figure S2.II.4 – Values of permeability obtained for the species conservation (CONS) indicator.

- *Land cover (LAN)*: The land cover of the study area is represented by forest (35.24%), followed by herbaceous vegetation (25.06%), shrubland (23.69%), cropland (7,81%), permanent water bodies (4.17%), herbaceous wetland (3.79%), urban areas (0.22%), bare soil/sparse vegetation (0.0085%) and ice and snow areas (0.0001%). Thus, most of the study area has permeability values greater than 5 (Figure S2.II.5).

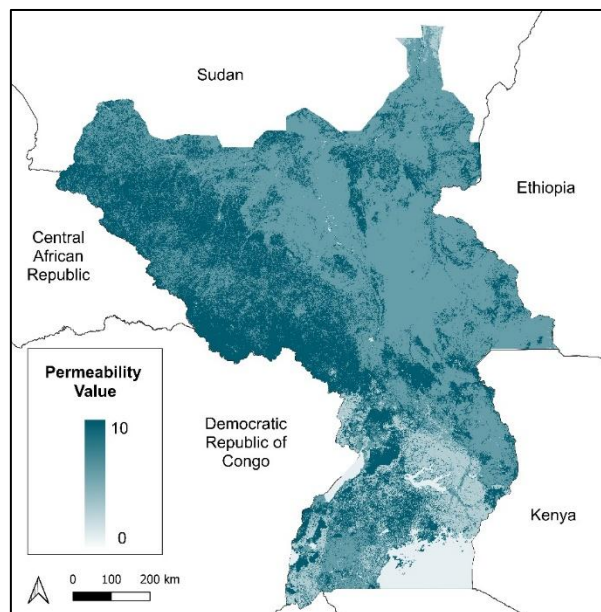


Figure S2.II.5 – Values of permeability obtained for land cover (LAN) indicator.

- *Human population (POP)*: Population pressure is much higher in Uganda, where there are more densely populated areas, than in South Sudan, where it is low, except in a few major cities (Figure S2.II.6).

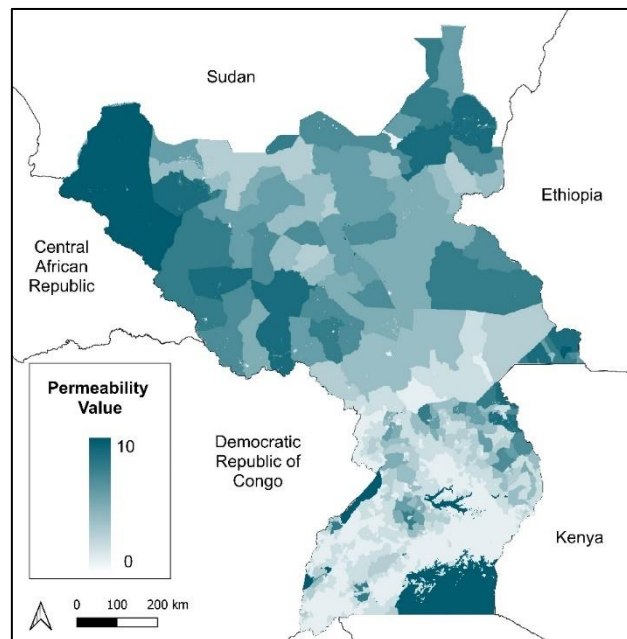


Figure S2.II.6 - Values of permeability obtained for the human population (POP) indicator.

- *Environmental protection (ENV)*: There are a total of 738 protected areas in the study area, 27 from South Sudan and 711 from Uganda (Figure S2.II.7). The total area of protected areas is 133,980 km² (16.10% of the total area), of which 97,714 km² (11.74%) are in South Sudan and 35,580 km² in Uganda (4.27%). The remaining 83.90% of the area has a zero value and represents areas without any level of protection.

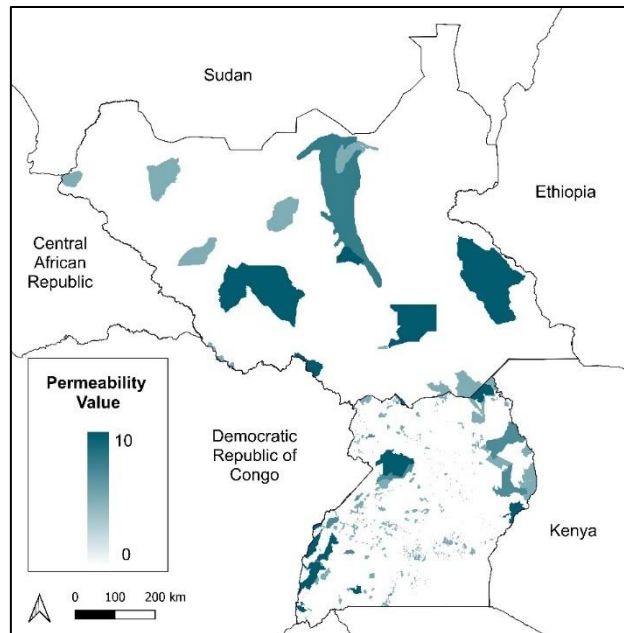


Figure S2.II.7 - Values of permeability obtained for the environmental protection (ENV) indicator.

- *Topography (TOP)*: The values are mostly 10 (Figure S2.8) and mainly reflect the contribution of low slope values, which are less than 30° for 94.62% of the study area. Most of the lowest values are 5 and represent mountainous areas with altitudes up to 5,000 metres and slopes up to 40° .

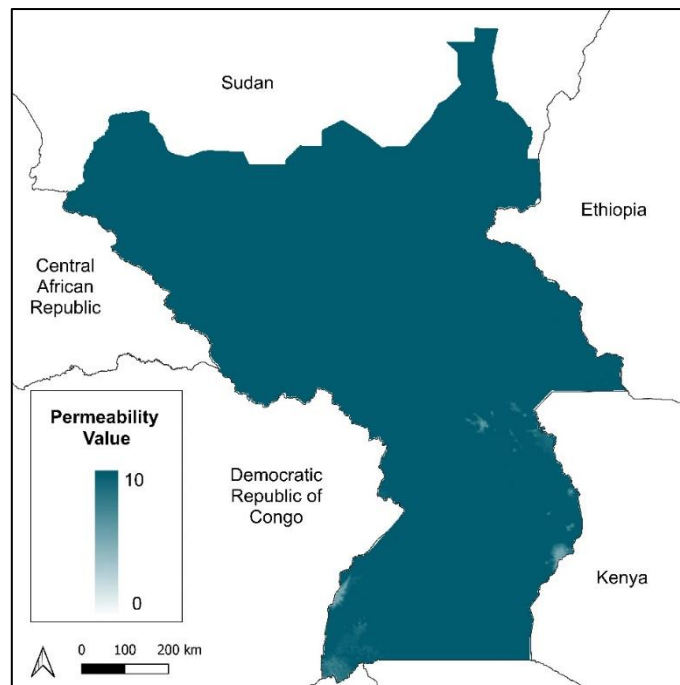


Figure S2.II.8 - Values of permeability obtained for the Topography (TOP) indicator.

Core areas in present and future scenarios:

Table S2.II.1 – Details of the impact on priority conservation areas due to the implementation of the planned linear infrastructure. The area and extent of areas lost in terms of km² and percentage have been expressed for each priority conservation areas in the present and future scenarios.

Country	Present		Future		Impact	Lost area (km ²)	%
	ID	Area (km ²)	ID	Area (km ²)			
South Sudan	core1	11	core1	11	No	0	0.00
South Sudan	core2	15	core2	15	No	0	0.00
South Sudan	core3	10	core3	10	No	0	0.00
South Sudan	core4	12	core4	12	No	0	0.00
South Sudan	core5	33	core5	33	No	0	0.00
South Sudan	core6	15	core6	15	No	0	0.00
South Sudan	core7	14	core7	14	No	0	0.00
South Sudan	core8	17	core8	17	No	0	0.00
South Sudan	core9	16	core9	16	No	0	0.00
South Sudan	core10	12	core10	12	No	0	0.00
South Sudan	core11	11	core11	11	No	0	0.00
South Sudan	core12	24	core12	24	No	0	0.00
South Sudan	core13	11	core13	11	No	0	0.00
South Sudan	core14	27	core14	27	No	0	0.00
South Sudan	core15	117	core15	117	No	0	0.00
South Sudan	core16	12	core16	12	No	0	0.00
South Sudan	core17	30	core17	30	No	0	0.00
South Sudan	core18	531	core18	531	No	0	0.00
South Sudan	core19	11	core19	11	No	0	0.00
South Sudan	core20	157	core20	157	No	0	0.00
South Sudan	core21	139	core21	133	Yes	6	4.32
South Sudan	core22	10	-	0	Yes	10	100.00
South Sudan	core23	13	core23	13	No	0	0.00
South Sudan	core24	11	core24	11	No	0	0.00
South Sudan	core25	20	core25	20	No	0	0.00
South Sudan	core26	41	core26	41	No	0	0.00
South Sudan	core27	41	core27	41	No	0	0.00
South Sudan	core28	12	core28	12	No	0	0.00
South Sudan	core29	15	core29	15	No	0	0.00
South Sudan	core30	66	core30	66	No	0	0.00
South Sudan	core31	127	core31	127	No	0	0.00
South Sudan	core32	13	core32	13	No	0	0.00
South Sudan	core33	52	core33	52	No	0	0.00
South Sudan	core34	13	core34	13	No	0	0.00
South Sudan	core35	12	core35	12	No	0	0.00
South Sudan	core36	10	core36	10	No	0	0.00
South Sudan	core37	11	core37	11	No	0	0.00
South Sudan	core38	20	core38	20	No	0	0.00

South Sudan	core39	14	core39	14	No	0	0.00
South Sudan	core40	41432	core40	41253	Yes	179	0.43
South Sudan	core41	59	core41	59	No	0	0.00
South Sudan	core42	76	core42	74	Yes	2	2.63
South Sudan	core43	62	core43	62	No	0	0.00
South Sudan	core44	25	core44	25	No	0	0.00
South Sudan	core45	17	core45	17	No	0	0.00
South Sudan	core46	12	core46	12	No	0	0.00
South Sudan	core47	30	core47	30	No	0	0.00
South Sudan	core48	10	core48	10	No	0	0.00
South Sudan	core49	404	core49	404	No	0	0.00
South Sudan	core50	16	core50	16	No	0	0.00
South Sudan	core51	18	core51	18	No	0	0.00
South Sudan	core52	80	core52	80	No	0	0.00
South Sudan	core53	198	core53a	13	Yes	1	0.51
South Sudan			core53b	184			
South Sudan	core54	11	core54	11	No	0	0.00
South Sudan	core55	26	core55	26	No	0	0.00
South Sudan	core56	13	core56	13	No	0	0.00
South Sudan	core57	93	core57	93	No	0	0.00
South Sudan	core58	37	core58	37	No	0	0.00
South Sudan	core59	10	core59	10	No	0	0.00
South Sudan	core60	393	core60	393	No	0	0.00
South Sudan	core61	102	core61	102	No	0	0.00
South Sudan	core62	83	core62	83	No	0	0.00
South Sudan	core63	10	core63	10	No	0	0.00
South Sudan	core64	19	core64	19	No	0	0.00
South Sudan	core65	28	core65	28	No	0	0.00
South Sudan	core66	63	core66	63	No	0	0.00
South Sudan	core67	50	core67	44	Yes	6	12.00
South Sudan	core68	79	core68	79	No	0	0.00
South Sudan	core69	14	core69	14	No	0	0.00
South Sudan	core70	40	core70	40	No	0	0.00
South Sudan	core71	10	core71	10	No	0	0.00
South Sudan	core72	15	core72	15	No	0	0.00
South Sudan	core73	13	core73	13	No	0	0.00
South Sudan	core74	10	core74	10	No	0	0.00
South Sudan	core75	42	core75	42	No	0	0.00
South Sudan	core76	142	core76	142	No	0	0.00
South Sudan	core77	13	core77	13	No	0	0.00
South Sudan	core78	37	core78	37	No	0	0.00
South Sudan	core79	27	core79	27	No	0	0.00
South Sudan	core80	48	core80	46	Yes	2	4.17
South Sudan	core81	20	core81	20	No	0	0.00
South Sudan	core82	483	core82	483	No	0	0.00
South Sudan	core83	10	core83	10	No	0	0.00
South Sudan	core84	102	core84	102	No	0	0.00

South Sudan	core85	10	core85	10	No	0	0.00
South Sudan	core86	518	core86	518	No	0	0.00
South Sudan	core87	76	core87	76	No	0	0.00
South Sudan	core88	10	core88	10	No	0	0.00
South Sudan	core89	67	core89	67	No	0	0.00
South Sudan	core90	20	core90	20	No	0	0.00
South Sudan	core91	12	core91	12	No	0	0.00
South Sudan	core92	13	core92	13	No	0	0.00
South Sudan	core93	13	core93	13	No	0	0.00
South Sudan	core94	10	core94	10	No	0	0.00
South Sudan	core95	21	core95	21	No	0	0.00
South Sudan	core96	35	core96	35	No	0	0.00
South Sudan	core97	70	core97	70	No	0	0.00
South Sudan	core98	928	core98a	50	Yes	39	4.20
South Sudan			core98b	32			
South Sudan			core98c	807			
South Sudan	core99	10	core99	10	No	0	0.00
South Sudan	core100	14	core100	14	No	0	0.00
South Sudan	core101	27	core101	27	No	0	0.00
South Sudan	core102	11	core102	11	No	0	0.00
South Sudan	core103	10	core103	10	No	0	0.00
South Sudan	core104	13	core104	13	No	0	0.00
South Sudan	core105	18	core105	17	Yes	1	5.56
South Sudan	core106	23	core106	23	No	0	0.00
South Sudan	core107	55	core107	55	No	0	0.00
South Sudan	core108	43	core108	43	No	0	0.00
South Sudan	core109	10	core109	10	No	0	0.00
South Sudan	core110	78	core110	78	No	0	0.00
South Sudan	core111	29	core111	29	No	0	0.00
South Sudan	core112	168	core112a	12	Yes	17	10.12
South Sudan			core112b	139			
South Sudan	core113	24	core113	24	No	0	0.00
South Sudan	core114	10	core114	10	No	0	0.00
South Sudan	core115	11	core115	11	No	0	0.00
South Sudan	core116	390	core116	390	No	0	0.00
South Sudan	core117	31	core117	31	No	0	0.00
South Sudan	core118	17	core118	17	No	0	0.00
South Sudan	core119	10	core119	10	No	0	0.00
South Sudan	core120	12	core120	12	No	0	0.00
South Sudan	core121	87	core121	87	No	0	0.00
South Sudan	core122	13	core122	13	No	0	0.00
South Sudan	core123	193	core123	178	Yes	15	7.77
South Sudan	core124	24	core124	24	No	0	0.00
South Sudan	core125	35	core125	34	Yes	1	2.86
South Sudan	core126	36	core126	36	No	0	0.00
South Sudan	core127	10	core127	10	No	0	0.00
South Sudan	core128	192	core128	192	No	0	0.00

South Sudan	core129	19	core129	19	No	0	0.00
South Sudan	core130	30	core130	30	No	0	0.00
South Sudan	core131	1571	core131	1571	No	0	0.00
South Sudan	core132	4438	core132	4438	No	0	0.00
South Sudan	core133	18652	core133	18652	No	0	0.00
South Sudan	core134	19	core134	19	No	0	0.00
South Sudan	core135	107	core135	103	Yes	4	3.74
South Sudan	core136	1318	core136	1318	No	0	0.00
South Sudan	core137	17	core137	17	No	0	0.00
South Sudan	core138	15	core138	15	No	0	0.00
South Sudan	core139	15	core139	15	No	0	0.00
South Sudan	core140	20	core140	19	Yes	1	5.00
South Sudan	core141	15	core141	15	No	0	0.00
South Sudan	core142	121	core142	121	No	0	0.00
South Sudan	core143	17	core143	17	No	0	0.00
South Sudan	core144	12	core144	12	No	0	0.00
South Sudan	core145	69	core145a	12	Yes	8	11.59
South Sudan			core145a	49			
South Sudan	core146	20	core146	20	No	0	0.00
South Sudan	core147	12	core147	12	No	0	0.00
South Sudan	core148	11	core148	11	No	0	0.00
South Sudan	core149	36	core149	36	No	0	0.00
South Sudan	core150	25859	core150a	23737	Yes	46	0.18
South Sudan			core150b	12			
South Sudan			core150c	2029			
South Sudan			core150d	35			
South Sudan	core151	20	core151	20	No	0	0.00
South Sudan	core152	17	core152	17	No	0	0.00
South Sudan	core153	10	core153	10	No	0	0.00
South Sudan	core154	11	core154	11	No	0	0.00
South Sudan	core155	62	core155	62	No	0	0.00
South Sudan	core156	13	core156	13	No	0	0.00
South Sudan	core157	14	core157	14	No	0	0.00
South Sudan	core158	297	core158	297	No	0	0.00
South Sudan	core159	273	core159	273	No	0	0.00
South Sudan	core160	14	core160	14	No	0	0.00
South Sudan	core161	36	core161	36	No	0	0.00
South Sudan	core162	12	core162	12	No	0	0.00
South Sudan	core163	154	core163	154	No	0	0.00
South Sudan	core164	10	core164	10	No	0	0.00
South Sudan	core165	65	core165	65	No	0	0.00
South Sudan	core166	10	core166	10	No	0	0.00
South Sudan	core167	23	core167	23	No	0	0.00
South Sudan	core168	11	core168	11	No	0	0.00
South Sudan	core169	10	core169	10	No	0	0.00
South Sudan	core170	16	core170	16	No	0	0.00
South Sudan	core171	25	core171	25	No	0	0.00

South Sudan	core172	85	core172	85	No	0	0.00
South Sudan	core173	189	core173	189	No	0	0.00
South Sudan	core174	45	core174	45	No	0	0.00
South Sudan	core175	334	core175	334	No	0	0.00
South Sudan	core176	22	core176	22	No	0	0.00
South Sudan	core177	31	core177	31	No	0	0.00
South Sudan	core178	171	core178	171	No	0	0.00
South Sudan	core179	22	core179	19	Yes	3	13.64
South Sudan	core180	157	core180	157	No	0	0.00
South Sudan	core181	302	core181	302	No	0	0.00
South Sudan	core182	88	core182	88	No	0	0.00
South Sudan	core183	1348	core183	1303	Yes	45	3.34
South Sudan	core184	167	core184	167	No	0	0.00
South Sudan	core185	14	core185	14	No	0	0.00
South Sudan	core186	116	core186	116	No	0	0.00
Uganda	core187	2076	core187	2070	Yes	6	0.29
Uganda	core188	20	core188	20	No	0	0.00
Uganda	core189	189	core189	189	No	0	0.00
Uganda	core190	246	core190	244	Yes	2	0.81
Uganda	core191	53	core191	53	No	0	0.00
Uganda	core192	107	core192	107	No	0	0.00
Uganda	core193	10	core193	10	No	0	0.00
Uganda	core194	32	core194	32	No	0	0.00
Uganda	core195	59	core195	59	No	0	0.00
Uganda	core196	50	core196	50	No	0	0.00
Uganda	core197	11	core197	11	No	0	0.00
Uganda	core198	12	core198	12	No	0	0.00
Uganda	core199	15	core199	15	No	0	0.00
Uganda	core200	25	core200	25	No	0	0.00
Uganda	core201	20	core201	20	No	0	0.00
Uganda	core202	18	core202	18	No	0	0.00
Uganda	core203	2305	core203a	2209	Yes	7	0.30
Uganda			core203b	89			
Uganda	core204	16	core204	16	No	0	0.00
Uganda	core205	20	core205	20	No	0	0.00
Uganda	core206	19	core206	19	No	0	0.00
Uganda	core207	21	core207	21	No	0	0.00
Uganda	core208	14	core208	14	No	0	0.00
Uganda	core209	23	core209	23	No	0	0.00
Uganda	core210	33	core210	33	No	0	0.00
Uganda	core211	13	core211	13	No	0	0.00
Uganda	core212	11	core212	11	No	0	0.00
Uganda	core213	99	core213	99	No	0	0.00
Uganda	core214	94	core214	94	No	0	0.00
Uganda	core215	409	core215	398	Yes	11	2.69
Uganda	core216	82	core216	82	No	0	0.00
Uganda	core217	285	core217	285	No	0	0.00

Uganda	core218	95	core218	95	No	0	0.00
Uganda	core219	166	core219a	14	Yes	10	6.02
Uganda			core219b	142			
Uganda	core220	194	core220	194	No	0	0.00
Uganda	core221	77	core221	77	No	0	0.00
Uganda	core222	109	core222	109	No	0	0.00
Uganda	core223	13	core223	11	Yes	2	15.38
Uganda	core224	26	core224	26	No	0	0.00
Uganda	core225	38	core225	38	No	0	0.00
Uganda	core226	13	core226	13	No	0	0.00
Uganda	core227	828	core227	823	Yes	5	0.60
Uganda	core228	12	core228	12	No	0	0.00
Uganda	core229	14	core229	14	No	0	0.00
Uganda	core230	332	core230	332	No	0	0.00
Uganda	core231	30	core231	30	No	0	0.00
Uganda	core232	111	core232	111	No	0	0.00
Total		114647		114218		429	0.37

Macro-regional ecological network in the present and future scenarios:

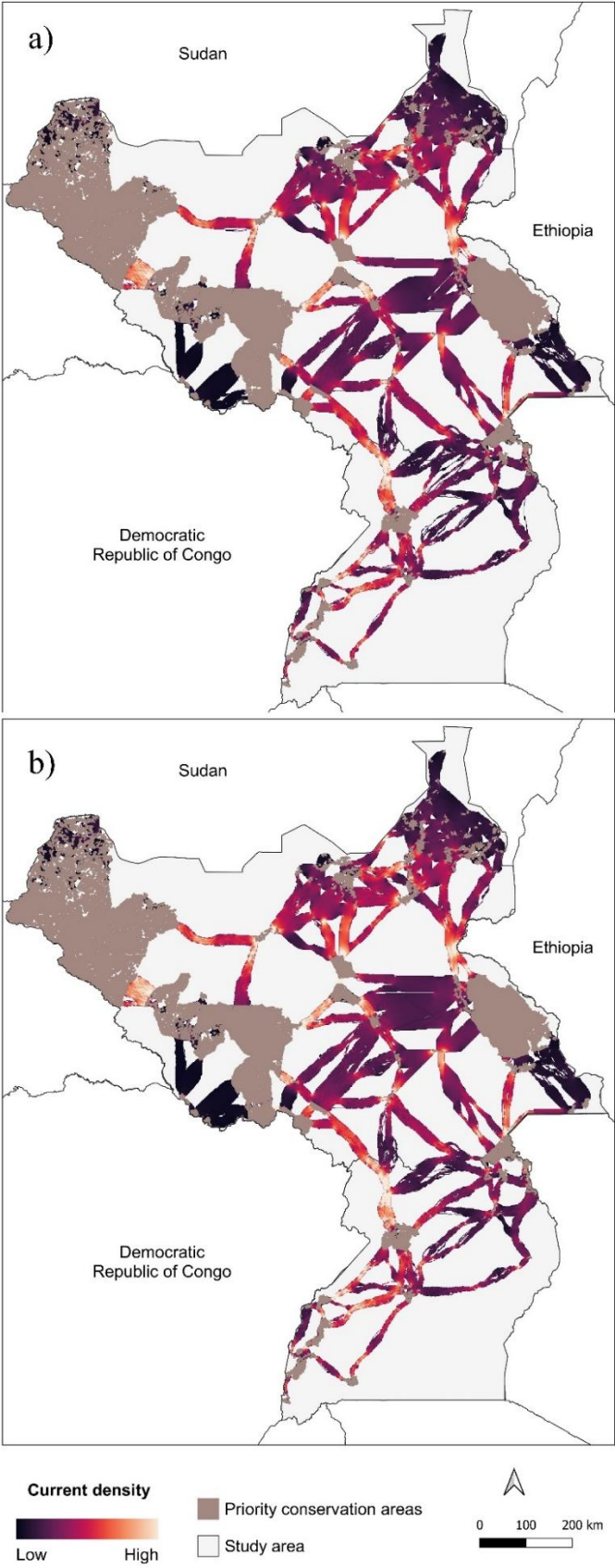


Figure S2.II.9 – Macro-regional ecological networks in the present (a) and future (b) scenarios.

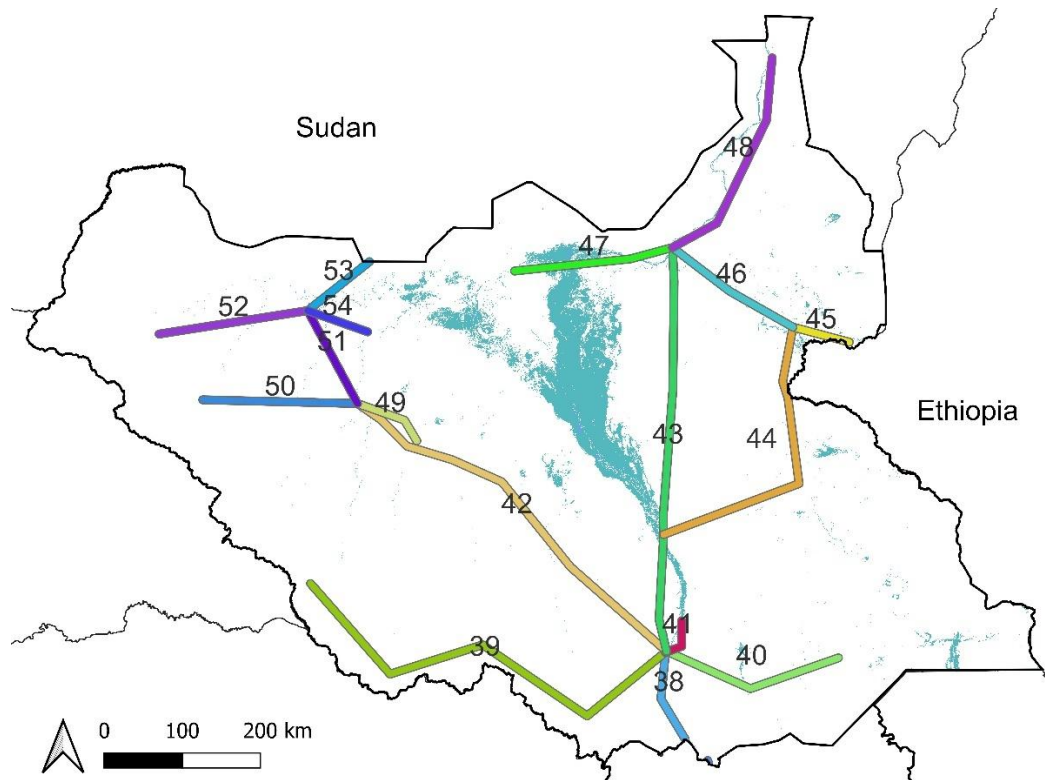


Figure S2.II.10 – Planned linear infrastructure in South Sudan.

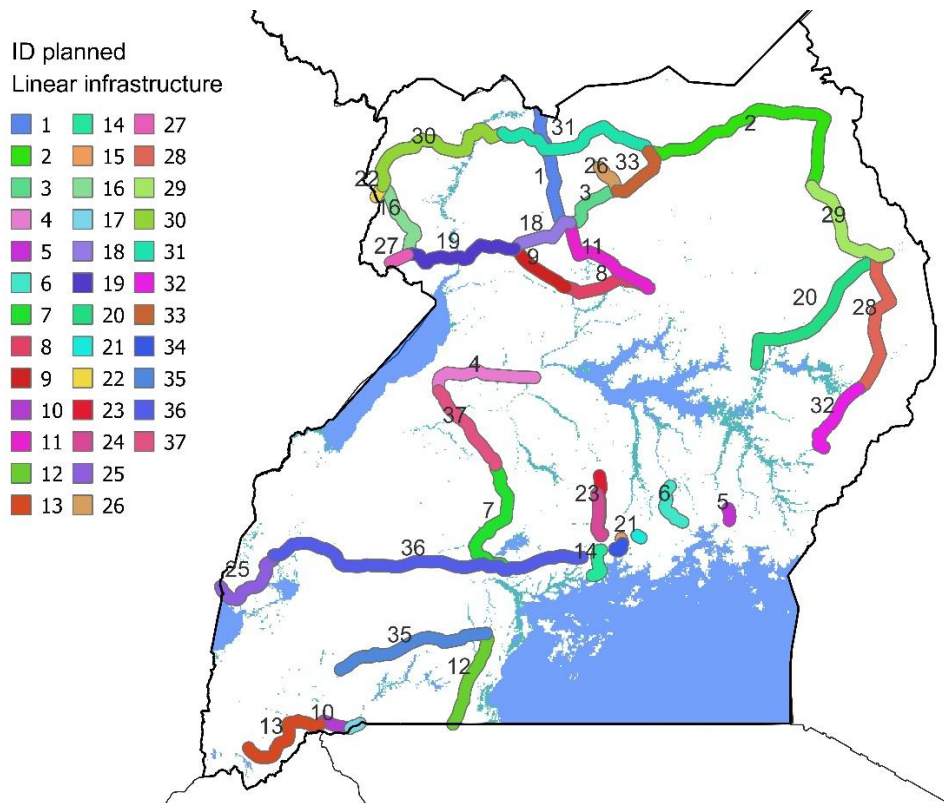


Figure S2.II.11 – Planned linear infrastructure in Uganda.

Table S2.II.2 - Details of the 54 planned linear infrastructures analysed in this study and comparison of ecological network characteristics in the present and future scenarios within the 5 km radius buffer around them. The number and length of LCPs refer to the Least-Cost Paths identified by the Linkage mapper pathway tool that intersect the 5 km buffer of each planned linear infrastructure; the current density refers to the Circuitscape outputs and the pinch points area refers to all areas with current densities above the 95th quantile. In bold, the planned linear infrastructure that will have a greater negative impact on landscape connectivity.

ID	Country	Voltage (kV)	Linear infrastructure length (km)	Number of LCPs		Length of LCP (km)			Current density			Pinch points area (km ²)		
				Present	Future	Present	Future	Change (%)	Present	Future	Change (%)	Present	Future	Change (%)
1	Uganda	400	149	2	2	25.11	25.11	0.00	21100.55	25301.00	19.91	0.00	0.00	-
2	Uganda	132	216	5	5	50.88	51.71	1.63	88486.67	92314.36	4.33	5.00	9.39	87.71
3	Uganda	132	53	1	0	26.59	0.00	-100.00	37263.44	473.30	-98.73	24.02	0.00	-100.00
4	Uganda	220	92	1	1	11.18	10.89	-2.63	59834.21	58979.48	-1.43	5.75	11.75	104.50
5	Uganda	132	10	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
6	Uganda	132	40	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
7	Uganda	132	122	1	1	10.72	10.72	0.00	34019.33	33950.65	-0.20	11.87	1.00	-91.58
8	Uganda	132	76	0	0	0.00	0.00	-	12815.22	11638.63	-9.18	0.00	0.00	-
9	Uganda	400	54	0	1	0.00	2.41	-	1134.42	4062.86	258.14	0.00	0.00	-
10	Uganda	132	27	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
11	Uganda	132	96	3	2	36.37	24.21	-33.44	53816.48	43720.25	-18.76	2.76	0.00	-100.00
12	Uganda	220	82	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
13	Uganda	132	85	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
14	Uganda	132	31	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
15	Uganda	132	5	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
16	Uganda	132	69	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
17	Uganda	132	9	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
18	Uganda	132	55	1	0	3.97	0.00	-100.00	4731.18	0.00	-100.00	0.93	0.00	-100.00
19	Uganda	132	101	4	4	19.02	19.02	0.00	71033.66	86353.42	21.57	114.60	179.23	56.39
20	Uganda	132	158	2	2	22.11	22.11	0.00	15428.54	17900.14	16.02	0.00	0.00	-
21	Uganda	220	4	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
22	Uganda	132	10	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
23	Uganda	132	53	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-

ID	Country	Voltage (kV)	Linear infrastructure length (km)	Number of LCPs		Length of LCP (km)			Current density			Pinch points area (km ²)		
				Present	Future	Present	Future	Change (%)	Present	Future	Change (%)	Present	Future	Change (%)
24	Uganda	220	38	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
25	Uganda	220	72	3	4	19.65	29.57	50.47	38236.75	41093.90	7.47	42.85	44.90	4.79
26	Uganda	132	28	1	0	13.25	0.00	-100.00	16340.60	473.30	-97.10	0.00	0.00	-
27	Uganda	132	15	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
28	Uganda	132	133	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
29	Uganda	132	99	4	4	53.91	53.91	0.00	30206.73	34766.02	15.09	0.00	0.00	-
30	Uganda	132	145	3	3	45.61	36.49	-20.00	86546.96	96529.51	11.53	202.04	218.66	8.23
31	Uganda	132	142	3	2	35.56	24.89	-30.01	37599.58	37153.98	-1.19	0.00	0.00	-
32	Uganda	132	67	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
33	Uganda	132	52	0	0	0.00	0.00	-	19057.95	11056.03	-41.99	0.00	0.00	-
34	Uganda	132	14	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
35	Uganda	220	131	2	2	19.52	20.35	4.24	29136.96	32334.66	10.97	1.86	2.86	53.68
36	Uganda	220	271	2	3	14.79	15.63	5.68	22895.22	30843.45	34.72	10.99	19.97	81.82
37	Uganda	132	81	3	3	40.24	40.24	0.00	50445.76	55863.41	10.74	2.00	4.00	100.00
38	South Sudan	220	120	1	1	26.46	14.24	-46.16	61753.21	64761.69	4.87	7.00	0.00	-100.00
39	South Sudan	220	573	8	14	89.19	182.32	104.42	114471.7 5	137108.5 6	19.78	3.21	2.77	-13.82
40	South Sudan	220	238	4	4	73.67	70.52	-4.27	126989.3 5	130430.9 6	2.71	12.82	9.82	-23.41
41	South Sudan	220	55	5	5	55.60	64.80	16.53	94532.19	105181.0 7	11.26	113.64	109.56	-3.59
42	South Sudan	220	519	7	7	78.84	79.66	1.05	226719.2 7	240713.9 0	6.17	203.97	198.86	-2.50
43	South Sudan	220	521	15	18	172.96	206.29	19.27	307054.1 3	345212.5 2	12.43	127.69	93.33	-26.91
44	South Sudan	220	391	24	27	427.85	480.04	12.20	405491.3 9	416281.5 1	2.66	375.76	344.38	-8.35
45	South Sudan	220	75	2	2	21.00	21.30	1.40	26228.59	26948.14	2.74		0.00	-
46	South Sudan	220	186	8	11	71.71	97.61	36.12	160889.1 1	184659.6 7	14.77	74.81	150.46	101.12

ID	Country	Voltage (kV)	Linear infrastructure length (km)	Number of LCPs		Length of LCP (km)			Current density			Pinch points area (km ²)		
				Present	Future	Present	Future	Change (%)	Present	Future	Change (%)	Present	Future	Change (%)
47	South Sudan	220	206	9	15	119.34	166.17	39.24	110347.63	124913.55	13.20	40.89	47.89	17.12
48	South Sudan	220	293	15	17	121.62	142.69	17.32	112585.79	111531.15	-0.94	35.2	26.19	-25.58
49	South Sudan	220	95	0	0	0.00	0.00	-	1044.53	1133.74	8.54	0.00	0.00	-
50	South Sudan	220	198	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
51	South Sudan	220	135	1	1	25.45	24.26	-4.68	88581.47	87815.21	-0.87	2.66	11.60	335.67
52	South Sudan	220	192	2	2	2.54	2.54	0.00	644.64	629.79	-2.30	0.00	0.00	-
53	South Sudan	220	101	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-
54	South Sudan	220	82	0	0	0.00	0.00	-	0.00	0.00	-	0.00	0.00	-

Table S2.II.3 – Comparison of the centrality and impact of each corridor in each planned linear infrastructure (ID) between present and future scenarios.

ID	Present			Future			Corridor	Type of impact
	From	To	Centrality class	From	To	Centrality class		
1	core187	core197	Medium	core187	core197	Medium	same	
	core192	core197	Medium	core192	core197	Medium	same	
2	core187	core190	High	core187	core190	High	same	
	core187	core192	High	core187	core192	High	same	
	core190	core193	Low	core190	core193	Low	same	
	core190	core195	Low	core190	core195	Low	same	
	core192	core197	Medium	core192	core197	Medium	same	
3	core187	core203	High				different	Corridor loss
4	core203	core210	High	core203a	core210	High	same	
7	core214	core230	Medium	core214	core230	Medium	same	
9				core203a	core203b	High	different	New corridor
11	core187	core203	High				different	Corridor loss
	core192	core203	High	core192	core203b	High	same	
	core200	core203	Medium	core200	core203b	High	same	Higher centrality
18	core187	core203	High				different	Corridor loss
19	core197	core202	High	core197	core202	High	same	
	core197	core204	High	core197	core204	High	same	
	core202	core204	High	core202	core204	High	same	
	core202	core206	High	core202	core206	High	same	
20	core196	core208	Medium	core196	core208	Medium	same	
	core201	core208	Medium	core201	core208	Medium	same	
25	core216	core223	Medium	core216	core223	Medium	same	
	core221	core222	High	core221	core222	High	same	
	core222	core223	Low	core222	core223	Low	same	
			core223	core228	Medium	different	No impact in present scenario	
26	core187	core203	High				different	Corridor loss
29	core195	core198	Low	core195	core198	Medium	same	Higher centrality
	core195	core201	Medium	core195	core201	Medium	same	
	core196	core201	Medium	core196	core201	Medium	same	
	core196	core208	Medium	core196	core208	Medium	same	
30	core179	core197	High	core179	core197	High	same	
	core183	core197	High	core183	core197	High	same	
	core185	core197	High	core185	core197	High	same	
31	core187	core197	Medium	core187	core197	Medium	same	
	core187	core203	High				different	Corridor loss
	core192	core197	Medium	core192	core197	Medium	same	
35	core214	core230	Medium	core214	core230	Medium	same	
	core226	core230	Medium	core226	core230	Medium	same	
36	core214	core230	Medium	core214	core230	Medium	same	
	core218	core219	High	core218	core219a	High	same	

				core219a	core219b	High	different	New corridor
37	core210	core215	Medium	core210	core215	Medium	same	
	core214	core215	Medium	core214	core215	Medium	same	
	core214	core217	High	core214	core217	High	same	
38	core179	core197	High	core179	core197	High	same	
39	core132	core178	Low	core132	core178	Low	same	
	core150	core178	Low	core150a	core178	Low	same	
				core150a	core150b	High	different	New corridor
				core150a	core150c	High	different	New corridor
	core150	core184	Low	core150a	core184	Low	same	
	core150	core186	Low	core150a	core186	Low	same	
	core176	core183	Low	core176	core183	Low	same	
				core150b	core150c	High	different	New corridor
				core150c	core150d	High	different	New corridor
				core150c	core186	Low	different	New corridor
	core181	core183	High	core181	core183	High	same	
				core150d	core186	Low	different	New corridor
	core183	core197	High	core183	core197	High	same	
core185	core197	High	core185	core197	High	same		
40	core171	core187	High	core171	core187	High	same	
	core177	core187	High	core177	core187	High	same	
	core179	core187	High	core179	core187	High	same	
	core179	core197	High	core179	core197	High	same	
41	core171	core177	High	core171	core177	High	same	
	core174	core177	High	core174	core177	High	same	
	core177	core187	High	core177	core187	High	same	
	core179	core187	High	core179	core187	High	same	
	core179	core197	High	core179	core197	High	same	
42	core130	core150	High	core130	core150a	High	same	
	core136	core161	High	core136	core161	High	same	
	core158	core161	High	core158	core161	High	same	
	core158	core176	High	core158	core176	High	same	
	core158	core181	Medium	core158	core181	Medium	same	
	core172	core181	High	core172	core181	High	same	
	core179	core185	High	core179	core185	High	same	
43				core84	core99	High	different	New corridor
	core84	core98	High	core84	core98c	High	same	
	core98	core112	High	core98c	core112b	Medium	same	Lower centrality
	core98	core116	High	core98c	core116	Medium	same	Lower centrality
	core116	core121	High	core116	core121	Medium	same	Lower centrality
	core116	core124	High	core116	core124	Medium	same	Lower centrality
	core116	core131	High	core116	core131	High	same	
	core131	core134	Medium	core131	core134	Medium	same	
	core131	core135	Medium	core131	core135	Medium	same	
	core134	core158	Medium	core134	core158	Medium	same	
				core135	core136	Medium	different	New corridor
			core138	core158	Medium	different	New corridor	

	core141	core158	Medium	core141	core158	Medium	same	
	core156	core158	Medium	core156	core158	Medium	same	
	core158	core171	Medium	core158	core171	Medium	same	
	core158	core172	High	core158	core172	High	same	
	core172	core181	High	core172	core181	High	same	
	core179	core185	High	core179	core185	High	same	
44	core96	core133	High	core96	core133	High	same	
	core96	core134	High	core96	core134	High	same	
	core102	core133	High	core102	core133	High	same	
	core103	core133	High	core103	core133	High	same	
	core116	core134	High	core116	core134	High	same	
	core133	core135	High	core133	core135	Medium	same	Lower centrality
	core133	core140	Medium	core133	core140	Medium	same	
	core133	core145	Medium	core133	core145b	Medium	same	
	core135	core137	High	core135	core137	High	same	
	core135	core139	High	core135	core139	High	same	
	core135	core140	Medium	core135	core140	High	same	Higher centrality
	core137	core140	Medium	core137	core140	Medium	same	
				core138	core158	Medium	different	New corridor
	core139	core140	Medium	core139	core140	Medium	same	
	core140	core144	High	core140	core144	High	same	
	core141	core158	Medium	core141	core158	Medium	same	
	core143	core145	Medium	core143	core145a	Medium	same	
	core144	core145	High	core144	core145a	High	same	
				core145a	core145b	High	different	New corridor
				core145a	core148	Medium	different	New corridor
	core145	core148	Low	core145b	core148	Low	same	
	core145	core156	Medium	core145b	core156	Medium	same	
core148	core155	Low	core148	core155	Low	same		
core148	core156	Medium	core148	core156	Medium	same		
core156	core158	Medium	core156	core158	Medium	same		
core158	core171	Medium	core158	core171	Medium	same		
core158	core172	High	core158	core172	High	same		
45	core102	core133	High	core102	core133	High	same	
	core103	core133	High	core103	core133	High	same	
46				core84	core99	High	different	New corridor
	core84	core98	High	core84	core98c	High	same	
	core96	core116	Medium	core96	core116	Medium	same	
	core96	core133	High	core96	core133	High	same	
	core96	core134	High	core96	core134	High	same	
	core106	core112	High	core106	core112a	High	same	
				core112a	core112b	High	different	New corridor
	core112	core114	Medium	core112a	core114	Medium	same	
				core112a	core116	Medium	different	New corridor
	core112	core116	High	core112b	core116	High	same	
core114	core116	High	core114	core116	High	same		
47	core34	core98	High	core34	core98c	Medium	same	Lower centrality

				core84	core99	High	different	New corridor
	core84	core98	High	core84	core98c	High	same	
	core86	core108	High	core86	core108	High	same	
	core86	core115	Medium	core86	core115	Medium	same	
	core97	core108	Medium	core97	core108	Medium	same	
	core97	core128	High	core97	core128	High	same	
	core97	core129	High	core97	core129	High	same	
				core98a	core98b	Low	different	New corridor
				core98a	core98c	Medium	different	New corridor
	core98	core105	Low	core98a	core105	Low	same	
				core99	core98c	Medium	different	New corridor
				core98b	core98c	High	different	New corridor
				core98c	core105	Medium	different	New corridor
	core98	core112	High	core98c	core112b	Medium	same	Lower centrality
48	core3	core7	Low	core3	core7	Low	same	
	core4	core9	Low	core4	core9	Low	same	
	core4	core11	Low	core4	core11	Low	same	
	core5	core11	Medium	core5	core11	Medium	same	
	core5	core21	Low	core5	core21	Medium	same	Higher centrality
	core5	core22	Low				different	Corridor loss
				core5	core24	Low	different	New corridor
	core11	core22	Medium				different	Corridor loss
				core20	core53a	Low	different	New corridor
	core21	core22	High				different	Corridor loss
				core21	core24	High	different	New corridor
	core21	core42	High	core21	core42	High	same	
	core21	core45	Medium				different	Corridor loss
				core21	core53a	Low	different	New corridor
	core22	core24	Medium				different	Corridor loss
	core34	core53	Medium	core34	core53a	Low	same	Lower centrality
				core42	core53a	Medium	different	New corridor
	core42	core53	High	core42	core53b	High	same	
				core53a	core53b	Medium	different	New corridor
	core53	core67	High	core53a	core67	High	same	
			core53b	core67	High	different	New corridor	
core67	core80	High	core67	core80	High	same		
51	core40	core130	High	core40	core130	High	same	
52	core123	core126	Low	core123	core126	Low	same	
	core125	core126	Low	core125	core126	Low	same	

CHAPTER 3

ROADKILL SUITABILITY AND ROAD CROSSABILITY: IMPLEMENTING TWO NOVEL CONCEPTS FOR PRIORITIZATION OF ROAD MITIGATION

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ABSTRACT

Roads play a critical role in biodiversity loss by reducing species survival and promoting habitat fragmentation. Most roadkill studies focus on single species or localized areas, using roadkill as a direct measure of risk, often overlooking or misinterpreting inherent biases (i.e. carcass-location, persistence and observation biases). In this study, we propose two novel concepts to better understand the relationship between wildlife-vehicle collisions and habitat connectivity. For the first time, we use roadkill locations, modelled using species distribution models, as indicators of detection suitability ('roadkill suitability') rather than actual risk. Additionally, we introduce 'road crossability', a measure of habitat connectivity along roads, assessed using circuit theory. We adopt a multispecies approach, analyzing roadkill data from 15 forest mammals with different mobility across different landscapes (natural and anthropized) in northeastern Italy, to investigate the relationship between roadkill suitability and road crossability. Our results show positive correlations between roadkill suitability and road crossability for *medium* and *high* mobility species, particularly in anthropized landscape, while *low* mobility species exhibit a weaker correlation. By combining these concepts, we offer a novel perspective on road ecology, classifying the regional road network into zones with different conservation and mitigation priorities: Priority Areas for Barrier Effect Mitigation (PABEMs), Potential Areas for Roadkill Mitigation (PARoMs), and Potential Areas for Connectivity Preservation (PACoPs). Our study suggests that assessing roadkill suitability and road crossability for multiple species holds promises to facilitate more effective conservation strategies and mitigation measures to maintain habitat connectivity and reduce the impact of roads in different landscapes.

KEYWORDS

Habitat connectivity, mammals, road ecology, road impact, wildlife-vehicle collision, wildlife corridor.

3.1 INTRODUCTION

Roads have numerous negative impacts on wildlife and habitats worldwide (Laurance et al., 2014; van der Ree et al., 2015), affecting biodiversity and ecosystems both directly and indirectly (Forman and Alexander, 1998). Roads are well known to cause direct mortality through vehicle collisions (hereafter roadkill, Ament et al. 2023) and significantly alter wildlife movements (Passoni et al., 2021), leading to modified behaviour patterns. In addition to these immediate impacts, roads contribute to habitat loss and fragmentation, which result in population declines, isolation, and a subsequent loss of genetic variability (Lesbarrères et al., 2006; Taylor and Goldingay, 2010). The effects of roads extend beyond individual species, as they fragment habitats, alter ecological connectivity and species interactions (Ament et al., 2023; Laurance et al., 2006). Ultimately, entire communities and ecosystems can be destabilized, leading to long-term ecological consequences.

Among the numerous adverse impacts of roads, wildlife roadkill is one of the most studied (Barrientos et al., 2021; D'Amico et al., 2018). Indeed, several studies have focused on both intrinsic (e.g., life-history traits) and extrinsic (e.g., road characteristics, habitat type) factors influencing roadkill (D'Amico et al., 2015; Visintin et al., 2016). For example, Cook and Blumstein (2013) found that vulnerability of mammals and birds to roadkill was influenced by their diet, with omnivorous mammals and herbivorous birds being more vulnerable. González-Suárez et al. (2018) identified body size, reproductive speed and ecological specialisation of the species as factors explaining the roadkill mortality of mammals and birds in Brazil. Among the extrinsic factors, previous studies analysed the relationships between roadkill and road characteristics and traffic volume (Jaeger and Fahrig, 2004; Trombulak and Frissell, 2000), as well as between habitat and landscape features (Fabrizio et al., 2019; Grilo et al., 2011).

Despite the spatial distribution of roadkill is probably the most studied topic in road ecology (D'Amico et al., 2015; Kreling et al., 2019), the majority of the research has focused on single charismatic and/or threatened species, typically evaluated at local scales, with limited evidence on how wildlife populations are affected (Barrientos et al., 2021). Only recently, more complex multi-species analyses and landscape-scale projects have been carried out, highlighting in particular the critical relationship between habitat connectivity and the spatial distribution of roadkill (Ament et al., 2023). However, achieving a comprehensive understanding of roadkill patterns in relation to habitat connectivity remains challenging due to multitude of influencing factors and the intrinsic characteristics of individual species. Indeed, the scientific literature provides contrasting results. For example, the spatial distribution of supposed roadkill hotspots did not coincide with highly connected areas for felids in Brazil (Cerqueira et al., 2021), and in Canada the relationship between roadkill density and connectivity for moose (*Alces americanus*) was observed to be weak (Laliberté and St-

Laurent, 2020). Boyle et al. (2017) found a discrete overlap for herpetofauna, but none at all for mammals. This can obviously vary depending on the species: for example Grilo et al. (2011) found higher mortality of stone marten (*Martes foina*) in well-connected areas, while Girardet et al. (2015) observed that landscape connectivity influenced roadkills for roe deer (*Capreolus capreolus*). These results are contrasting probably because the distribution of detected roadkills is usually interpreted as a faithful representation of the wildlife-vehicle collisions occurred in a given area, whereas the recent literature showed that approximately one third of roadkilled wildlife dies far from the road and consequently it's no available to be detected by traditional roadkill surveys (Román et al., 2024). Additionally, this source of error is spatially structured: for example crippling bias is more likely to occur on minor roads compared to highways (Román et al., 2024), as are other biases related to roadkill surveys, such as carcass-persistence bias and carcass-observation bias (Barrientos et al., 2021; Santos et al., 2011). This issue is especially relevant for opportunistic data (such as roadkill data from citizen science), in which not all the roads are surveyed with the same sampling effort (Vercayie and Herremans, 2015). Consequently, we propose that the amount of recorded roadkills in a given area should be interpreted as a roadkill suitability to be detected (hereafter refereed as roadkill suitability), rather than a direct measure of roadkill risk. In this article we will demonstrate that, despite its intrinsic limitations, this metric can be used to deepen our understanding of how roadkill patterns are related to habitat connectivity.

Our aim is to contribute to the understanding of the relationship between roadkill suitability and habitat connectivity using a multi-species approach across different landscapes, ultimately supporting more informed conservation planning and road management decisions. Specifically, we investigated roadkill suitability in relation to habitat connectivity among species with different movement abilities across two contiguous landscape types: one characterised by relatively intact, natural habitats (i.e. natural landscape), and the other by highly anthropized and fragmented areas (i.e. anthropized landscape). Here we implemented a second novel concept: road crossability, intended as a specific measure of habitat connectivity across the whole road network of the study area. By examining the relationship between roadkill suitability and road crossability, we considered contrasting landscapes and a broad spectrum of species with different dispersal capabilities, ultimately contributing to the potential development of more effective conservation strategies to mitigate the impact of roads in different contexts. Indeed, we used these two novel concepts to propose zoning plans for the road network, identifying potential areas for mitigating road impacts and areas for maintaining connectivity. This approach allowed us to categorize the regional road network into distinct zones, each characterised by different levels of conservation, management and mitigation priorities. Specifically, we defined “Priority Areas for Barrier Effect Mitigation” (PABEMs), zones of high

roadkill suitability and high road crossability, where mitigation measures such as wildlife crossings may be required to prevent roadkill and maintain connectivity. Potentially, the PABEMs might represent areas of high roadkill concentration or areas where a higher number of roadkill could be observed, but at the same time these areas may also have higher wildlife crossings due to high connectivity. We also defined “Potential Areas for Roadkill Mitigation” (PARoM), which are zones of high roadkill suitability but low road crossability. These zones could have high numbers of roadkill or higher roadkill detection, but are unlikely to be frequently crossed, suggesting that other factors influencing roadkill patterns should be considered. Finally, we defined the zones of low roadkill suitability and high road crossability as “Potential Areas for Connectivity Preservation” (PACoP), since these areas could be roads with high wildlife crossings but with characteristics that favour safe crossing or that favour carcass-location bias. The road network zoning approach based on the assessment of roadkill suitability and road crossability provides an initial assessment that can guide mitigation and conservation actions to address road impacts.

3.2 MATERIALS AND METHODS

3.2.1 Study area

The study was conducted in Friuli Venezia Giulia region in northeastern Italy, covering 7,908 km² (Figure 3.1). Characterized by a complex geology, an altitudinal range from 0 to 2,780 m a.s.l., the study area support high biodiversity, including over 90 mammals (Loy et al., 2019). According to EEA (2024), the region encompasses two biogeographical regions: the alpine and the continental (Figure 3.1), covering 47% and 53% of the area. The alpine (hereinafter 'natural landscape') is characterized by predominantly natural habitats, with only 6.4% of the area being affected by human activities (i.e. farming, urbanisation). This region is largely composed of extensive montane mixed forests, featuring species such as *Fagus sylvatica*, *Picea abies*, and *Abies alba* (FVG 2013). In contrast, the continental region (hereinafter 'anthropized landscape') is dominated by densely populated urban areas and agriculture (75.2%; Appendix 3, Table S3.1). However, in the southeastern area, the broadleaved deciduous woods and Mediterranean scrub of the karstic landscape, with species like *Fraxinus ornus*, *Ostrya carpinifolia*, and *Quercus pubescens*, offer more semi-natural conditions. The road network of the study area covers 13,392 km, mostly located in the lowland (10,994 km in anthropized landscape and 2,398 km in natural landscape). Of this network, 86% are local roads, 5% regional roads, 4% national roads and 5% of highways (Figure 3.1).

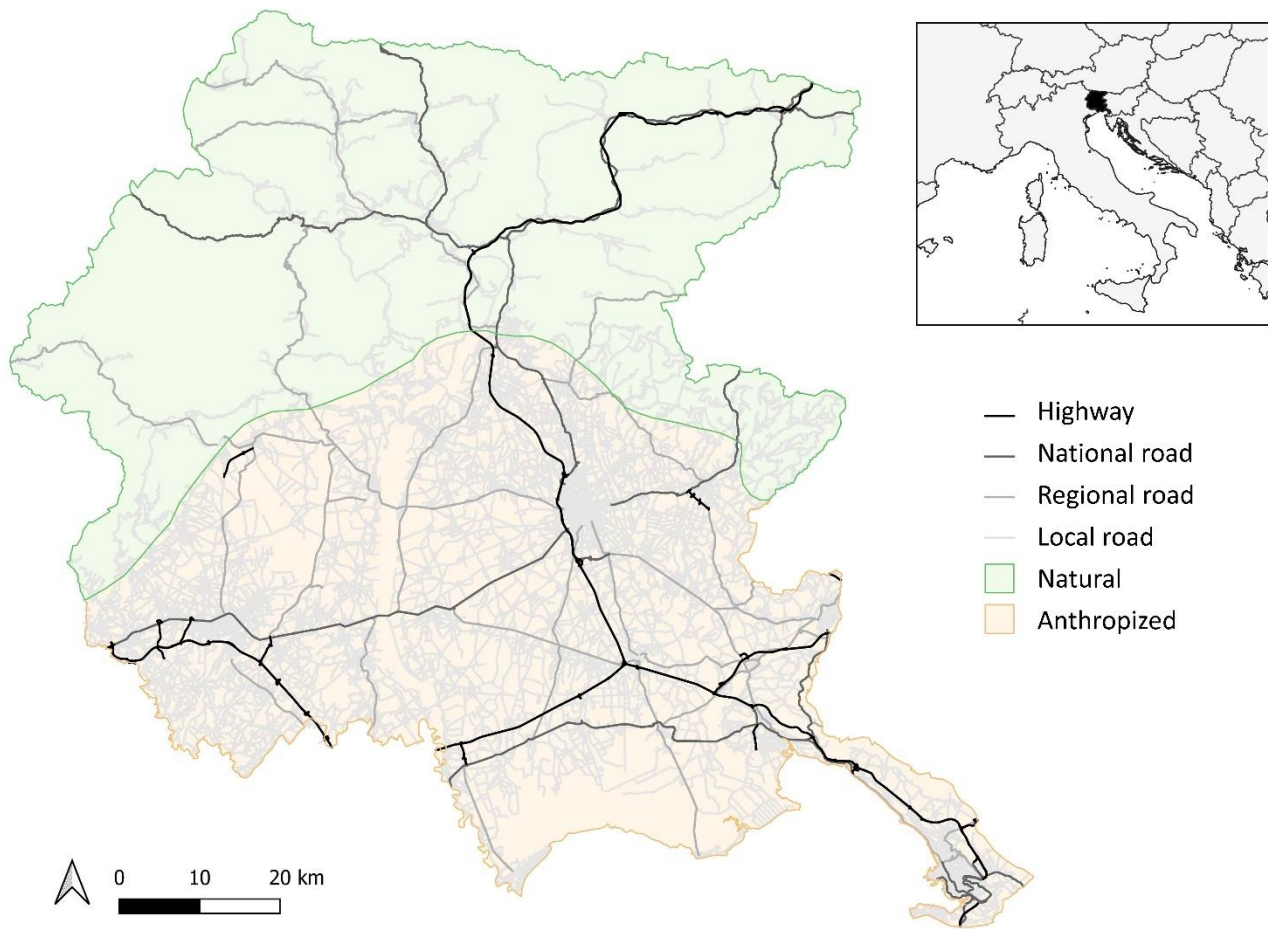


Figure 3.1 - The road network and landscape types of the study area are depicted, with the 'natural' landscape shown in green and the 'anthropized' in orange. These areas correspond to the alpine and continental biogeographical regions of Friuli Venezia Giulia in northeastern Italy. Shades of black represent various road types, ranging from highways to local roads.

3.2.2 Roadkill and species mobility group classification

Roadkill data were recorded from November 2019 to January 2023 and were obtained via the InfoFaunaFVG data repository, created for the monitoring, rescue and veterinary care of debilitated and/or dead wildlife species in the study area (Tomè et al., 2023). All data were opportunistically collected and verified to ensure accurate species identification and determination of the cause of injury or death. From this repository, we selected records of forest mammals injured or dead by vehicle identified at species level.

We divided forest mammals into three different groups according to their movement ability and body size (Kang et al., 2016). We calculated the median dispersal capacity for each species using allometric equations (Santini et al., 2013), utilizing body size and home range, obtained from the PanTHERIA database (Jones et al., 2009), as input data. Species with a median dispersal distance of less than 5 km were classified as *low* mobility, those with a median dispersal distance between 5 and 11 km were

classified as *medium* mobility, and those with a median dispersal distance greater than 11 km were classified as *high* mobility (Appendix 3, Table S3.2).

3.2.3 Roadkill suitability models

We modelled roadkill suitability along the road network separately for each species mobility group using the maximum entropy algorithm (MaxEnt; Phillips et al. 2006; Elith et al. 2006) with the “*ENMeval*” v.2.0.4 R (v.4.3.1, R Core Team, 2023) package (Kass et al., 2021). This method outperformed other presence-only models (Valavi et al., 2022) and it has been previously used to predict road mortality in other studies (e.g., Cerqueira et al., 2021; Fabrizio et al., 2019). To avoid spatial autocorrelation issues and prior to model fitting, we thinned the roadkill data based on home range information using the “*spThin*” v.0.2.0 R package (Aiello-Lammens et al., 2015). This process involves two steps: (i) species-specific thinning, where roadkill data were filtered for each species based on its specific home range; (ii) group-specific thinning, where roadkill data were filtered using the mean weighted home range of each species’ mobility group. The home range of each species was obtained from the PanTHERIA database (Jones et al., 2009) and the mean home range was calculated as the average of the species-specific home range values weighted by the species-specific number of roadkill (Appendix 3, Table S3.2).

In the models, we included predictors likely to influence roadkill suitability (Clevenger et al., 2003; D’Amico et al., 2015), such as elevation and the distance from urban areas, forests, nearest water bodies, cultivated areas, and protected areas calculated in QGIS v.3.28.4. We also included the density of highways and national, regional and local roads as predictors in our models, which were calculated using moving windows equal in size to the weighted mean home range of each species mobility group (Fabrizio et al., 2019). All predictors were calculated with a resolution of 30 m, 60 m and 120 m for the *low*, *medium* and *high* mobility groups to match the subsequent connectivity analyses. To avoid multicollinearity among predictors we removed those with Variance Inflation Factor > 3 (Zuur et al., 2010). Given the possibility that the non-random distribution of our data could lead to biased predictions from MaxEnt models (Kramer-Schadt et al., 2013), we created bias maps for each species group by constructing Gaussian kernel density maps of their roadkill (Worton, 1995). We subsequently overlaid to these bias maps 10,000 background points (Fourcade et al., 2014) constrained within a buffer around the road network of 220 m (for *low*), 660 m (for *medium*) and 2,400 m (for *high*) radius matching the weighted mean home range size for each species mobility group (Fabrizio et al., 2019).

MaxEnt models were trained and tuned using the ENMevaluate function in the “*ENMeval*” v.2.0.4 R package (Kass et al., 2021) with the maxent.jar algorithm (“*dismo*” v.1.3-14 R package; Hijmans et

al., 2020). We chose the ‘block’ method for data partitioning because it is particularly useful to generalize the models beyond the specific environmental conditions present in the training data, thus evaluating transferability to new conditions (Kass et al., 2021). We used the linear and quadratic feature combinations to ensure more ecologically realistic response curves (Bateman et al., 2016) and we tested regularization multipliers between 0.5 and 2, with 0.5 steps, resulting in a total of 12 models (Kass et al., 2021). The model with the lowest Akaike Information Criterion corrected for small sample size (AICc) was selected (Anderson and Burnham, 2002). We used the area under the receiver operating characteristic curve (AUC; Boyce et al., 2002), the difference between calibration and evaluation AUCs (AUCdiff; Warren and Seifert, 2011), the Boyce index (CBI; Hirzel et al. 2006), and the omission rate at 10th percentile to assess models performance.

3.2.4 Road crossability modelling

We applied circuit theory to model forest habitat connectivity in the study area and consequently road crossability along the road network (McRae et al., 2008) using the *Circuitscape* package in Julia v.1.8.0 (Hall et al., 2021). In *Circuitscape*, the landscape is represented as a conductive surface where low resistances denote ease of movement and high resistances indicate barriers (McRae et al., 2009). Focal nodes represent locations from and to which movement flow is to be modelled (McRae et al., 2009). Applying circuit theory, areas with higher current density represent greater animal movement, i.e. wildlife corridors (Wade et al., 2015). The critical step in movement flow modelling is the definition of resistance surfaces, which can be parameterised by several approaches (Dutta et al., 2022). Considering that the multispecies focus of our research required the representation of different landscape permeabilities for distinct species, we chose the alternative approach proposed by de Sousa Miranda et al. (2021) to design the resistance surface. This implied the development of a set of resistance surfaces where possible combinations of resistance values were given for each land cover class. According to ecologically meaningful classes for our species, we reclassified the Corine Land Cover 2018 (CLC; <https://land.copernicus.eu/en/products/corine-land-cover/clc2018>) by merging classes with similar environmental characteristics in order to obtain five classes: forested areas, urban areas, agricultural areas, heterogeneous and non-forested natural areas (see Appendix 3, Table S3.1 for more details). Heterogeneous areas included diverse land covers like cultivation with significant areas of natural vegetation and agroforestry, while non-forested natural areas covered natural features without trees, such as grassland and pastures. We used the reclassified map of land cover as the basis for designing the set of resistance surfaces. As in de Sousa Miranda et al. (2021) and Bowman et al. (2020), we considered the resistance values ranging from 1 (no resistance) to 100 (maximum resistance) to animal movement. For all the resistance surfaces, we assigned the lowest resistance to

forest class, as we have considered mammals with high forest habitat suitability, and the highest resistance to urban areas. For the three remaining land cover classes, we assigned three resistance values, i.e. high (90), medium (50) and low (10), taking into account the different levels of resistance for each class (de Sousa Miranda et al., 2021). Altogether, we defined 27 distinct resistance surfaces based on all possible combinations of the resistance values.

Our multi-species approach required us to consider not only the different levels of landscape permeability to species movement, but also the different grains of resistance surface (pixel resolution). The grain should match the perceptual grain of the species, depending on the specific type of connectivity being modelled, and should be selected based on the species characteristics such as organism size, dispersal and movement type (Wade et al., 2015). Since we included species with different characteristics, we selected three different spatial resolutions of the resistance surfaces. Based on the movement capacity of the species, we chose a pixel size of 30 m for species with *low* dispersal ability, 60 m for species with *medium* dispersal ability and 120 m for species with *high* dispersal ability (Wade et al., 2015). This resulted in a total of 81 resistance surfaces (i.e. 27 resistance surfaces for each spatial resolution).

For each of the resistance surfaces, we run a model setting the 8-cell neighbourhood rule and the pairwise modelling mode (McRae et al., 2013). We randomly placed 50 focal nodes in a 30 km buffer around the study area, corresponding to approximately 20% of the maximum length in our study area, to remove the effects of high current densities near the node placement (Koen et al., 2014). Each model returned a cumulative current density map. We then summed these to obtain a final consensus map for each resolution, thus obtaining a 30 m pixel map, a 60 m pixel map and a 120 m pixel map (de Sousa Miranda et al., 2021).

3.2.5 Roadkill suitability and road crossability relationship

To assess the correlation between roadkill suitability and road crossability we used the Sperman's correlation coefficient (ρ ; Zar 2005). Specifically, we calculated ρ by considering the pixel values of roadkill suitability and road crossability for the whole study area and separately for the natural and the anthropized landscapes, to test whether the correlation between roadkill suitability and road crossability differs between areas with different environmental conditions. Before estimating the correlation, we recalculated both roadkill suitability and road crossability using moving windows with a size equal to the weighted mean home range for each species mobility group. In this way, we accounted for the effects of the surrounding environments within the species' home range. To consider only the relationship along the road, we then clipped both roadkill suitability and road crossability

layers for each group using a buffer around the road network of 30 m, 60 m and 120 m for *low*, *medium* and *high* mobility.

Finally, we categorised both roadkill suitability and road crossability maps into terciles, thus dividing their values into low, medium and high (Medrano-Vizcaíno et al., 2023). Nine joint categories were obtained and mapped using bivariate choropleth maps in QGIS v.3.28.4. In this way, we identified and mapped the PABEMS (both roadkill suitability and road crossability high), PARoMs (high roadkill suitability and low road crossability) and PACoPs (low roadkill suitability and high road crossability). This procedure was repeated for the entire study area and separately for the natural and anthropized landscapes. Then, for each of the nine categories, we calculated the density of roadkill and the percentage of the road network included in each category.

3.3 RESULTS

From November 2019 to January 2023, 4,882 roadkill (involving dead or injured animals) of 15 mammals were recorded across the road network in our study area (Appendix 3, Table S3.2). Species characteristics vary widely, from the body size and home range of the edible dormouse (*Glis glis*) (0.13 kg and 0.001 km²) to those of the Eurasian wolf (*Canis lupus*) (31.76 kg and 159.860 km²; Appendix 3, Table S3.2). The *low* mobility group included a total of 81 roadkill of five species: *Glis glis*, *Sciurus vulgaris*, *Erinaceus europeaeus*, *Mustela nivalis* and *Mustela putorius* (Appendix 3, Table S3.2). The *medium* mobility group included a total of 3,961 roadkill of seven species: *Meles meles*, *Felis silvestris*, *Martes martes*, *Martes foina*, *Capreolus capreolus*, *Canis aureus* and *Vulpes vulpes* (Appendix 3, Table S3.2). The *high* mobility group included 840 roadkill of three different species: *Sus scrofa*, *Cervus elaphus* and *Canis lupus* (Appendix 3, Table S3.2). The most common species recorded was roe deer *Capreolus capreolus*, followed by red fox *Vulpes vulpes*, European badger *Meles meles*, wild boar *Sus scrofa* and red deer *Cervus elaphus*. The *low* mobility group had a weighted mean home range of 0.12 km², the *medium* mobility group 1.38 km² and the *high* mobility group 18.18 km².

Model performance values of the best fitting models for roadkill suitability ranged from 0.63 to 0.70 AUC testing and 0.49 to 0.80 CBI (Table 3.1). The differences between training and testing AUCs (AUCdiff) were low for all species groups, ranging from 0.08 to 0.12, indicating limited overfitting problems, and the 10th percentile omission rates ranged from 0.13 to 0.20, indicating good prediction accuracy (Scridel et al., 2021; Table 3.1).

Table 3.1 - Sample sizes ("thinned roadkill") used in the roadkill suitability analyses, alongside the MaxEnt best-performing model settings and performance metrics for each species mobility group. "FC" denotes the feature classes: "Linear" (L), "Quadratic" (Q), and the hybrid (LQ) model; "RM" refers to the Regularization Multiplier; "AUC" stands for the Area Under the Curve; and "CBI" denotes the Continuous Boyce Index. "OM-10" represents the 10th percentile threshold omission rates.

Species mobility group	Thinned roadkill	FC	RM	AUC training	AUC testing	AUC diff	CBI training	CBI testing	OM-10
<i>Low</i>	79	LQ	0.5	0.782	0.698	0.085	0.945	0.698	0.204
<i>Medium</i>	2656	Q	0.5	0.655	0.632	0.098	0.995	0.802	0.133
<i>High</i>	164	LQ	1	0.678	0.644	0.125	0.960	0.489	0.165

For the *low* mobility group, the variables that contributed more in the final model were the distance from cultivated and urban areas (quadratic relationship), as well as the density of national roads (quadratic) and highways (negative) (Appendix 3, Figure S3.1 and S3.2, Table S3.3). The roadkill suitability for the *medium* mobility group was mostly affected by density of local roads (negative), the distance from cultivated (positive) and forested areas (negative), and the density of national roads (positive) (Appendix 3, Figure S3.3 and S3.4, Table S3.4). The best model for the *high* mobility group showed that roadkill suitability increased at lower altitudes, near forested areas and at greater distances from cultivated areas (Appendix 3, Figure S3.5 and S3.6, Table S3.5). The outputs of the MaxEnt models indicated high roadkill suitability for all mobility groups located in the natural landscape (Figure 3.2). In contrast, in the anthropized landscape, *medium* and *high* mobility groups showed a higher roadkill suitability near natural and forested areas, especially in the south-eastern region (karst), while for the *low* mobility group higher roadkill suitability is predicted near urban areas (Figure 3.2). The *Circuitscape* outputs showed significantly higher cumulative current in the northern part of the study area (natural landscape) and in the south-east region (karst), while current values decreased towards the south-west (Figure 3.2).

We found notable differences in the correlations between roadkill suitability and road crossability across species mobility groups and landscapes (Table 3.2). In the entire study area, our results showed no correlation for *low* mobility group ($\rho = -0.06$), and a positive correlation for *medium* ($\rho = 0.53$) and *high* mobility groups ($\rho = 0.73$; Table 3.2). We also found notable differences in the correlations between road crossability and roadkill suitability between the natural and anthropized landscapes. Indeed, positive correlations were found in the anthropized landscape, similar to those found for the whole study area, with higher coefficient values associated with species movement ability (Table 3.2).

Conversely, in the natural landscape, where roadkill suitability and crossability were generally higher, correlations were weaker or absent compared to those in the anthropized landscape (Table 3.2).

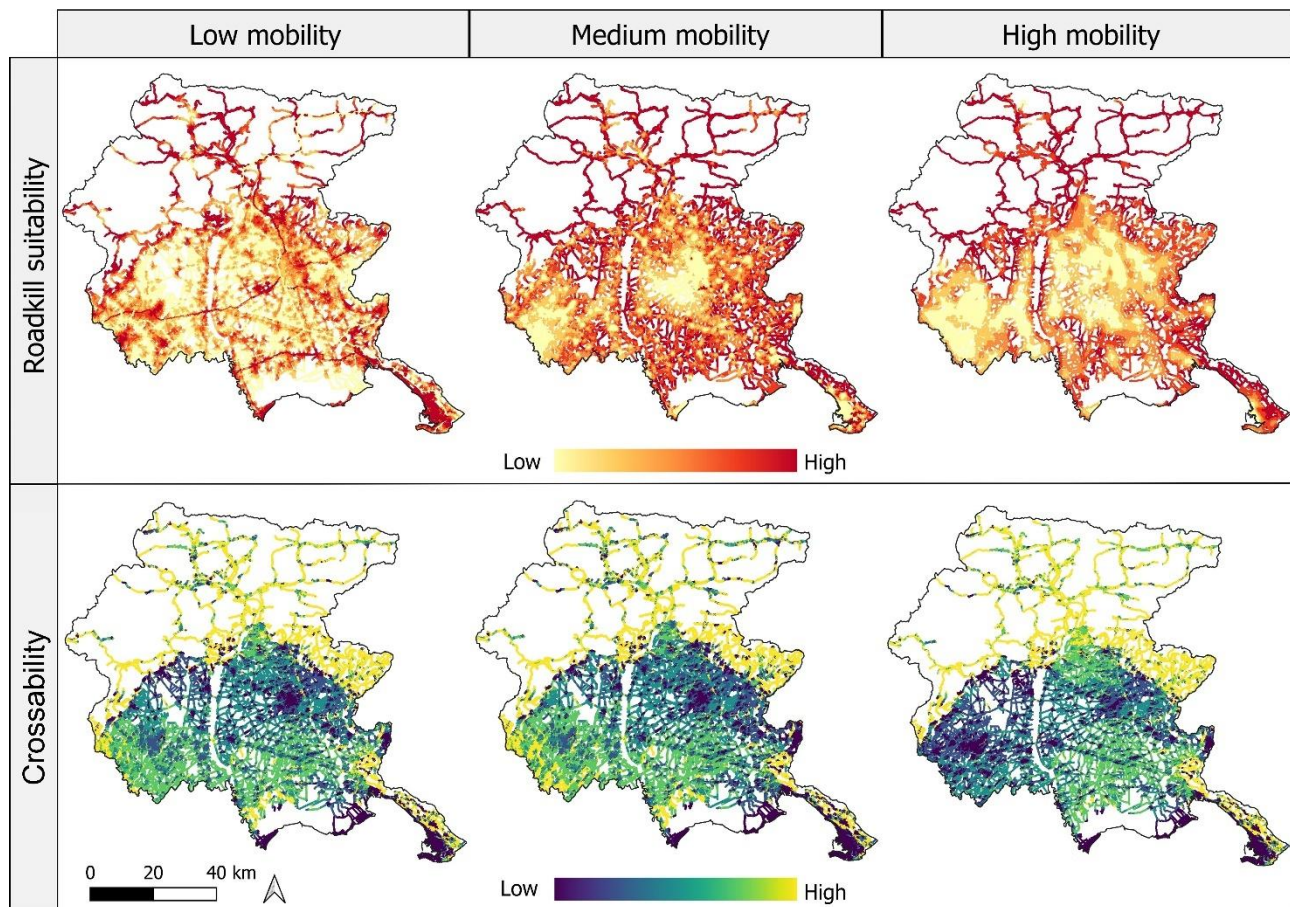


Figure 3.2 - Roadkill suitability and road crossability recalculated using moving windows equal in size to the weighted mean home range of low, medium and high mobility species groups along the road network of the study area.

Table 3.2 - Results of the Spearman (ρ) correlations between roadkill suitability and crossability, recalculated using moving windows equal to the weighted mean home range for the study area and the two landscapes for each mobility species group.

Species mobility group	Study area	Natural landscape	Anthropized landscape
Low	-0.058	-0.165	-0.266
Medium	0.527	0.229	0.374
High	0.726	0.100	0.602

The bivariate choropleth map (Figure 3.3) determined the location of the PABEMs, PARoMs and PACoPs (Figure 3.4) for each species mobility group and landscape. The maps of the *low* mobility group showed less overlap of the PABEMs compared to those of the *medium* and *high* mobility group (Figure 3.3 and 3.4; Appendix 3, Tables S3.6, S3.7 and S3.8). This difference was more pronounced in the anthropized landscape, where the percentage of the road network classified as high road crossability and high roadkill suitability was 8.86% for the *low* mobility group, 16.04% and 21.93% for *medium* and *high* mobility group (Appendix 3, Table S3.8). In the natural landscape, only areas with high roadkill suitability, i.e. PARoMs, contained higher roadkill densities (Appendix 3, Table S3.7). In contrast, in the anthropized landscape, higher roadkill densities were found in areas with both high roadkill suitability and road crossability, i.e. PABEMs, and in areas with high roadkill suitability only, i.e. PARoMs (Figure 3.3 and 3.4, Appendix 3, Table S3.8). The PABEMs of the *low* mobility group were more limited and scattered than those of the *medium* and *high* mobility groups, which are particularly concentrated in the south-east and north of the anthropized landscape, corresponding to the presence of more natural areas (e.g. karst, Figure 3.4). Similarly, PARoMs are dispersed for *low* mobility group and concentrated in the central-east of the anthropized landscape for *medium* and *high* mobility groups. On the other hand, PACoPs are widespread for the *low* mobility group and more restricted for the *high* mobility group (Figure 3.4).

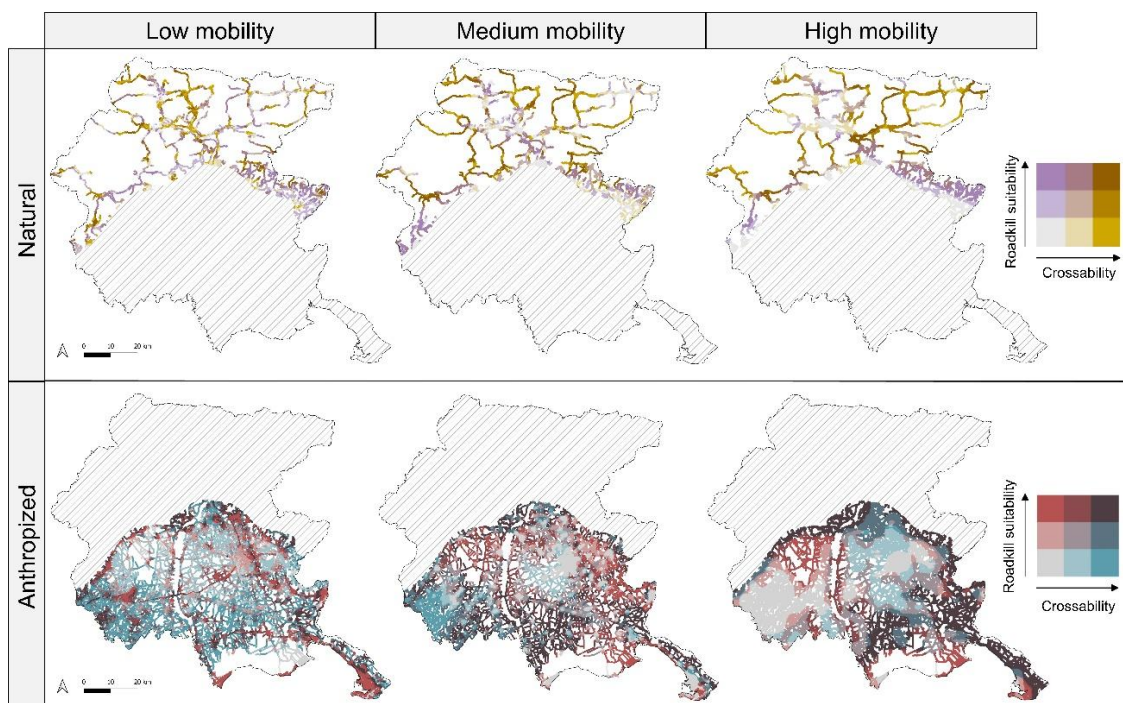


Figure 3.3 - Bivariate choropleth maps highlighting the nine categories based on terciles values for roadkill suitability and road crossability. Class values were calculated using moving windows according to the weighted mean home range. The terciles were calculated separately for the two landscape type (natural and anthropized) and for each species mobility group (low, medium and high).

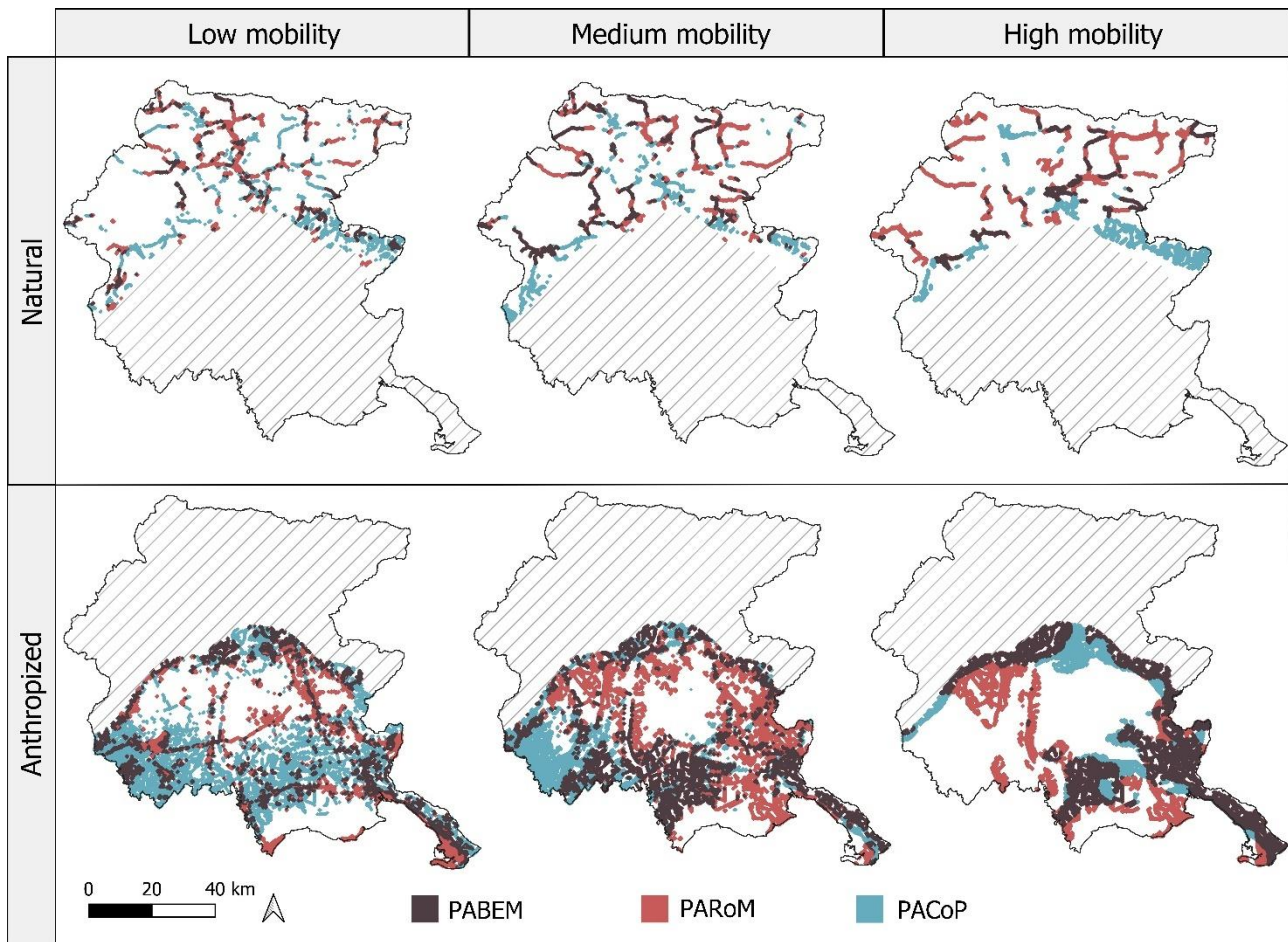


Figure 3.4 - Spatial distribution of the Potential Areas for Barrier Effect Mitigation (PABEM), Potential Areas for Roadkill Mitigation (PARoM) and Potential Areas for Connectivity Preservation (PACoP) across the two landscape types (natural and anthropized) and for low, medium and high species mobility groups.

3.4 DISCUSSION

By introducing two novel concepts in road ecology, the roadkill suitability and road crossability, our study provided new insights into the complex relationship between road mortality and habitat connectivity. The integration of these two concepts enabled us to propose a new approach to prioritising roads for connectivity conservation (PACoPs), and road impact mitigation (PARoMs and PABEMs). Our findings demonstrate the complexity of the relationship between roadkill suitability and road crossability, highlighting the variability among species with different movement abilities and across distinct landscapes. Indeed, our results revealed a positive correlation between roadkill suitability and road crossability for *medium* and *high* mobility species groups, whereas no correlation was observed for *low* mobility species. Furthermore, a clear distinction emerged between the two landscapes we considered, the natural and anthropized landscape. Correlation patterns within the anthropized landscape resembled those of the entire study area, where the degree of overlap between wildlife corridors crossing roads and areas of high roadkill suitability increased with increasing

species mobility. In contrast, in the natural landscape, correlations were weaker or absent for all the species groups, suggesting region-specific factors influencing wildlife mortality and movement.

Species with different movement abilities respond differently to the presence of roads due to their distinct ecological and behavioural traits (Rytwinski and Fahrig, 2012). *High* and *medium* mobility species tend to cover larger areas, making them more susceptible to encountering roads (González-Suárez et al., 2018), and therefore have higher roadkill suitability in areas where the movement is facilitated, i.e. with high road crossability. This may explain the relationship found for these species groups, which have a higher overlap of high roadkill suitability areas with high road crossability areas. Conversely, *low* mobility species have smaller home ranges and fewer dispersal movements, limiting their exposure to roads (Rytwinski and Fahrig, 2012). This limited movement range and the weak correlation found between road crossability and roadkill suitability suggest that interactions with roads are less frequent and the roadkill pattern is more dependent on local habitat characteristics rather than wider landscape connectivity. Furthermore, studies have demonstrated the barrier effect of roads on mammals (Rytwinski and Fahrig, 2015), affecting species with varying mobility (Chen and Koprowski, 2019; Grilo et al., 2018). Chen and Koprowski (2019) found that the barrier effects of roads decrease as species' body size, and consequently movement abilities, increase. Medium-sized carnivores and large ungulates can easily cross minor roads but tend to avoid high-traffic roads (Underhill and Angold, 2000), whereas narrow, low-traffic roads may inhibit small mammals' movement (Galantinho et al., 2022). Though with species-specific variations, large mammals are generally less susceptible to roads' barrier effect than small mammals, as even narrow roads can significantly reduce their crossing. The barrier effect may also explain the low correlation found between road crossability and roadkill suitability for the *low* mobility species group: although our modelling identified wildlife corridors for *low* mobility species, some of these corridors crossing roads could not be effectively used because of the barrier effect.

Another interesting result was the landscape-level difference in the relationships between road crossability and roadkill suitability. Both factors varied greatly between natural and anthropized landscape, with generally higher crossability and roadkill suitability in the natural (Figure 3.2). However, for *medium* and *high* mobility species, correlations were weaker or absent compared to the anthropized landscape, suggesting that in fragmented areas, connectivity may play a more important role in shaping roadkill patterns. This can be attributed to the natural landscape's higher permeability and more extensive forested areas, which facilitate multiple movement pathways for wildlife (Pither et al., 2023). Consequently, the dispersed movements in this landscape could reduce the likelihood of wildlife being channelled into specific road crossings where there would be higher likelihood of roadkill. *Circuitscape* models are also designed to highlight movement bottlenecks where high

current densities are more concentrated due to high resistance in the surrounding areas (McRae et al., 2008). These movement bottlenecks are particularly evident in the anthropized landscape, where high fragmentation of forested areas force wildlife to move more frequently through human-altered environments (Hilty et al., 2019). As animals move between isolated forest habitat patches using well-defined and concentrated movement corridors, they frequently encounter roads, increasing the likelihood of roadkill. Considering this, the positive correlation observed for *medium* and *high* mobile species could be attributed to increased movement along these corridors, increasing their exposure to specific road crossing points with higher roadkill suitability.

Our multi-species approach was similarly used in both connectivity (de Sousa Miranda et al., 2021) and roadkill (Kang et al., 2016) studies. One of the main advantages of this approach is its ability to create general models that can be applied to a wide range of species, facilitating more comprehensive conservation strategies, but it has inherent limitations. The *Circuitscape* and *Maxent* models used may suffer from reduced accuracy when different species are grouped together, potentially lacking the precision of species-specific models. This could lead to less accurate predictions for individual species, as the unique ecological and behavioural characteristics of each species may not be fully captured. Despite this, our results are coherent with those from species-specific studies. For example, in our same study area the habitat connectivity and roadkill models highlight similar results for golden jackal, one of our *medium* mobility species (Frangini et al., 2022; Torretta et al., 2020). Mayer et al. (2021) found that more vehicle collisions of red deer occurred in areas with high forest cover as found for the *high* mobility species in our study, while the occurrence of roadkilled hedgehogs was positively associated with cultivated areas, as for the *low* mobility species (Canova and Balestrieri, 2019).

Recent attention to biases in roadkill data is increasingly highlighting their importance and potentially revolutionising road ecology studies (Barrientos et al., 2021, 2018; Román et al., 2024). Indeed, roadkill data, especially those collected opportunistically, are often subject to biases such as carcass-location, persistence and observation bias, which can distort the interpretation of roadkill risk and distribution. By redefining roadkill locations as a measure of suitability for detection rather than actual risk, our approach provides a more nuanced understanding and, while acknowledging the limitation, presents a more realistic interpretation of what roadkill locations mean. By using roadkill suitability combined with the other new concept of road crossability, we provided a first assessment of road impacts and zoned the road network based on the potential conservation and/or management measures required. This assessment could guide conservation and mitigation efforts by identifying different areas that require further investigation to accurately place mitigation measures. The PABEMs could represent true roadkill hotspots, as many animals could be roadkilled or more detected

and road crossability is potentially high. In these areas, once the roadkill hotspot has been confirmed by further analysis, mitigation measures will be required to prevent roadkill and maintain connectivity, such as wildlife crossings. Once confirmed by further analysis, the PARoMs may represent roads with high mortality due to some road characteristics that increase the risk to be roadkilled that should be removed as a mitigation measure. Finally, the PACoPs should be further investigated to understand whether these areas actually have few roadkill or whether they are areas particularly suited to roadkill data bias. If roadkill numbers are indeed low, the factors influencing them (e.g., low traffic) should be preserved to maintain connectivity.

Our zoning approach included the complex and varied relationships between species groups and different landscape types, but the method can be reproduced and adapted to other species or taxa and different environmental conditions, providing a versatile tool for guiding road impact mitigation and conservation planning.

APPENDIX 3

Figure S3.1 - Percentage contribution of variables in the best model for the group of species with low mobility according to MaxEnt models.

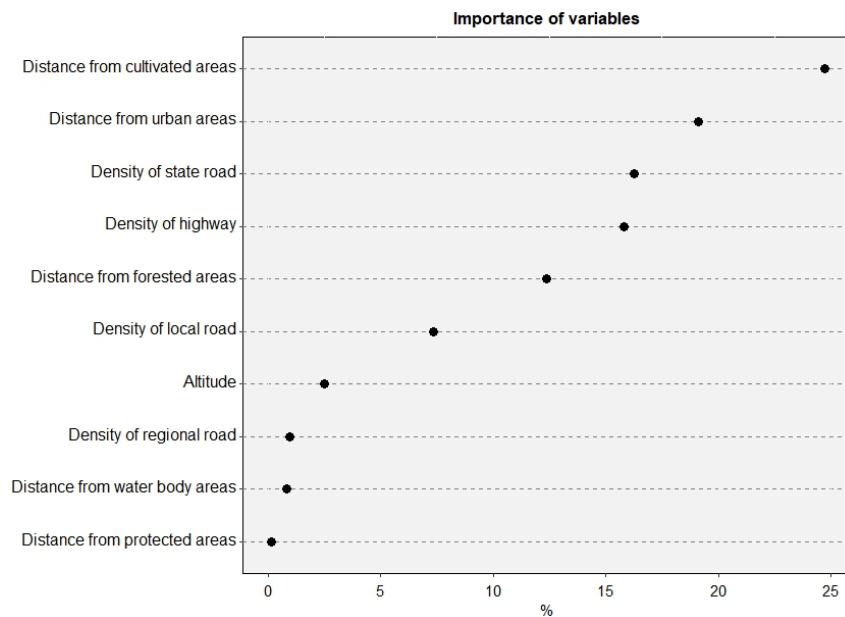


Figure S3.2 - Response curves of the variables included in the best MaxEnt model of the low mobility species group, 'predicted values' represent the roadkill suitability.

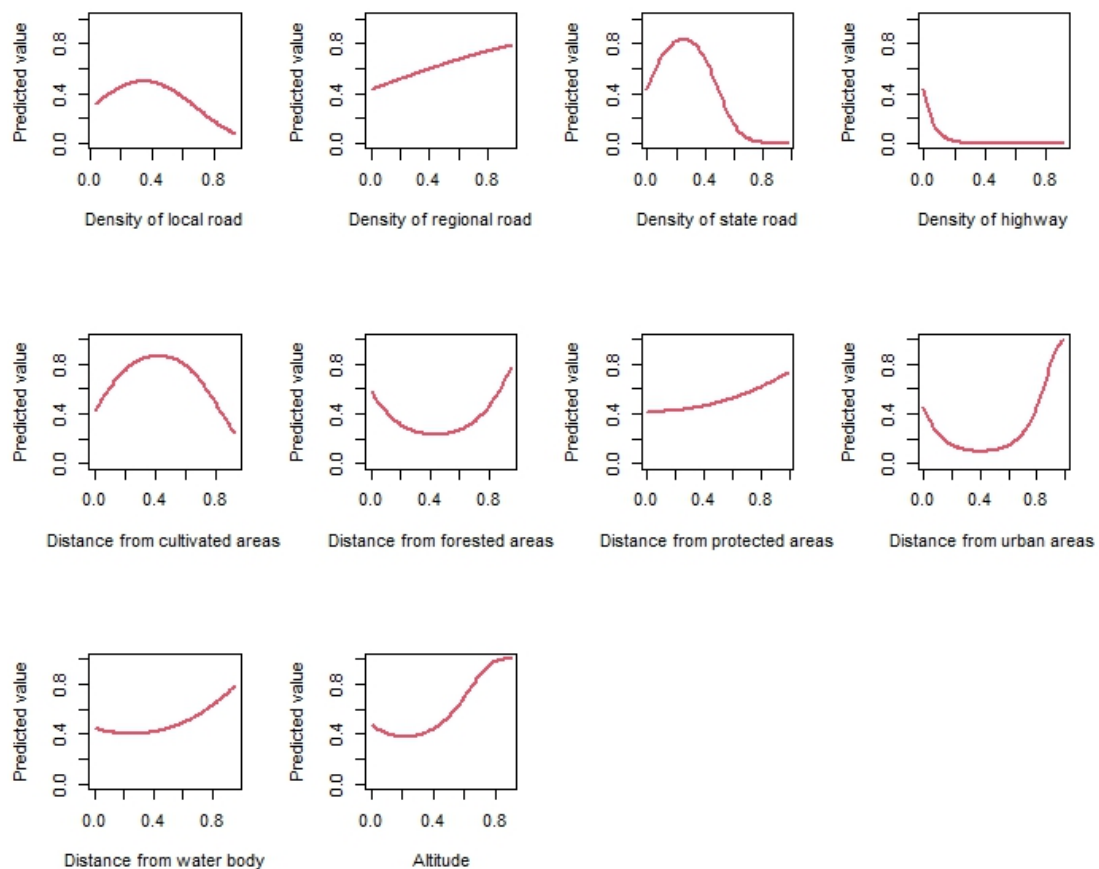


Figure S3.3 - Percentage contribution of variables in the best model for the group of species with medium mobility according to MaxEnt models.

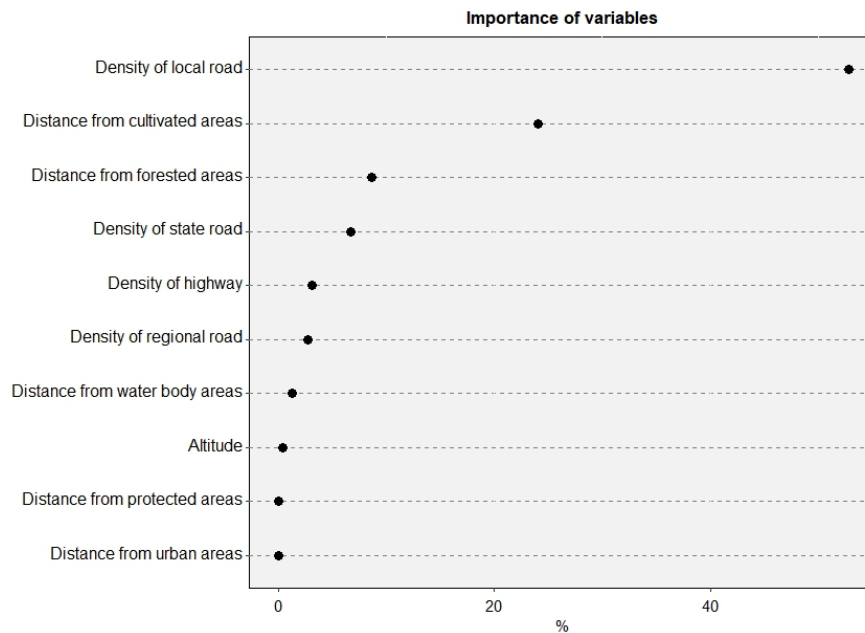


Figure S3.4 - Response curves of the variables included in the best MaxEnt model of the medium mobility species group, 'predicted values' represent the roadkill suitability.

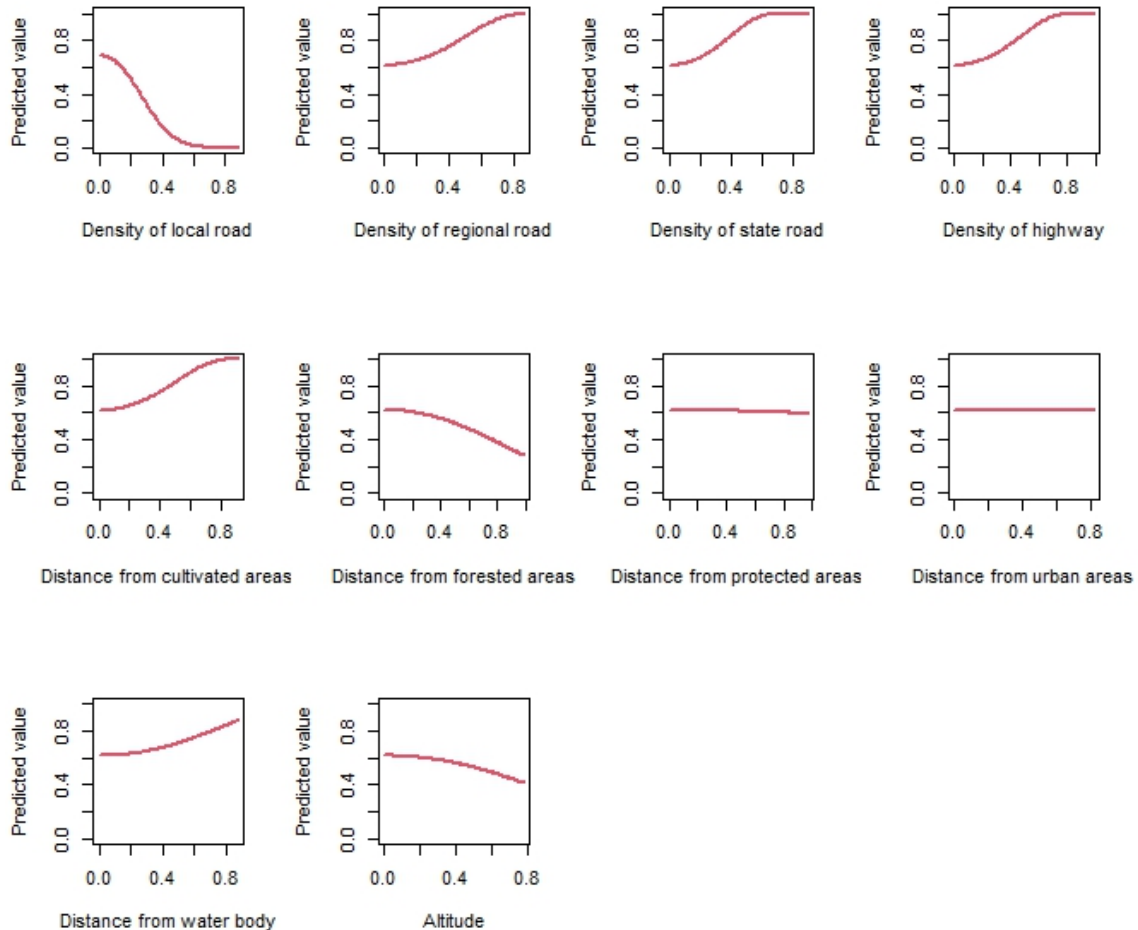


Figure S3.5 - Percentage contribution of variables in the best model for the group of species with high mobility according to MaxEnt models.

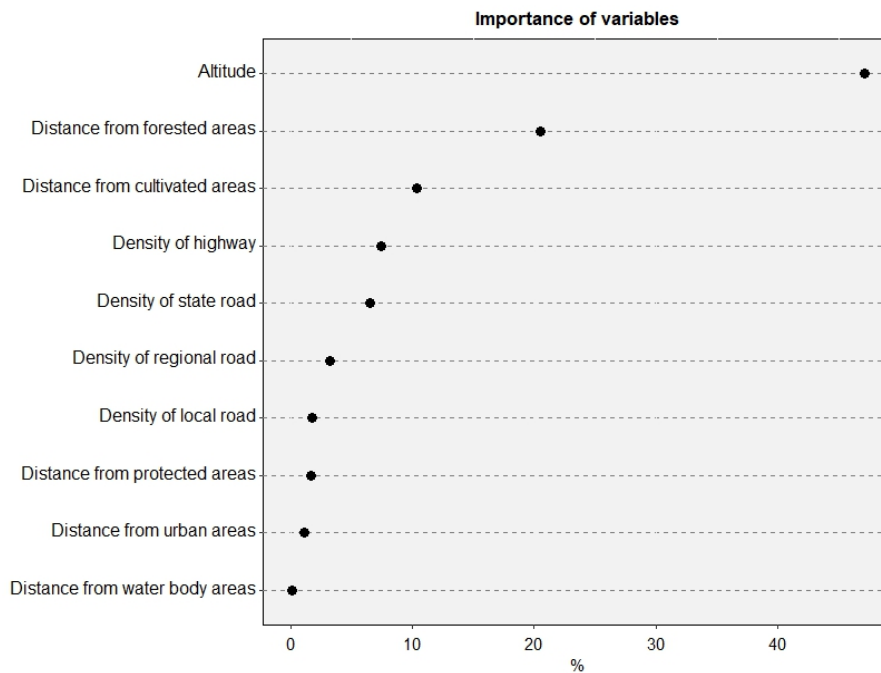


Figure S3.6 - Response curves of the variables included in the best MaxEnt model of the high mobility species group, 'predicted values' represent the roadkill suitability.

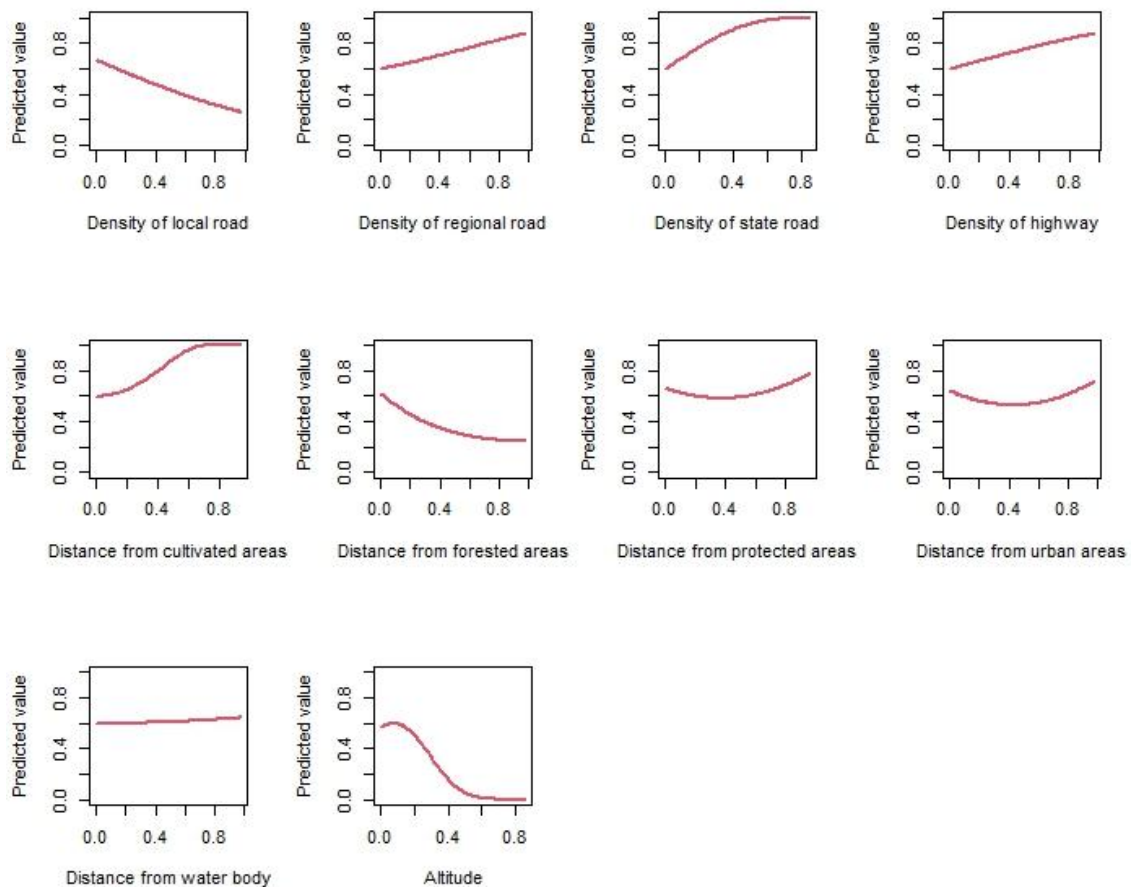


Table S3.1 - Corine Land Cover 2018 (CLC18) categories merged into the five classes used in the Circuitscape models, and the landscape types associated with each land cover category.

CLC18	Description	Class	Landscape type
111	Continuous urban fabric	Urban areas	Anthropized
112	Discontinuous urban fabric	Urban areas	Anthropized
121	Industrial or commercial units	Urban areas	Anthropized
122	Road and rail networks and associated land	Urban areas	Anthropized
123	Port areas	Urban areas	Anthropized
124	Airports	Urban areas	Anthropized
131	Mineral extraction sites	Urban areas	Anthropized
132	Dump sites	Urban areas	Anthropized
133	Construction sites	Urban areas	Anthropized
141	Green urban areas	Urban areas	Anthropized
142	Sport and leisure facilities	Urban areas	Anthropized
211	Non-irrigated arable land	Cultivated areas	Anthropized
212	Permanently irrigated land	Cultivated areas	Anthropized
213	Rice fields	Cultivated areas	Anthropized
221	Vineyards	Heterogeneous areas	Anthropized
222	Fruit trees and berry plantations	Heterogeneous areas	Anthropized
223	Olive groves	Heterogeneous areas	Anthropized
231	Pastures	Non-forested natural areas	Anthropized
241	Annual crops associated with permanent crops	Heterogeneous areas	Anthropized
242	Complex cultivation patterns	Cultivated areas	Anthropized
243	Land principally occupied by agriculture, with significant areas of natural vegetation	Heterogeneous areas	Natural
244	Agro-forestry areas	Heterogeneous areas	Natural
311	Broad-leaved forest	Forested areas	Natural
312	Coniferous forest	Forested areas	Natural
313	Mixed forest	Forested areas	Natural
321	Natural grasslands	Non-forested natural areas	Natural
322	Moors and heathland	Non-forested natural areas	Natural
323	Sclerophyllous vegetation	Forested areas	Natural
324	Transitional woodland-shrub	Forested areas	Natural
331	Beaches, dunes, sands	Non-forested natural areas	Natural
332	Bare rocks	Non-forested natural areas	Natural
333	Sparsely vegetated areas	Non-forested natural areas	Natural
334	Burnt areas	Non-forested natural areas	Natural
335	Glaciers and perpetual snow	Non-forested natural areas	Natural
411	Inland marshes	Non-forested natural areas	Natural
412	Peat bogs	Non-forested natural areas	Natural
421	Salt marshes	Non-forested natural areas	Natural
422	Salines	Non-forested natural areas	Natural
511	Water courses	Non-forested natural areas	Natural

CLC18	Description	Class	Landscape type
512	Water bodies	Non-forested natural areas	Natural

Table S3.2 - Details and numbers of roadkill of the species selected in this study and their classification into low, medium and high mobility species groups. Body size and home range were obtained from the PanTHERIA database (Jones et al., 2009), while median dispersal distances were calculated using the allometric equation of Santini et al. (2013).

Mobility species group	Scientific Name	Common Name	Body Size (kg)	Home range (km ²)	Median dispersal distance (km)	N of roadkill	Thinned roadkill	
							species-specific	weighted home range
Low Median dispersal distance < 5 km	<i>Glis glis</i>	Edible dormouse	0.128	0.001	0.279	1	1	79
	<i>Sciurus vulgaris</i>	Eurasian red squirrel	0.333	0.050	0.688	35	33	
	<i>Erinaceus europaeus</i>	Western European hedgehog	0.778	0.080	1.059	33	33	
	<i>Mustela nivalis</i>	Least weasel	0.078	0.070	1.482	2	2	
	<i>Mustela putorius</i>	Western polecat	0.976	0.530	4.077	10	10	
Medium 5 < Median dispersal distance < 11 km	<i>Capreolus capreolus</i>	Roe deer	22.502	0.520	5.848	2,320	1,409	2,656
	<i>Meles meles</i>	Eurasian badger	11.884	1.200	6.134	605	495	
	<i>Felis silvestris</i>	European wildcat	4.573	1.290	6.360	70	62	
	<i>Martes martes</i>	Pine marten	1.300	2.150	8.211	18	18	
	<i>Martes foina</i>	Stone marten	1.675	2.150	8.211	97	93	
	<i>Canis aureus</i>	Golden jackal	9.659	2.950	9.618	63	51	
High Median dispersal distance > 11 km	<i>Vulpes vulpes</i>	Red fox	4.820	3.500	10.477	788	528	164
	<i>Sus scrofa</i>	Wild boar	84.472	1.180	11.584	470	224	
	<i>Cervus elaphus</i>	Red deer	240.867	58.420	31.390	361	70	
	<i>Canis lupus</i>	Wolf	31.757	159.860	70.804	9	7	

Table S3.3 - Values of the models performed for the low mobility species group. In bold the best model, i.e., with $\Delta AICc = 0$.

	FC	RM	AUC training	CBI training	AUC testing	AUC diff	CBI testing	OM-10	AICc	Delta AICc
1	L	0.5	0.728	0.814	0.696	0.079	0.591	0.128	2323.017	34.109
2	Q	0.5	0.675	0.654	0.622	0.047	0.596	0.128	2362.411	73.503
3	LQ	0.5	0.782	0.945	0.698	0.085	0.698	0.204	2288.908	0.000
4	L	1	0.731	0.788	0.698	0.078	0.578	0.128	2323.904	34.995
5	Q	1	0.676	0.808	0.623	0.048	0.597	0.128	2362.841	73.932
6	LQ	1	0.780	0.964	0.699	0.079	0.616	0.191	2294.193	5.285
7	L	1.5	0.733	0.776	0.698	0.076	0.571	0.128	2324.763	35.855
8	Q	1.5	0.676	0.871	0.627	0.048	0.615	0.128	2360.643	71.735
9	LQ	1.5	0.778	0.962	0.702	0.075	0.595	0.178	2299.727	10.819
10	L	2	0.735	0.772	0.699	0.075	0.575	0.115	2322.973	34.065
11	Q	2	0.675	0.847	0.625	0.051	0.668	0.128	2358.205	69.297
12	LQ	2	0.776	0.935	0.707	0.067	0.560	0.115	2305.828	16.919

Table S3.4 - Values of the models performed for the medium mobility species group. In bold the best model, i.e., with $\Delta AICc = 0$.

	FC	RM	AUC training	CBI training	AUC testing	AUC diff	CBI testing	OM-10	AICc	Delta AICc
1	L	0.5	0.667	0.997	0.652	0.080	0.925	0.118	46331.87	139.381
2	Q	0.5	0.654	0.995	0.632	0.098	0.802	0.133	46192.49	0.000
3	LQ	0.5	0.671	0.997	0.669	0.080	0.939	0.117	46280.18	87.693
4	L	1	0.667	0.996	0.652	0.082	0.916	0.119	46334.40	141.910
5	Q	1	0.653	0.995	0.629	0.100	0.797	0.132	46208.00	15.508
6	LQ	1	0.669	0.996	0.663	0.079	0.927	0.112	46296.53	104.040
7	L	1.5	0.666	0.996	0.652	0.085	0.909	0.118	46337.40	144.909
8	Q	1.5	0.650	0.992	0.626	0.102	0.783	0.126	46216.57	24.083
9	LQ	1.5	0.667	0.996	0.655	0.085	0.908	0.117	46309.20	116.707
10	L	2	0.665	0.996	0.652	0.087	0.897	0.119	46339.96	147.476
11	Q	2	0.648	0.996	0.623	0.103	0.761	0.121	46209.40	16.908
12	LQ	2	0.667	0.996	0.652	0.088	0.896	0.119	46322.62	130.130

Table S3.5 - Values of the models performed for the high mobility species group. In bold the best model, i.e., with $\Delta AICc = 0$.

	FC	RM	AUC training	CBI training	AUC testing	AUC diff	CBI testing	OM-10	AICc	Delta AICc
1	L	0.5	0.662	0.973	0.629	0.112	0.597	0.110	4218.651	18.142
2	Q	0.5	0.654	0.966	0.619	0.116	0.476	0.184	4214.012	13.503
3	LQ	0.5	0.681	0.981	0.645	0.129	0.429	0.208	4206.380	5.871
4	L	1	0.663	0.977	0.629	0.114	0.603	0.110	4218.752	18.243
5	Q	1	0.654	0.958	0.619	0.116	0.469	0.184	4214.350	13.841
6	LQ	1	0.678	0.960	0.644	0.125	0.489	0.165	4200.509	0.000
7	L	1.5	0.663	0.973	0.629	0.116	0.623	0.110	4218.949	18.441
8	Q	1.5	0.654	0.956	0.617	0.114	0.400	0.178	4212.599	12.090
9	LQ	1.5	0.677	0.956	0.645	0.122	0.526	0.153	4204.072	3.563
10	L	2	0.663	0.973	0.628	0.118	0.622	0.116	4219.245	18.737
11	Q	2	0.655	0.957	0.616	0.114	0.412	0.172	4213.285	12.776
12	LQ	2	0.675	0.958	0.647	0.121	0.535	0.165	4211.181	10.672

Table S3.6 - Percentage of road network categorised based on roadkill risk and connectivity terciles for the entire FVG for each of the mobility species groups. The colours of the categories refer to those in the bivariate maps (Figure 3.3, main text).

Category		% of road network		
		Low	Medium	High
1	Low connectivity - Low roadkill risk	5.36	17.13	19.92
2	Medium connectivity - Low roadkill risk	13.95	9.32	11.34
3	High connectivity - Low roadkill risk	11.82	9.14	8.10
4	Low connectivity - Medium roadkill risk	10.91	13.39	14.23
5	Low connectivity - High roadkill risk	16.04	6.95	5.39
6	Medium connectivity - Medium roadkill risk	14.01	6.89	2.51
7	High connectivity - Medium roadkill risk	8.53	10.67	7.77
8	Medium connectivity - High roadkill risk	10.60	10.79	10.97
9	High connectivity - High roadkill risk	8.77	15.71	19.77

Table S3.7 - Percentage of road network categorised based on roadkill risk and connectivity terciles for the Alpine biogeographical region in FVG for each of the mobility species groups. The colours of the categories refer to those in the bivariate maps (Figure 3.3, main text).

Category		% of road network			Density of roadkill (n total roadkill/area km ²)		
		Low	Medium	High	Low	Medium	High
1	Low connectivity - Low roadkill risk	7.43	16.08	14.50	0.10	3.71	0.92
2	Medium connectivity - Low roadkill risk	14.24	8.89	8.06	0	2.14	0.06
6	High connectivity - Low roadkill risk	10.42	9.67	11.21	0	1.87	0.17
3	Low connectivity - Medium roadkill risk	9.61	12.93	10.55	0.22	5.73	0.89
5	Low connectivity - High roadkill risk	15.48	7.58	7.48	0.35	6.64	1.29
4	Medium connectivity - Medium roadkill risk	11.66	8.37	11.07	0	3.18	0.35
8	High connectivity - Medium roadkill risk	9.48	11.52	14.87	0.06	3.08	0.36
7	Medium connectivity - High roadkill risk	13.30	10.71	11.60	0.33	4.96	1.46
9	High connectivity - High roadkill risk	8.37	14.25	10.66	0	4.04	0.49

Table S3.8 - Percentage of road network categorised based on roadkill risk and connectivity terciles for the Continental biogeographical region in FVG for each of the mobility species groups. The colours of the categories refer to those in the bivariate maps (Figure 3.3, main text).

Category		% of road network			Density of roadkill (n total roadkill/area km ²)		
		Low	Medium	High	Low	Medium	High
1	Low connectivity - Low roadkill risk	4.90	17.37	21.21	0.04	1.53	0.07
2	Medium connectivity - Low roadkill risk	13.89	9.42	12.12	0.01	1.74	0.11
6	High connectivity - Low roadkill risk	12.13	9.02	7.36	0.01	1.72	0
3	Low connectivity - Medium roadkill risk	11.20	13.50	15.11	0.07	3.02	0.24
5	Low connectivity - High roadkill risk	16.16	6.81	4.90	0.32	5.39	0.55
4	Medium connectivity - Medium roadkill risk	14.54	6.55	0.48	0.05	2.56	0.14
8	High connectivity - Medium roadkill risk	8.31	10.48	6.09	0.02	2.80	0.50
7	Medium connectivity - High roadkill risk	10.00	10.81	10.82	0.21	4.36	0.44
9	High connectivity - High roadkill risk	8.86	16.04	21.93	0.25	3.98	0.82

CHAPTER 4

AN OPTIMISED FRAMEWORK FOR ASSESSING LOSS OF FOREST HABITAT CONNECTIVITY AND A REFORESTATION PLAN FOR A HYDROPOWER PROJECT

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ABSTRACT

The development of renewable energy, such as hydropower, often leads to the loss and fragmentation of terrestrial habitats, with significant effects on biodiversity. However, these impacts are often overlooked or underestimated in Environmental Impact Assessments (EIAs). In this study, we proposed a framework that explicitly consider forest habitat connectivity into EIAs, focusing on both impact assessment and providing recommendation for compensation measures. The framework included (i) an evaluation of forest habitat connectivity loss by comparing before- and after-construction scenarios and (ii) a spatial analysis to prioritise reforestation activities aimed at restoring connectivity for wildlife species with varying movement abilities. We applied this framework to a proposed hydropower project in Nepal and observed major loss of forest habitat connectivity within the project footprint and up to 15 km away, indicating substantial loss of riverine forest connectivity and a wide-scale impact on connectivity. To compensate for this impact, we identified deforested areas by analysing land cover changes from 2000 to 2019 in the study area and along rivers. These areas were ranked using the Integral Index of Connectivity to assess their importance for enhancing habitat connectivity, if reforested. The analysis considered different wildlife dispersal distances (500 m, 1 km and 2 km) to identify priority reforestation areas suitable for species with different movement abilities. Our findings highlight the importance of including habitat connectivity in EIAs and how this approach can guide effective compensation measures, thereby promoting a better balance between energy demand and biodiversity conservation.

KEYWORDS

Compensatory reforestation, Environmental Impact Assessment, hydroelectric, reservoir, terrestrial habitat, wildlife corridors.

HIGHLIGHTS

- EIAs overlook impacts on terrestrial habitat connectivity
- We propose a framework to include habitat connectivity assessment into EIAs and guide compensation measures
- We include an assessment of forest habitat connectivity, comparing before- and after-construction scenarios
- To compensate the loss of habitat connectivity, we identify priority areas for reforestation to improve connectivity

4.1 INTRODUCTION

The transition to renewable energy production is indispensable for reducing greenhouse gas (GHG) emissions and limiting global warming to 1.5 °C, as targeted in the Paris Agreement (2015). The world's largest sources of renewable electricity generation - hydro, solar and wind - have low GHG emissions, and according to the IEA (2024), global renewable capacity is expected to grow 2.7 times by 2030. While hydropower remains the largest and most extensively deployed renewable energy source, its importance is expected to grow less than that of solar and wind (IEA, 2024). Nevertheless, hydropower is anticipated to expand further, particularly in emerging and developing countries, as new projects are planned and commissioned (IEA, 2024; Moran et al., 2018). Hydropower and other renewable energy sources require considerable financial investment and offer substantial energy generation potential. However, they also raise critical environmental concerns and pose complex challenges related to biodiversity conservation (Gibson et al., 2017; Moran et al., 2018). Among renewables, reservoir-based hydropower has the greatest environmental impacts (Gibson et al., 2017), mainly due to the loss and fragmentation of habitats. Most of the scientific literature has focused on the impacts of hydropower on freshwater ecosystems (Japoshvili et al., 2021; Winemiller et al., 2016), riverine biodiversity (He et al., 2024) and mitigation measures for fish species (Haraldstad et al., 2019; Zarri et al., 2022). In contrast, although land use change has been considered as a major impact of hydropower development (Gracey and Verones, 2016), deforestation of natural, biodiversity-rich areas has been documented (Pandit and Grumbine, 2012) and impacts on habitats of terrestrial species have been recognised (Palmeirim and Gibson, 2021), relatively little attention has been paid to terrestrial habitats and their connectivity, even though impacts can be relevant (Dorber et al., 2020; Gracey and Verones, 2016; Pandit and Grumbine, 2012). Ecological connectivity, which is defined as “the unimpeded movement of species and the flow of natural processes that sustain life on Earth” (CMS 2020), plays a critical role in long-term conservation strategies. It is essential for maintaining viable populations, supporting gene flow and allowing species to move and to adapt to environmental changes (Fischer and Lindenmayer, 2007; Hilty et al., 2020). While connectivity impacts of hydropower have been studied in rivers (Anderson et al., 2018; Finer and Jenkins, 2012), its effects on forest connectivity underrepresented in EIAs, with fragmentation often not being quantitatively assessed. Forest fragmentation isolates forest patches and exacerbates edge effect, disrupting habitats and altering biotic and abiotic conditions, and favours the introduction of invasive alien species (Fahrig, 2003). These changes alter wildlife movement, reduce habitat quality and affect ecological networks. Dorber et al. (2023) demonstrated the impact of a hydropower project in Norway on the connectivity of the migratory wild reindeer (*Rangifer tarandus tarandus*). Furthermore, they found that the cumulative effect of hydropower and associated infrastructure extends far beyond the

reservoir, affecting the entire ecological network of reindeer. Similarly, Lan et al. (2024) found that reservoirs in the Indochina Peninsula altered habitat connectivity and exacerbated habitat fragmentation for terrestrial mammals. These examples among the others, clearly confirm the negative effect of reservoir-based hydropower projects on terrestrial habitat connectivity.

The lack of consideration of connectivity in Environmental Impact Assessments (EIAs) is not a new issue (Patterson et al., 2022; Torres et al., 2022). Although many connectivity studies have been published and a wide range of connectivity metrics and modelling techniques are available (CCSG, 2024; Hilty et al., 2020; Keeley et al., 2021), their practical applications in EIAs remains limited (Torres et al., 2022). The main reasons appear to be related to difficulties in quantitative assessment of connectivity and inadequate guidance and national/international legislation (Patterson et al., 2022; Torres et al., 2022). EIAs play a pivotal role in sustainable development, including renewable energy projects (Dorber et al., 2023), and must identify and predict all possible environmental impacts of a proposed project. A key objective of EIAs is to achieve *no net loss* or *net gain* of biodiversity, as outlined by the International Finance Corporation, Performance Standard 6 (IFC, 2019). To achieve this goal, EIAs must include detailed and specific mitigation and/or compensation measures that effectively address environmental impacts. However, impacts on forest habitat connectivity are often not adequately addressed in the measures proposed for hydropower projects.

Here we propose the application of a framework to explicitly include the impact of reservoir-based hydropower on forest habitat connectivity in EIA. This study aims to assess the changes in forest habitat connectivity resulting from the construction of a proposed hydropower project in Nepal, and to support reforestation activities as a compensatory measure committed in the EIA designed to restore and enhance connectivity after project implementation. Nepal, a developing country and a globally recognised biodiversity hotspot (Mittermeier et al., 2011), along with other Himalayan countries, is experiencing a rapid expansion of hydropower development (Pandit and Grumbine 2012; Dhyani 2023; NEA 2024). This is largely due to the mountainous environment of the region, which is particularly suitable for this type of projects and represents a good example to apply the framework of this study. To provide a practical and general framework for enhancing forest habitat connectivity into the implementation of EIA actions, we (i) assessed the extent of forest habitat fragmentation caused by a proposed hydropower project on the Dudh Koshi River in Nepal by modelling habitat connectivity before and after construction, and (ii) used the connectivity models to prioritise potential reforestation areas to compensate for connectivity loss and enhance habitat connectivity.

4.2 MATERIALS AND METHODS

4.2.1 Study area

The framework of this study was applied to a proposed hydropower project located on the Dudh Koshi River in the eastern Nepal, within the Okhaldhunga, Khotang and Solukhumbhu districts (Figure 4.1). The Dudh Koshi River is one of the primary tributaries of the larger Koshi River Basin and is a major tributary of the Sapta Koshi River system. Originating from Imja Peak at an elevation of 6,189 m, the Dudh Koshi River is situated within the Himalayan region near Mount Everest. To set an adequate area of analysis for the application of the proposed methodology, a 25 km buffer around the hydropower project footprint was defined, resulting in a total study area of 3,792 km² (Figure 4.1). This buffer radius was selected considering the median dispersal distance of the common leopard (*Panthera pardus*), a species known to inhabit the area and recognised for its high movement ability. This ensured that study area effectively captured potential impacts also on wide-ranging terrestrial wildlife. The dispersal distance of the common leopard was calculated using the allometric equations of Santini et al. (2013), with home range data from the PanTHERIA database (Jones et al., 2009) as input. Elevation in the study area ranges between 234 to 3859 m asl, with an average of 1500 m asl, resulting in significant climatic variation from severe cold at higher altitudes to warm, humid conditions at lower elevations. Data from the Okhaldhunga meteorological station, close to the expected location of the hydropower project site, indicate a minimum recorded temperature of 3.4°C in January, characteristic of the cold winter conditions in the region. In contrast, the maximum temperature reaches 23.7°C in June, reflecting the warmer climate typical of early summer. Annual rainfall at this station is approximately 1,700 mm per year. The study area spans three main physiographic zones of Nepal (Heinen and Kattel, 1992): the Terai and Inland Terai (below 450 m asl), with most of the area situated in the Middle Hills (between 450 and 3,600 m asl) and a small portion extending into the Himalayan zone (above 3,600 m asl). The vegetation in these zones is very diverse, ranging from subtropical Sal forests with *Dalbergia sissoo* and *Bombax ceiba* in the river plains and lower slopes, to temperate and cold temperate forests with species such as spruce and fir near the tree line, and deciduous species such as oak and rhododendron in the higher elevations (DFRS, 2015). Based on a screening on international open database (IUCN, 2024), the study area hosts 115 mammals, 654 birds, 66 fish, 67 reptiles, and 27 amphibians. Among these, seven species are classified as Critically Endangered (*Indotestudo elongata*, *Manis pentadactyla*, *Aythya baeri*, *Gyps bengalensis*, *Gyps tenuirostris*, and *Sarcogyps calvus*), and ten are categorized as “Amazing Species” due to their unique ecological or cultural significance (*Tor putitora*, *Elephas maximus*, *Axis porcinus*, *Cuon alpinus*, *Ailurus fulgens*, *Panthera tigris*, *Pardofelis marmorata*) (IUCN, 2024).

4.2.2 Before and after habitat connectivity assessment

4.2.2.1. Land cover maps

For the proposed framework, the assessment of impacts on habitat connectivity was carried out for a range of forest wildlife species inhabiting the study area, following the methodology outlined by de Sousa Miranda et al. (2021). Land cover map for 2019 was obtained from the National Land Cover Monitoring System for Nepal (Aryal, 2022) at a spatial resolution of 30 m, and subsequently resampled using the nearest neighbour technique at a resolution of 60 m due to computational limitations. In addition, due to the limited extent of some land cover classes in the study area, we combined the original classes into five categories: Forest, grassland, cropland, water bodies and unsuitable areas (Table 4.1). The mixed forest class included the original *forest* and *other wooded land* classes, the water bodies class included *water body* and *riverbed*, and unsuitable areas included *glaciers*, *snow*, *built-up areas*, *bare soil* and *bare rock*. The classes of cropland and grassland remained unchanged from the original ones. Furthermore, considering the high elevation of some portion of the study area, all areas higher than 3,600 m asl (above the tree line; Sharma et al., 2019) were classified as unsuitable areas. This aggregated land cover map was used to analyse habitat connectivity under current conditions representing the state of habitat connectivity in the study area before the construction of the hydropower project. After-construction, all areas affected by the hydropower project were reclassified in the land cover map as unsuitable areas (Figure 4.1), thus, to obtain the land cover used for the after-construction. All spatial analyses were performed in QGIS v.3.28.10 and R v4.3.1 (R Core Team 2023).

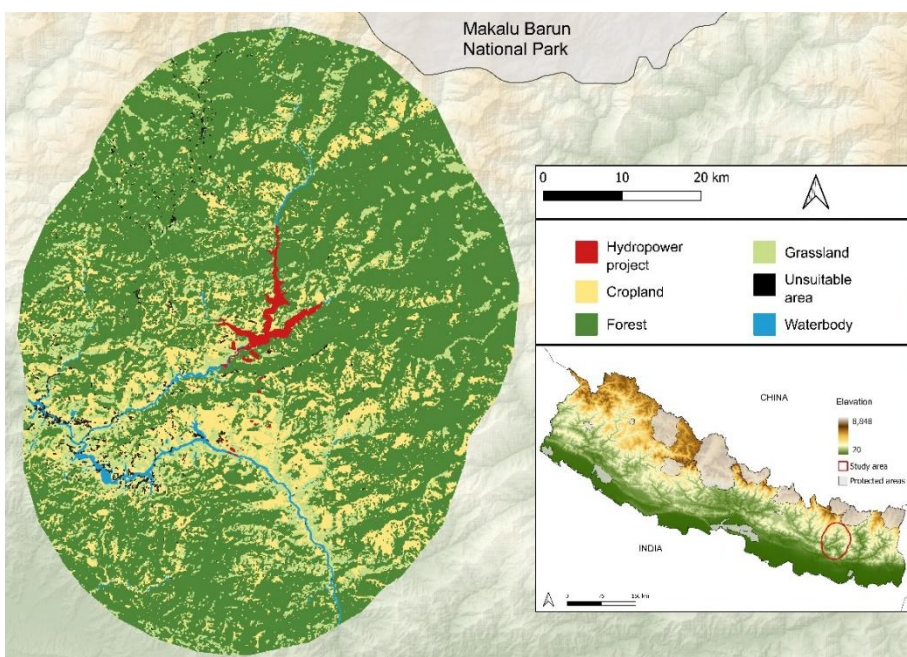


Figure 4.1 - Maps showing the location of the study area in Nepal and the land cover. The footprint of the project is outlined in red. Spatial data have been retrieved from www.nea.org.np/publications and manually georeferenced.

4.2.2.2 Connectivity models

The final reclassified maps (referred hereafter as before- and after-construction land covers) were used to estimate habitat connectivity models before- and after-construction. In particular, we used the circuit theory (McRae et al., 2008) to model forest habitat connectivity in our study area using *Circuitscape* package in Julia v.1.8.0 (Hall et al., 2021). *Circuitscape* represents the landscape through which wildlife has to move as a resistance surface, where each element of the landscape has a resistance value: lower resistance values indicate easier movement and higher resistance values indicate obstacles to movement (McRae et al., 2009). Focal nodes represent the sites from which and to which movement flows (current densities) are to be modelled (McRae et al., 2009). Through the application of circuit theory, areas of higher current density represent greater wildlife movement (Wade et al., 2015). Following de Sousa Miranda et al. (2021), we used the novel approach to parameterise the resistance surfaces by analysing different resistance profiles representing different landscape permeability of ecologically distinct species. In this way, although simplified, this approach allowed us to generalise habitat connectivity for multiple species or taxa, rather than focusing on a single species. This novel approach involved creating a set of resistance surfaces where different combinations of resistance values, ranging from 1 (lowest resistance) to 100 (highest resistance), were assigned to each land cover class (de Sousa Miranda et al., 2021). For all resistance surfaces, the forest class was assigned the minimum resistance value of 1, reflecting its optimal habitat suitability for forest wildlife movement. In contrast, unsuitable areas were assigned the maximum resistance value of 100, indicating their highest level of resistance to wildlife movement (Bowman et al., 2020; de Sousa Miranda et al., 2021). A low (10), medium (50) and high (90) resistance values were alternatively assigned to cropland, grassland and waterbodies classes. By considering all possible combinations of these resistance values, a total of 27 resistance surfaces were defined ($1 \text{ (Forest)} \times 1 \text{ (Unsuitable areas)} \times 3 \text{ (Cropland)} \times 3 \text{ (Grassland)} \times 3 \text{ (Waterbodies)} = 27$ resistance surfaces) for both the before- and after-construction scenarios. For each of the 27 resistance surface, we ran a model setting (i) the 8-cell neighbourhood rule, (ii) the pairwise modelling mode (McRae et al., 2013). We randomly located 50 focal nodes in a 16 km buffer around the study area, i.e. 20% of the maximum length in our study area (Koen et al., 2014), to avoid the effects of high current densities near the focal node. Each of the 27 models generated a raster of cumulative current density, and by summing the results of all models, we obtained a single final map for both the before- and after-construction scenarios.

The change in current density between the two scenarios was quantified for each grid cell as the percentage increase or decrease in current density, with positive values representing an increase in current density and negative values indicating a decrease (Leskova et al., 2022). This was calculated

by subtracting the before-construction map from the after-construction map, dividing the resulting change by the before-construction current density, and then multiplying by 100.

4.2.3 *Optimising the selection of reforestation sites*

4.2.3.1 *Identification of potential areas for reforestation*

To identify all areas suitable for reforestation, we compared the most recent land cover data (2019) with the oldest available (2000; Aryal, 2022) to detect areas that had experienced deforestation in recent years. Specifically, we first reclassified the 2000 land cover raster using the same classes and pixel resolution as the 2019 land cover (Table 4.1) and then compared the change per pixel to identify areas that were forested in 2000 but converted to cropland or unsuitable areas by 2019, and areas that remained forested in 2019. Next, based on the results of the after-construction connectivity model, we selected deforested areas with >20th percentile of current density (de Sousa Miranda et al., 2021). Finally, we created a hexagonal grid of 10 ha cells (de Sousa Miranda et al., 2021), which reduces edge effects and better aligns grid cells with Euclidean distances (Birch et al., 2007), and overlaid it on the identified forested and deforested areas. Hexagonal cells that overlapped 100% of the forested areas were classified as forested, while those that overlapped at least 10% of the deforested areas were classified as deforested. All adjacent forested hexagonal cells were merged (Tambosi et al., 2014), while deforested cells were no merged.

The procedure above described for the identification of potential areas for reforestation was carried out for the whole study area. After this first assessment, we selected deforested hexagonal cells that overlap, intersect or are within the rivers to obtain a set of potential reforestation areas specifically associated with riparian zones. This targeted analysis was conducted because riparian habitats are among the most significantly impacted by the hydropower project. Enhancing connectivity in these areas is crucial as a compensatory measure, given the ecological importance of riparian zones in supporting biodiversity and maintaining habitat continuity along the river corridor. All the analysis to identify potential areas for reforestation were done in QGIS v.3.28.10.

4.2.3.2 *Integral Index of Connectivity*

The Integral Index of Connectivity (IIC) is a widely used metric that evaluates the structural connectivity of habitat patches, accounting for their spatial arrangement, and quantifies the contribution of each patch to maintaining or increasing habitat connectivity (Pascual-Hortal and Saura, 2006; Saura and Rubio, 2010). The IIC is a binary connectivity index, where two patches are connected or not if they are within of beyond a threshold distance (Saura and Rubio, 2010). The IIC

was applied to identify optimal locations for reforestation activities aimed at promoting and enhancing habitat connectivity (Pascual-Hortal and Saura, 2006). Following de Sousa Miranda et al. (2021), we calculated the IIC for each potential reforestation area, represented as deforested hexagonal cells, to determine their contribution to improving habitat availability and connectivity, if reforested. Using Conefor Sensinode 2.6 (Saura and Torné, 2012), we simulated the reforestation of each deforested hexagonal cell, converting them into forested areas (function in Conefor Sensinode 2.6 “node to add”) (Tambosi and Metzger, 2015), and considered forested areas as habitat patches, using the current density from the after-construction scenario divided by patch area as the patch attribute. The importance of each deforested cell was quantified using the variation of the ICC (varIIC), a metric that captures the relative change in connectivity resulting from reforesting a specific cell. Higher varIIC indicated a greater importance on connectivity, helping to prioritise cells for reforestation efforts to achieve maximum benefit. Furthermore, as IIC evaluates connectivity by considering the presence or absence of connections between hexagonal cells based on distance thresholds, we performed the IIC calculations using different distance thresholds (500 m, 1 km and 2 km). These thresholds were selected to simulate species movements with varying dispersal capabilities. After estimating the area of forest loss caused by the project construction, reforestation scenarios were considered by selecting a number of hexagonal cells for each dispersal distance, corresponding to the total estimated area of forest removed.

This analysis was applied to the selected deforested areas throughout the study area to ensure that all potential reforestation sites were assessed for their contribution to improving overall habitat connectivity. Additionally, an alternative approach was also taken focusing exclusively on riparian deforested areas. These were evaluated using the same method described above, including the calculation of varIIC under different dispersal distances (500 m, 1 km and 2 km). By focusing on riparian zones as a subset of the study area, we were able to assess their specific contribution to improving riparian habitat connectivity and to integrate a targeted restoration strategy to compensate for the impacts of a water-related project such as hydropower.

4.3 RESULTS

4.3.1 Forest habitat connectivity loss and changes

The land cover of the study area in 2019 is predominantly forested (60%), with forests being more extensive and continuous in the northern region, while in southern they are more fragmented and interspersed with agricultural land. Croplands (33%) and unsuitable areas, including built-up areas, are primarily located around the water bodies (Figure 4.1 and Table 4.1). The proposed hydropower

project is expected to occupy an area of 23 km², currently dominated by forests and croplands, with a smaller part covered by other land cover classes (Table 4.1). According to the used land cover, a total of 8 km² of the forest class will be lost due to the construction of the hydropower project (Table 4.1).

Table 4.1 - Change in land cover and percentage before and after the construction of the hydropower project. Original land cover classes from Aryal (2022) were reclassified into broader categories and used in this study. Δ represents the comparison between the before and after construction scenarios.

Original land cover class	Land cover class reclassified	Before construction		After construction		Δ	
		Area (km ²)	%	Area (km ²)	%	Area (km ²)	%
Glacier	Unsuitable areas	11	0.29	34	0.90	+23	+0.61
Snow							
Built-up area							
Bare soil							
Bare rock							
Hydropower project							
Water body	Waterbodies	28	0.74	25	0.66	-3	-0.08
Riverbed							
Cropland	Cropland	1271	33.52	1261	33.25	-10	-0.27
Grassland	Grassland	197	5.19	195	5.14	-2	-0.05
Forest	Forest	2285	60.26	2277	60.05	-8	-0.21
Other wooded land							

As the study area is sparsely populated and predominantly forested, all connectivity models identified numerous corridors, with only minor differences throughout the area (Figure 4.2). In the northern region, the higher in term of mean elevation value, the corridors are wider and exhibit a more dispersed current density due to the presence of contiguous forests. In contrast, the southern region shows a more concentrated current density, resulting in narrower and more defined corridors (Figure 4.2). In the project area, current density in the before-construction scenario is generally high but is expected to be entirely lost in the after-construction scenario (Figure 4.2). The construction of the hydropower project will have major impact on habitat connectivity, resulting in the complete loss of corridors within project area and a substantial decrease beyond the project footprint (Figure 4.2). Indeed, reduced current densities of around 10% were observed up to 15 km from the project footprint. Conversely, an increase in current density was observed in the northern and southern surrounding areas of the project, reflecting the adjustment of current to find alternative routes around the project (Figure 4.2b,e).

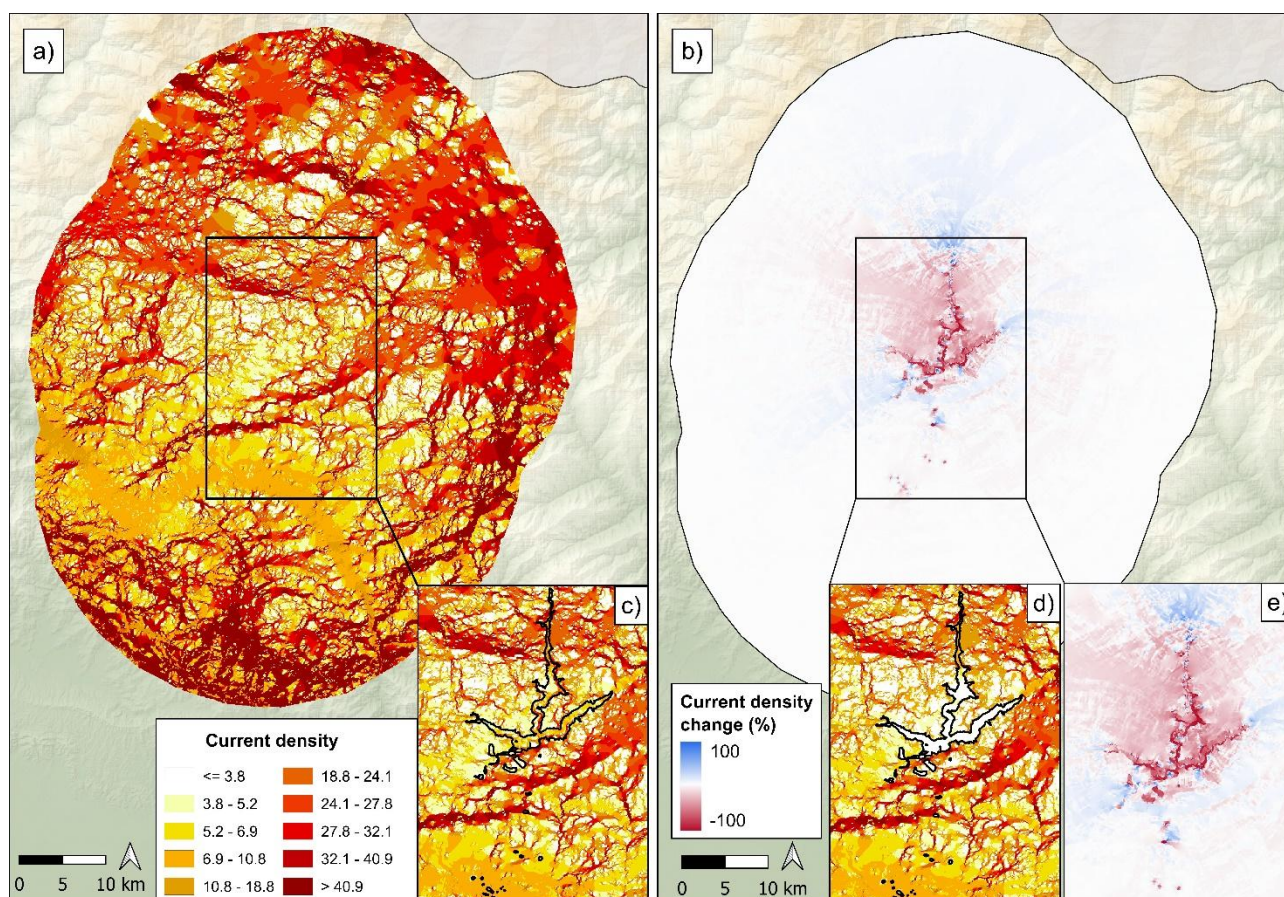


Figure 4.2 - Outputs of connectivity models generated using Circuitscape in the before construction scenarios (a), and the percentage of current density change between the before and after construction scenarios (b); Panels (c) and (d) provide zoomed-in view of the connectivity models within the project area for the before construction and after construction scenarios, respectively. Panel (e) highlights the zoomed-in of the percentage change in current density within and around the project area.

4.3.2 Reforestation priorities

Based on the assessment of land cover change between 2000 and 2019, we identified a total of 94.1 km² of deforested areas within the study area (25 km buffer area from the project footprint). Of these, 41.8 km² had a current density above the 20th percentile in the after-construction scenario, representing all potential sites for reforestation activities. These areas were converted into hexagonal cells, resulting in 2827 hexagons throughout the study and 560 hexagons that overlapped, intersected or were within the rivers, i.e. those related to riparian zones. Considering the estimated 8 km² of forest loss due to the construction of the proposed hydropower project, we prioritised the first 80 hexagonal cells for each dispersal distance threshold, evaluated separately for the entire study area and the riparian zones. Among the 80 prioritised hexagons for the whole study area, varIIC values varied notably across the dispersal distances. Lower varIIC values were observed for the 500 m threshold

(ranging from 0.12 to 0.76), intermediate values for the 1 km threshold (ranging from 1.40 to 0.29), and higher values for the 2 km threshold (ranging from 34.50 to 5.20). Similarly, for the 80 hexagons within riparian zones, varIIC values varied across dispersal distances, with lower values for the 500 m threshold (ranging from 0.28 to 0.02), intermediate values for the 1 km threshold (ranging from 1.31 to 0.05), and higher values for the 2 km threshold (ranging from 32.50 to 1.41). Overall, priority areas for reforestation across all dispersal distances were predominantly located in the southern part of the study area, where forest fragmentation is more pronounced (Figure 4.3). When considering the whole study area, most of the areas were prioritised for only one dispersal distance, with only 6% being prioritised for all dispersal distances. Specifically, 33% of the hexagons were prioritised exclusively for the largest dispersal distance (2 km), 22% for the intermediate distance (1 km) and 18% for the smallest dispersal distance (500 m) (Figure 4.3a). In contrast, when focusing exclusively on riparian deforested areas, the priority classifications showed greater overlap among dispersal distance thresholds. Specifically, 37% were prioritised for all dispersal distances, while 20% were prioritised only for the largest dispersal distance (2 km), 11% for the intermediate distance (1 km) and only 6% for the smallest dispersal distance (500 m) (Figure 4.3b).

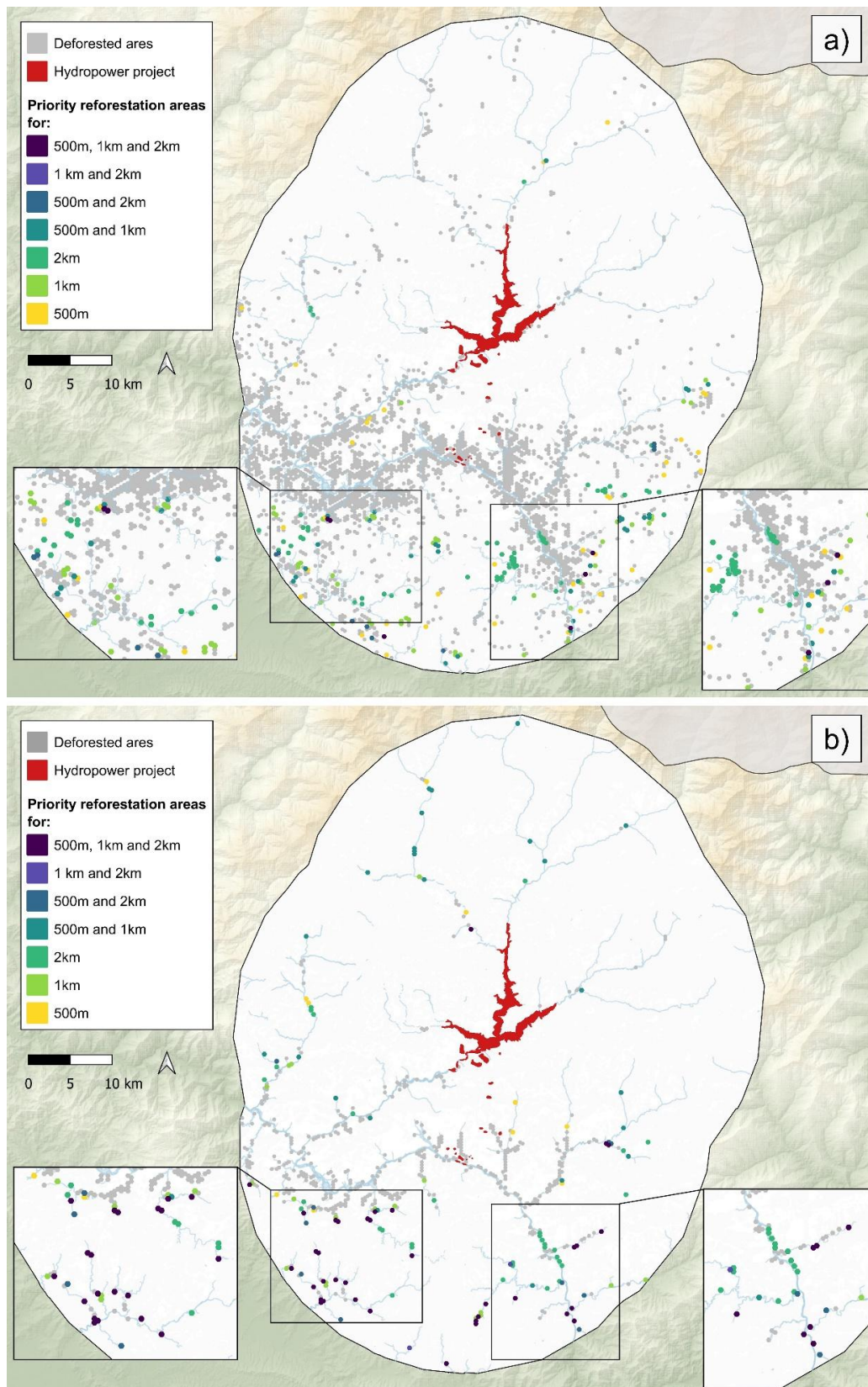


Figure 4.3 - Maps showing the locations of deforested areas identified comparing land cover between 2000 and 2019, along with the priority areas for reforestation activities based on different dispersal distances: 500 m, 1 km and 2 km. a) represent the reforestation priorities in the whole study area; b) represent the priorities identified by the deforested areas along the rivers.

4.4 DISCUSSION

In this study, we applied a framework for explicitly including forest habitat connectivity into Environmental Impact Assessments (EIAs) to evaluate the impact and guide compensation measures for large-scale hydropower projects. This approach enhances the accuracy of the assessment, making it more truthful, quantitative and representative of the actual impacts on terrestrial habitats of a reservoir-based hydropower project. The proposed framework comprised a first assessment of the change and loss of habitat connectivity comparing before- and after-construction scenarios and, secondly, a spatial prioritisation of reforestation activities to enhance connectivity for species with different movement abilities as an optimised compensation measure.

The application of this framework enabled us to identify the spatial extent and specific areas most affected by connectivity loss. As expected, our models predicted a complete loss of wildlife corridors within the proposed project area, particularly in inundated areas. Part of these lost lands are currently characterised by riparian forests, which have important ecological functions and can serve as corridors for many terrestrial wildlife species (Larsen-Gray and Loehle, 2022). Longitudinal (upstream and downstream along the river) and lateral connectivity (movement between riverbanks) of riparian forests are essential for enabling the movement of terrestrial species (Jeong et al., 2018). Particularly in countries with distinct dry and wet seasons, such as Nepal, dry or non-flowing rivers are increasingly recognised as priority ecosystems for the conservation of terrestrial species (Sánchez-Montoya et al., 2023; Steward et al., 2012). Consequently, the loss of these corridors is likely to disrupt both longitudinal and lateral wildlife movements, with relevant ecological implications. Our results further revealed that habitat connectivity loss extended well beyond the reservoir area, affecting regions up to 15 km from the project footprint. Similarly, Dorber et al. (2023) demonstrated that hydropower and associated infrastructure impacts on reindeer connectivity extended well beyond the project boundaries. These findings confirm the large-scale impacts of hydropower development on terrestrial habitat and connectivity, highlighting that using only the area occupied by hydropower projects as a metric for estimating terrestrial habitat impacts is overly simplistic and insufficient to capture the broader consequences (Dorber et al., 2023).

While hydropower offers low-carbon energy compared to fossil fuels, it poses relevant impacts on terrestrial habitats by increasing fragmentation, as demonstrated in this study. These impacts, along with their spatial extent, should not be underestimated and must be systematically considered into EIAs for hydropower or other renewable energy projects, given their current and future expansion (IEA, 2024). Renewable energy, including hydro, solar and wind, often require extensive geographical space, which can lead to potential conflicts between energy development and biodiversity conservation goals (e.g., Leskova et al., 2022; Patel et al., 2024). When alternatives

within the mitigation hierarchy (IFC, 2019) are not feasible and forest loss is unavoidable, reforestation activities can serve as a critical compensation measure. Moreover, in many countries, including Nepal, national legislation mandates reforestation following deforestation as a legal requirement (Forest Act, 2019 (2076)). To address the need for reforestation and the impact on terrestrial habitat connectivity, our study applied a method previously used for restoration efforts (e.g., de Sousa Miranda et al., 2021; Tambosi et al., 2014; Tambosi and Metzger, 2015) to spatially prioritise the most suitable areas for reforestation to enhance connectivity. Overall, our analysis revealed that most deforested areas are concentrated in the southern part of the study area, particularly along the Sun Koshi River. This pattern indicates relevant human-driven deforestation pressure on riparian habitats over the past 20 years, highlighting an additional stress factor impacting these important ecosystems (Iwata et al., 2003).

Our approach to selecting priority areas for reforestation was designed to address two different alternatives: a broad assessment of all deforested areas within the study area, and a targeted assessment of areas considering compensatory afforestation sites close to rivers. Focusing on the entire study area ensures that reforestation efforts improve habitat connectivity on a larger spatial scale, reducing fragmentation and supporting species with different movement abilities across the wider landscape. This comprehensive alternative prioritises deforested areas that could provide the greatest contribution on improving connectivity, regardless of their specific location. However, this strategy does not specifically target the restoration of riparian forests, which are among the most affected by the proposed hydroelectric project.

In contrast, prioritising reforestation efforts along riparian zones allows for the restoration of important habitats and, potentially, for restoring longitudinal and lateral connectivity along waterways. Riparian forests act as natural corridors connecting fragmented habitats, facilitating species dispersal and providing essential ecosystem services (Larsen-Gray and Loehle, 2022). However, this targeted approach is limited by the relatively small number of riparian areas available for reforestation, which may constrain its scope. Our analysis prioritised habitat connectivity as the primary criterion for reforestation, but we recognise that other critical factors should also be incorporated into offsetting plans. For example, social and economic considerations need to be included, as well as active stakeholder engagement to ensure alignment with local needs and priorities. Some areas that are highly valuable for habitat connectivity may ultimately be unsuitable for reforestation due to social, technical or economic constraints. This dual approach ensures a balanced prioritisation strategy, combining a broad assessment with a more targeted plan for riparian areas. By considering both widespread reforestation opportunities and the specific restoration needs of riparian habitats, the approach aims to optimise the ecological and practical effectiveness of

reforestation efforts. The results of the spatial prioritisation for reforestation efforts revealed different patterns and outcomes between the two alternatives. For the entire study area, the prioritised areas were often spatially dispersed, with limited overlap across the different dispersal distances. In contrast, the analysis of the riparian zone showed a more concentrated pattern of priority areas, with greater overlap across dispersal distances, partly due to the smallest number of cells available for reforestation. Importantly, considering multiple spatial scales in such assessments allows for a more comprehensive approach that accounts for species with different movement abilities. Areas identified as priorities across all dispersal distances should be given particular attention, as they have the greatest potential to support connectivity for a wider range of species. Combining these insights into conservation, management strategies and EIAs, together with active stakeholder engagement and social considerations, will facilitate the design of compensation plans that are ecologically sound, socially acceptable and effective in enhancing biodiversity and habitat connectivity.

4.5 CONCLUSIONS

In recent years, there has been growing concern about biodiversity loss, habitat fragmentation and ecosystem degradation associated with renewable energy development (Rehbein et al., 2020), highlighting the urgent need for effective planning to mitigate resulting impacts. While our approach provides a practical and generalisable method for prioritising reforestation efforts - applicable to other land-consuming projects, such as large-scale renewable energy developments - it remains a purely model-based assessment. As such, it does not fully account for species-specific ecological requirements, population dynamics or local constraints such as land availability and stakeholder interests. These limitations highlight the need for complementary studies and field validation when applying the framework. In addition, particularly in areas with threatened or protected species, reforestation activities alone may not be sufficient to offset the impacts of habitat degradation and connectivity loss. In such cases, intervention should be limited to exceptional circumstances, and projects must prioritise avoidance and minimisation of impacts before exploring compensation options. Overall, a precautionary and context-specific approach is needed to ensure that ecological integrity is not compromised by energy development, while balancing the urgent need for clean energy with biodiversity conservation.

CHAPTER 5

GENERAL CONCLUSIONS

5.1 KEY FINDINGS AND IMPLICATIONS

This thesis addresses the complex relationship between human infrastructure development and biodiversity conservation, focusing on preserving and enhancing ecological connectivity. The adverse impacts of human activities and infrastructure on connectivity were assessed through three distinct studies, each providing practical examples and recommendations for integrating aspects of ecological connectivity into environmental planning and impact assessments of current and future infrastructure projects. Furthermore, the thesis introduces innovative, advanced and reproducible tools and methods that are adaptable to diverse environmental contexts and various spatial scales. The scientific findings presented have direct and practical applications in Environmental Impact Assessments (EIAs) and environmental planning or management, offering insights for policymakers and conservationists to enhance efforts and prioritise connectivity conservation.

The common and overarching objective of the thesis, that connectivity needs to be considered to balance biodiversity conservation with infrastructure development, was elaborated and promoted in the three different case studies (Chapter 2-4). The case studies address and assess, at different spatial scales, the impacts on connectivity of linear infrastructure (Chapters 2 and 3) and land-consuming infrastructure (Chapter 4), and present suggestions to avoid and mitigate these impacts (Chapters 2 and 3) or, where no alternatives are possible, to compensate for them (Chapter 4).

Chapter 2 explored the integration of structural landscape connectivity into environmental planning and impact assessments of linear infrastructure in developing countries, South Sudan and Uganda. The landscape-scale study demonstrated how macro-regional ecological networks could be designed under current and future scenarios, taking into account both existing and planned linear infrastructure. The changes between these two scenarios allowed critical areas for connectivity conservation to be identified, direct and cumulative impacts to be assessed, and environmental planning for future development to be informed. Not less importantly, the study has enabled the use of open access databases to increase knowledge of biodiversity and connectivity, making the study even more useful for under-studied countries, where scientific research is difficult to conduct using traditional methods for several reasons, such as South Sudan.

In Chapter 3, the thesis advances road ecology by introducing the novel concepts of *roadkill suitability* and *road crossability* to assess the impact of roads on habitat connectivity for multiple mammal species. These concepts offer new perspectives on roadkill and contribute to the understanding of wildlife-road interactions. Using northeastern Italy as a regional case study (Friuli Venezia Giulia region, Italy), roadkill data and habitat connectivity were analysed for 15 mammals with different levels of mobility and across natural and anthropized landscapes. The results

highlighted the complexity of the relationship between roadkill suitability and road crossability, revealing differences depending on the type of landscape and species mobility. This suggests that a ‘one-size-fits-all’ approach to road mitigation may be insufficient and that different considerations should be used to plan mitigation measures and support multi-species road mitigations that maintain habitat connectivity. Considering this, in Chapter 3, a targeted zoning plan to prioritise conservation and management actions was proposed through the identification of Priority Areas for Barrier Effect Mitigation (PABEMs), Potential Areas for Roadkill Mitigation (PARoMs), and Potential Areas for Connectivity Preservation (PACoPs).

Chapter 4 examined renewable energy projects that require extensive land use, with a particular focus on the impacts of a proposed hydropower project in Nepal on forest habitat connectivity. This study addresses the need for connectivity considerations in renewable energy planning, highlighting the impacts on terrestrial habitat even in water-related projects such as hydropower. The novelty of this study lies in the proposal of a framework that not only assesses the loss of forest connectivity, but also guides compensation measures through reforestation priorities. This framework provides a systematic approach to address impacts that are often overlooked in EIAs, which is particularly relevant in the context of increasing global investments in renewable energy projects.

By developing methods that combine ecological modelling, multi-species analysis and spatial prioritisation, from linear infrastructure in developing countries to road networks in diverse landscapes and renewable energy projects in biodiverse regions, the thesis demonstrates the need of integrating ecological connectivity into environmental planning and management.

5.2 RESEARCH OUTLOOK AND FUTURE PERSPECTIVES

The findings presented in this thesis contribute to the understanding of several aspects of balancing connectivity and biodiversity conservation with infrastructure development, while also opening up new opportunities for further exploration and in-depth investigation. In Chapters 2, 3 and 4, the thesis outlines different future perspectives, highlighting specific avenues for further research and practical application, tailored to the unique challenges explored in each study.

In general, a major opportunity for refinement lies in the integration of functional connectivity considerations - including species-specific requirements and behaviour - with structural connectivity approaches. Significant advances in connectivity science over the past few decades, enabled in part by advances in computational tools and modelling techniques, have expanded the scope of research to include functional connectivity. Recent connectivity models have become increasingly

sophisticated, incorporating movement direction, distinguishing between different movement types and seasonality, and accounting for dynamic landscape and environmental change.

However, the choice of appropriate modelling methods, such as single- or multi-species, should be based on specific objectives, data availability and other constraints. In some cases, it may not be feasible to incorporate highly detailed species-specific data into connectivity models due to incomplete baseline information and tight decision timelines, which are common challenges in EIAs (Torres et al., 2022). In other cases, the approach may be driven by legislation, such as land-use planning frameworks that require multi-species connectivity, or conversely, legislation focused on endangered species that requires the production of single-species connectivity map. Comparing different models may be one way of understanding these trade-offs and determining where to allocate resources and effort for the greatest benefit. However, validation of connectivity models through field-based studies remains critical to ensure their reliability and practical applicability, both in research and in the context of management and EIAs. By incorporating species-specific functional connectivity, considering temporal scales and validating models, researchers can gain a deeper understanding of long-term changes and the cumulative impacts of infrastructure on ecological connectivity. This combination would allow the dynamic interactions between species and their habitats to be captured, promoting more effective and sustainable integration of biodiversity and connectivity conservation into infrastructure development and environmental management.

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LIST OF PUBLICATIONS

SCIENTIFIC PAPERS

Chapter 2

Fonda, F., Bullegas, F., Petruzzellis, F., and Bacaro, G. Assessing the impact of linear infrastructure on ecological connectivity: a worked example from South Sudan and Uganda. Under review in *Biodiversity and Conservation*

Chapter 3

Fonda, F., D'Amico, M., Petruzzellis, F., Scridel, D., Pesaro, S., Tomè, P., and Bacaro, G. Roadkill suitability and road crossability: implementing two novel concepts for prioritization of road mitigation. Under review in *Biological Conservation*

Chapter 4

Fonda, F., Petrillo, M., and Bacaro, G. An optimised framework for the assessment of habitat connectivity loss and restoration planning in a developing country. In preparation for *Environmental Impact Assessment Review*

Side papers published during the PhD

Lazzeri, L., Fazzi, P., Lucchesi, M., Mori, E., Velli, E., Cappai, N., Ciuti, F., Ferretti, F., **Fonda, F.**, Paniccia, C., Pavanello, M., Pecorella, S., Sangiuliano, A., Sforzi, A., Siclari, A., and Spada, A. 2022. The rhythm of the night: patterns of activity of the European wildcat in the Italian peninsula. *Mammalian Biology*, 102(5-6), 1769-1782.

Lopez, D., **Fonda, F.**, Monti, F., and Dal Zotto, M. 2023. Density estimates and habitat preferences of two sympatric bird species as potential bioindicators of neotropical forest alterations. *Diversity*, 15(2), 208.

Pecorella, S., De Luca, M., **Fonda, F.**, Viviano, A., Candelotto, M., Candotto, S., Mori, M., and Banea, O. 2023. First record of allonursing in golden jackal (*Canis aureus*, L. 1758): a case of

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Mortelliti, A., Bergamin, R., Bartolommei, P., Greco, I., Manzo, E., Rovero, F., and **Fonda, F.** 2024. Cost-effectiveness of lures in attracting mammals: a large scale camera-trapping field test on European species. *European Journal of Wildlife Research* 70, 90. <https://doi.org/10.1007/s10344-024-01840-0>

CONFERENCE CONTRIBUTIONS

Posters - National Congresses

Fonda, F., De Luca, M., Mori, e., and Pecorella, S. The density of badger setts in a natural river corridor (NE Italy). in: Chirichella, R., and Preatoni, D. G. (2022). XII Italian congress of Mammalogy. *Hystrix, the Italian Journal of Mammalogy*, 33(Supplement), 1-144.

Fonda, F., Vezzani, L., Mena Aguilar, L.A., Romeo, G., Sonetti, D., and Dal Zotto, M. Investigating ecotourism impacts on mammal activity in a Costa Rican protected area. in: Chirichella, R., and Preatoni, D. G. (2022). XII Italian congress of Mammalogy. *Hystrix, the Italian Journal of Mammalogy*, 33(Supplement), 1-144.

Cullati, C., **Fonda, F.**, Balestrieri, A., and Chiatante, G. A hair-tube survey of small mammals from Serra di Ivrea (NW Italy). in: Chirichella, R., and Preatoni, D. G. (2022). XII Italian congress of Mammalogy. *Hystrix, the Italian Journal of Mammalogy*, 33(Supplement), 1-144.

Dal Zotto, M., Mena Aquilar, L.A., Sonetti, D., **Fonda, F.**, and Romeo, G. The herpetofauna of a threatened and under-investigated region of Costa Rica: diversity and conservation. XIV Congress Societas Herpetologica Italica, Torino. 13-17 September 2022.

Oral presentation - National Congresses

Fonda, F., Bergamin, R., Bartolommei, P., Greco, I., Manzo, E., Rovero, F., and Mortelliti, A. Cost-effectiveness of lures in attracting mammals: a results of a large-scale camera-trapping field experiment. XIII Italian congress of Mammalogy. Pesche (Isernia), 3-5 Luglio 2024.

Oral presentations - International Congresses

Pecorella, S., De Luca, M., **Fonda, F.**, Viviano, A., Candelotto, M., Candotto, S., Mori, M., and Banea, O. First record of multiple breeding and communal nursing within one social unit of

European golden jackal (*Canis aureus*, L. 1758) in a low density area in NE Italy. 3rd International Jackal Symposium. Gödöllő, Hungary, 2-4 Novembre 2022. Speaker: Stefano Pecorella.

Fonda, F., D'Amico, M., Petruzzellis, F., Pesaro, S., Tomè, P., and Bacaro, G. Planning conservation strategies based on a multi-scalar and multispecies approach to assess habitat connectivity and roadkill risk area. Challenging conservation - Adattarsi al Cambiamento. Chapter Italiano Society for Conservation Biology. Roma, 19-21 Aprile 2023.

Fonda, F., D'Amico, M., Petruzzellis, F., Scridel, D., Pesaro, S., Tomè, P., and Bacaro, G. A multi-scale and multi-species approach to evaluate overlap between wildlife corridors and high roadkill risk areas. 4th International Conference on Community Ecology. Trieste, 20-22 September 2023.

Fonda, F., Bullegas, F., and Bacaro, G. Assessing the impact of planned linear infrastructure on ecological connectivity: an example from Uganda and South Sudan. 7th European Congress of Conservation Biology. Bologna, 17-21 Giugno 2024.

Bacaro, G., Petruzzellis, F., Tosti, V., Castello, M., **Fonda, F.**, Scridel, D., Thouverai, E., and Olmo, V. Flourishing diversity along sacred paths: unveiling habitat conservation through remote sensing analysis in the Henro Pilgrimage, Shikoku, Japan. 7th European Congress of Conservation Biology. Bologna, 17-21 Giugno 2024. Speaker: Elisa Thouverai.

