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Guidelines for connectivity conservation and planning in Europe

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Guidelines for connectivity conservation and planning in Europe

D6.1 Guidelines for connectivity conservation and planning in Europe with supporting web-based inventory and databases

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Project title	NATURACONNECT - DESIGNING A RESILIENT AND COHERENT TRANS- EUROPEAN NETWORK FOR NATURE AND PEOPLE

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Deliverable description	This guidelines will be the product of tasks 6.1 and 6.2 In 6.1 we will co-design a framework for multi-scale connectivity assessment and planning together with stakeholders from MS administrations, EU policy bodies and other relevant EU programs and platforms: LIFE projects, EuropaBON, KCBD, EEA, etc. This framework will be published in the connectivity guidelines together with the output of task 6.2 which include a synthesis report of the input data, statistical models and predictions of species dispersal kernels using agent-based models.
Keywords	Biodiversity policy, connectivity assessment, conservation planning, ecological corridors, landscape fragmentation, population models, species dispersal, species traits, user needs.

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Table of Contents

Funded by the European Union

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NATURA CONNECT

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List of Figures

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List of Tables

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Abbreviations

ABM	Agent-Based Model
ASCII	American Standard Code for Information Interchange
BGI	Blue and Green Infrastructure
CMS	Convention on Migratory Species
CSV	Comma-separated values
EC	European Commission
ES	Ecosystem Services
GBF	Global Biodiversity Framework
GI	Green Infrastructure
GIS	Geographic Information System
GUI	Graphical User Interface
IUCN	International Union for Conservation of Nature
LULC	Land Use / Land Cover
MAES	Mapping and Assessment of Ecosystems and their Services
OECM	Other Effective area-based Conservation Measure
PCA	Principal Component Analysis
PIT	Passive Integrated Transponder
RBMP	River Basin Management Plan
WFD	Water Framework Directive

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Executive summary

Ecological connectivity is key to maintaining a coherent and resilient network of protected areas in the EU. The EU Biodiversity Strategy for 2030 has identified the unhindered movement of species, nutrients and ecological processes across connected landscapes as a key feature of a coherent Trans-European Nature Network (TEN-N) of protected and conserved areas. However, to date, streamlined guidance on planning for and implementing connectivity measures specifically at the European scale has been limited.

This report presents a coherent methodological framework and guidelines for mapping functional and structural connectivity at the European scale, as part of the Horizon Europe NaturaConnect project, which is supporting EU Member States in developing a coherent TEN-N of protected and conserved areas.

It describes key ecological connectivity concepts and approaches; outlines methods and tools for estimating connectivity; presents an overview of connectivity projects across Europe; identifies connectivity priorities, gaps and challenges following a stakeholder consultation process; and provides practical and operational guidelines for implementing ecological connectivity for conservation projects ranging from regional to national and European levels. The guidelines present a strategic blueprint aimed at enhancing ecological connectivity across Europe, and address the specific challenges and opportunities related to planning ecological connectivity in the European context.

This report has been written for practitioners and individuals involved in the management and administration of protected areas and ecological connectivity projects across Europe. This includes professionals working in TEN-N implementation at national or regional levels, others involved in spatial planning outside protected areas, and professionals engaged in the implementation of connectivity projects and protected area management.

The primary focus is on the terrestrial realm, although challenges in freshwater connectivity are also addressed.

Key insights and results presented in the report include:

- **Connectivity is an integral component of protected area planning in Europe**. As highlighted by the EU Biodiversity Strategy for 2030, a coherent Trans-European Nature Network (TEN-N) depends on the setting up of ecological corridors “to prevent genetic isolation, allow for species migration, and maintain and enhance healthy ecosystems”.
- **When planning for and implementing connectivity, understanding and distinguishing between different connectivity concepts and approaches is vital**. For example, concepts such as the role of protected areas versus ecological corridors, structural and functional connectivity, Green and Blue Infrastructure, spatial scale and dispersal issues, design of corridors and stepping stones, integration of connectivity in spatial conservation prioritization, and freshwater and cross-realm connectivity (all defined in Chapter 2).

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- **Connectivity goals are being featured prominently in several recent global and EU policy instruments**, including the post-2020 Global Biodiversity Framework, the EU Biodiversity Strategy for 2030, the EU Forest Strategy for 2030, the Green and Blue Infrastructure (GBI) strategy, the Nature Restoration Regulation, the Water Framework Directive, and the EU pollinators initiative (Chapter 3).
- **To date, comprehensive assessments providing a pan-European overview of connectivity projects taking place across Europe, as well as connectivity implementation gaps and needs, have been limited**. To address this need, as part of the NaturaConnect project, an online survey and follow up webinar were carried out with stakeholders in the conservation community to gather this key information (Chapter 4). Key findings from the online survey which received submissions on 80 projects across 35 European countries include:
    - The most common connectivity goals of projects are connectivity between protected areas or between specific habitat types
    - Additional benefits of connectivity projects included recreation, climate regulation and pollination services
    - The most targeted taxa in projects were large carnivores, followed by arthropods and birds
    - The most targeted ecosystems were forests and grasslands (Fig. ES1)
    - The main target users of project results were regional or local administrations
    - The main funding sources were nature conservation funds from national and regional administrations, and private funds
    - The spatial scope of most projects was subnational
    - The most common targeted biogeographical region was Continental, followed by Alpine
    - Selected approaches for estimating connectivity were mainly land cover and expert-based
    - Most projects provided spatial information on locations for ecological corridors, stepping stones and locations for habitat restoration
    - In most cases (over 70%) there was no monitoring of project effectiveness, and the potential negative impacts of increased connectivity were often not considered (though mentioned ones included human-wildlife conflicts and increased spread of invasive species)

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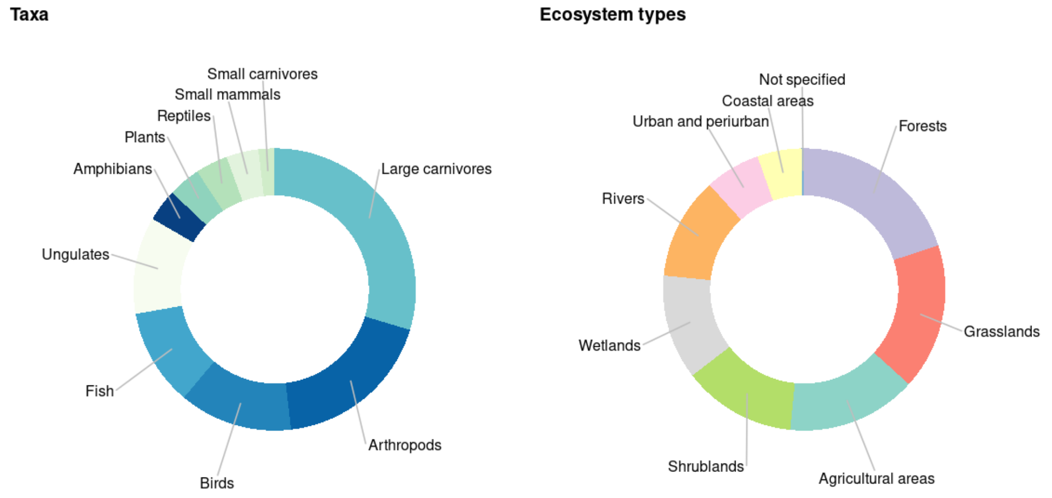

Figure ES1: Response rates for taxonomic groups and ecosystem types for the survey on ecological connectivity projects in Europe

- A companion online database presenting all 80 projects submitted to the online survey is publicly available online at https://naturaconnect.idiv.de/projects/. Its aim is to serve as a dynamic resource for researchers, policymakers, conservationists, and the public interested in connectivity conservation projects conducted in Europe.

- **Stakeholder priorities for future multi-scale connectivity planning and implementation across Europe are wide ranging and target multiple aspects and stages of connectivity planning (Chapter 4)**. Main priorities identified by stakeholders during a two-day NaturaConnect follow up webinar included:
  - Identification of climate and evolutionary refugia
  - Setting of stepping stones for long distance migrants (mainly birds)
  - Promoting connecting across realms
  - A focus on human well-being in the planning of multi-functional corridors, mainly in urban and peri-urban contexts
  - A focus on rivers as backbones of connectivity planning
  - Setting of policies and incentives targeting the promotion of connectivity, mainly on private land
  - Dam removal and the restoration of natural rivers
  - Increase the permeability of linear infrastructures as roads and railway

- **Connectivity planning and implementation challenges identified by stakeholder included those on gaps in data availability, lack of streamlined guidance on connectivity planning and implementation, and lack of opportunities for technical training (Chapter 4)**. Main challenges identified by stakeholders during a two-day NaturaConnect follow up webinar included:

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  - Gaps in data, mainly in what concerns species movement and dispersal
  - Species requirements during migration
  - The incorporation of management information in current maps of land cover
  - Lack of socio-economic data to better frame people's perceptions of corridors and connectivity
  - Lack of guidance and rules needed for future connectivity modelling and on-the-ground implementation
  - Land ownership issues
  - How to assign economic value to connectivity
  - Lack of a multi-level governance structure for the planning and management of connectivity networks
  - Lack of technical training opportunities

- **To adequately plan for and implement connectivity measures, it is often required to use models to estimate connectivity across regions**. A portfolio of publicly accessible tools and data sources are already available to help practitioners with this and are summarised in this report (Chapter 5).

- **The need exists for a dedicated framework for connectivity conservation and planning in Europe, which presents clear steps to consider when designing a connectivity project (Fig. ES2; Chapter 6).** The *NaturaConnect connectivity network design framework* presented in this report aims to address this need and outlines a set of five key steps for practitioners:

  (1) Scoping and Problem Assessment: Conduct a comprehensive analysis of the entire landscape to identify potential threats, connectivity actions, and impact of those actions, identify all relevant stakeholders and build an interdisciplinary collaboration team for connectivity analysis, communication, and implementation. Establish the general spatial extent at which your study will take place.

  (2) Setting of Objectives: Use the assessment of the connectivity problem to establish spatial and temporally explicit objectives and targets that will help mitigate the identified problem. Determine the appropriate width and characteristics of corridors and stepping stones based on the target species and landscape characteristics. Finalize the spatial extent and needed data resolution.

  (3) Analysis Selection and Data Preparation: Determine the correct model or models to analyse ecological connectivity. Given the model and your objectives collect and produce all the necessary data and spatial layers necessary to run the spatial analysis.

  (4) Assessment of connectivity: Use connectivity metrics and models to determine the most effective design for a connectivity network that integrates with the current network of protected areas. Present draft results to stakeholders, iterate new models, and prioritise corridors and stepping stones; and

  (5) Implementation, Monitoring and Evaluation: Develop a comprehensive management and monitoring plan for the ecological corridor and/or stepping stones. This includes activities such as habitat restoration, invasive species

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control, monitoring of species movement, and assessing the corridor's effectiveness in achieving the connectivity objectives.

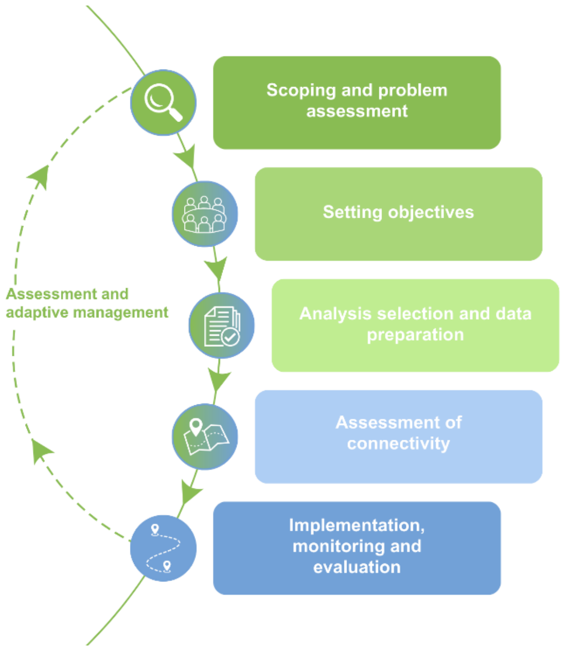

Figure ES2: Building blocks of the proposed framework for implementing ecological connectivity projects

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1. Introduction

1.1 Why is ecological connectivity important?

Earth's ecosystems have undergone substantial degradation and significant loss of ecosystem processes and functions caused by human activities. Approximately 75% of the land surface has been significantly modified, more than 85% of wetland areas have been lost, and an average of 25% of globally assessed animal and plant species are threatened with extinction due to land use changes and unsustainable logging, harvesting, hunting, and fishing (IPBES, 2022). Over the next few decades, climate change is expected to play an increasingly significant role as a direct driver of biodiversity loss (IPBES, 2022).

As climate change and direct human pressures increase in severity, ecosystems with high biodiversity value become smaller and increasingly isolated (Fahrig, 2019, 2003). Smaller and isolated species habitats harbour smaller populations with lower genetic diversity and higher threats of extinction (Frankham et al., 2010; Schlaepfer et al., 2018). These habitats are also vulnerable to edge effects (i.e., pressures on species populations at their habitat boundaries) (e.g., Weathers et al., 2001) and to the simplification of species community composition and interactions (e.g., Razafindratsima et al., 2018; Valladares et al., 2006). Synergistic effects of habitat loss and isolation interfere with critical ecological processes sustaining the ecosystem integrity, such as pollination, seed dispersal and the nutrients flow, which, in turn, has cascading effects on both ecosystem structure and functions (Haddad et al., 2015; Laurance and Bierregaard, 1997).

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Connectivity conservation and restoration are key to counteract the detrimental effects of ecosystem degradation, habitat loss, and fragmentation. Ecological connectivity

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encompasses the **functional and physical connections between different habitats and ecosystems that enable the movement of species, nutrients, and ecological processes across landscapes** (Crooks et al., 2011; Crooks and Sanjayan, 2006; Hilty et al., 2020). Ecological connectivity plays a pivotal role in preserving biodiversity, ensuring the long-term persistence and adaptability of species populations and communities (van Rees et al., 2021). Individuals are often compelled to move and disperse due to various ecological drivers, including reproduction, access to food sources, seasonal habitat and climate change, intraspecific competition, evasion from predators and competitors, and temporal or permanent habitat degradation and destruction. The seamless movement facilitated by ecological connectivity is fundamental for their survival and reproductive success (Crooks and Sanjayan, 2006). When populations are interconnected, the flow of individuals and genes are fostered, enhancing adaptability and resilience to environmental change and stochastic events. Moreover, as the climate changes, species may need to track spatial changes in the habitat quality. Therefore, connected landscapes are key to species adaptability since it can facilitate distribution shifts in response to climate and land-use changes (Heller and Zavaleta, 2009; Opdam and Wascher, 2004).

Ecological connectivity has an even broader impact on ecosystem-level processes. Critical ecological phenomena, such as nutrient cycling, pollination, and predator-prey interactions, hinge on the unhindered movement of species (Crooks et al., 2011; Razafindratsima et al., 2018). Furthermore, the interlinking of habitats provides a safety net against antropogenic disturbances. For example, when a particular habitat patch undergoes a catastrophic event like a fire or a disease outbreak, species can seek refuge in neighbouring, connected habitats. This not only allows for immediate survival but also facilitates recolonization processes and passive ecological restoration.

Recent international agreements have placed **connectivity at the core of the pathway towards nature recovery**. Goal A of the United Nations Global Biodiversity Framework aims to *maintain, enhance and restore the integrity, connectivity and resilience of all ecosystems* by 2050*.* Associated targets include reducing threats to biodiversity through enhancing connectivity with ecosystem restoration (Target 2), designing well-connected protected areas (Target 3) and increasing the connectivity of green and blue spaces in urban areas, contributing to the provision of ecosystem services (Target 12). The European Union Biodiversity Strategy for 2030 aims to enhance connectivity among habitats, protected areas and green and blue infrastructure, for instance, with the designation of additional protected areas and the creation of high diversity landscape features and ecological corridors.

1.2 Aims and target audience

This document aims to provide base knowledge and guidance for planning ecological connectivity conservation and restoration. It is designed to address the specific needs, opportunities, and challenges for connectivity planning, with a specific focus on supporting the implementation of policy commitments for biodiversity conservation and restoration. The report provides a thorough review of available methods, tools and data sources for connectivity planning, and proposes recommendations for designing connectivity projects supporting a **coherent and resilient Trans-European Network of Protected Areas (TEN-N)**.

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We also present an analysis of the characteristics of connectivity projects in Europe based on an extensive survey, and the identification of data and information gaps and needs for supporting connectivity assessments, conservation, and restoration. These analyses included the input of multiple stakeholders through online surveys and workshops.

The IUCN (International Union for Conservation of Nature) "Guidelines for conserving connectivity through ecological networks and corridors" (Hilty et al., 2020) introduced a set of recommendations for building ecological networks and for implementing ecological connectivity between protected areas and other conservation areas. They showcase different approaches for conserving ecological corridors by presenting case studies aimed at protecting or restoring ecological connectivity from around the world and in terrestrial, freshwater and marine ecosystems. The present report complements these guidelines and other existing literature by providing a thorough review of approaches, the information needs as identified by stakeholders, and practical recommendations.

This document is primarily intended for analysts, practitioners, and scientists involved in the design and management of nature conservation and restoration projects, e.g., from public National and regional administrations, environmental planners and managers within and outside protected areas, as well as private initiatives, foundations, etc. interested in connectivity planning. It is tailored to meet the needs of those responsible for developing and implementing strategies, policies, and management plans.

The document is focused on the terrestrial realm, although some aspects of freshwater connectivity are also addressed. The marine realm is only partly tackled, in the context of cross-realm connectivity (Section 2.6).

1.3 Summary of the content

Part I: Connectivity in Europe: Key concepts, policy context, and implementation

Chapter 2 discusses **connectivity concepts and approaches**. We contrast the different objectives of *protected areas versus ecological corridors*, that do not necessarily need to provide key habitats for *in situ* conservation. Then the distinction between *structural connectivity* (focusing on land use patterns) *and functional connectivity* (focusing on species traits, including dispersal movements) is made. Connectivity is also presented in the context of *Green and Blue Infrastructure (GBI)*, based on multi-functionality to incorporate both biodiversity and ecosystem services targets. The multi-functional perspective of GBI spans many policy sectors and raises some challenges to connectivity design, namely through defining the relative weight of the biodiversity *versus* ecosystem services objectives. *Spatial scale and dispersal* issues are also addressed. In fact, projects addressing the restoration and protection of connectivity may be implemented at various spatial scales, ranging from local to regional or even continental, depending on the specific objectives and the species being considered. The scale of analyses must be linked to the ecological traits of the species being considered, particularly on dispersal capacity. The key principles for the *design of corridors and stepping stones* is also presented, as well as the *integration of connectivity in spatial conservation prioritization*. This Chapter also includes a Section on *freshwater and cross-realm connectivity*.

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Chapter 3 focuses on **policy instruments addressing connectivity**. An overview is made of how connectivity is tackled in seven major policy instruments, the post-2020 Global Biodiversity Framework, the EU Biodiversity Strategy for 2030, the EU Forest Strategy for 2030, the Green and Blue Infrastructure (GBI) strategy, the Nature Restoration Law, the Water Framework Directive, and the EU pollinators initiative.

Chapter 4 focuses on **current connectivity projects and practices in Europe**. It presents the results from a *survey conducted to gather information on ecological connectivity projects in Europe* carried out at regional, national, and Pan-European levels. The survey consisted of 27 questions covering project information, scope, participants, and selected approaches. The survey was conducted between May 2023 and January 2024, and gathered information on 80 projects conducted in 35 European countries, regarding: goals and scope; targeted taxa and ecosystems; policy context, target users and funding; spatial scope; selected approaches and outputs; assessing effectiveness; and potential negative effects. The companion online connectivity projects database, containing all the projects included in the survey, is also presented.

Chapter 4 also includes a synthesis of identified stakeholder priorities and challenges for future multi-scale connectivity planning across Europe, identified during a two-day online NaturaConnect workshop in October 2023 on “Assessing Ecological Connectivity in Europe: Conservation goals and information gaps” which gathered ~ 90 experts and stakeholders.

Part II: Tools and guidelines for implementation of connectivity projects in Europe

Chapter 5 provides a comprehensive review of **available tools and data sources** for modelling connectivity. Here, we provide an overview of existing software and applications based on three major types of model families: *least-cost path and resistant kernels*, *graph theory* and *circuit theory*. The use of *agent-based models* is also addressed, as well as the *assessment of ecosystem services* in the case of multi-functional connectivity projects.

Chapter 6 proposes a framework for connectivity conservation and planning, where the steps to consider when designing a connectivity project are presented.

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Part I: Connectivity in Europe: Key concepts, policy context, and implementation

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2. Connectivity concepts and approaches

The term ***ecological connectivity*** has been defined in several ways, each of them with different implications for the management applications of the concept and the associated analytical and mapping approaches. In this Section, we give an overview of concepts underpinning different perspectives on connectivity used in nature conservation and assessments.

2.1 Protected areas and ecological corridors

Protected areas have long been the foundation of nature conservation strategies worldwide. Between 2010 and 2023 the global coverage of terrestrial protected areas (including inland waters) grew from 14.1% to 17.19%. In the European Union, the percentage of protected areas has been on a similar trajectory, with the Natura 2000 network currently covering 18.6% of the land area (Fig. 2.1).

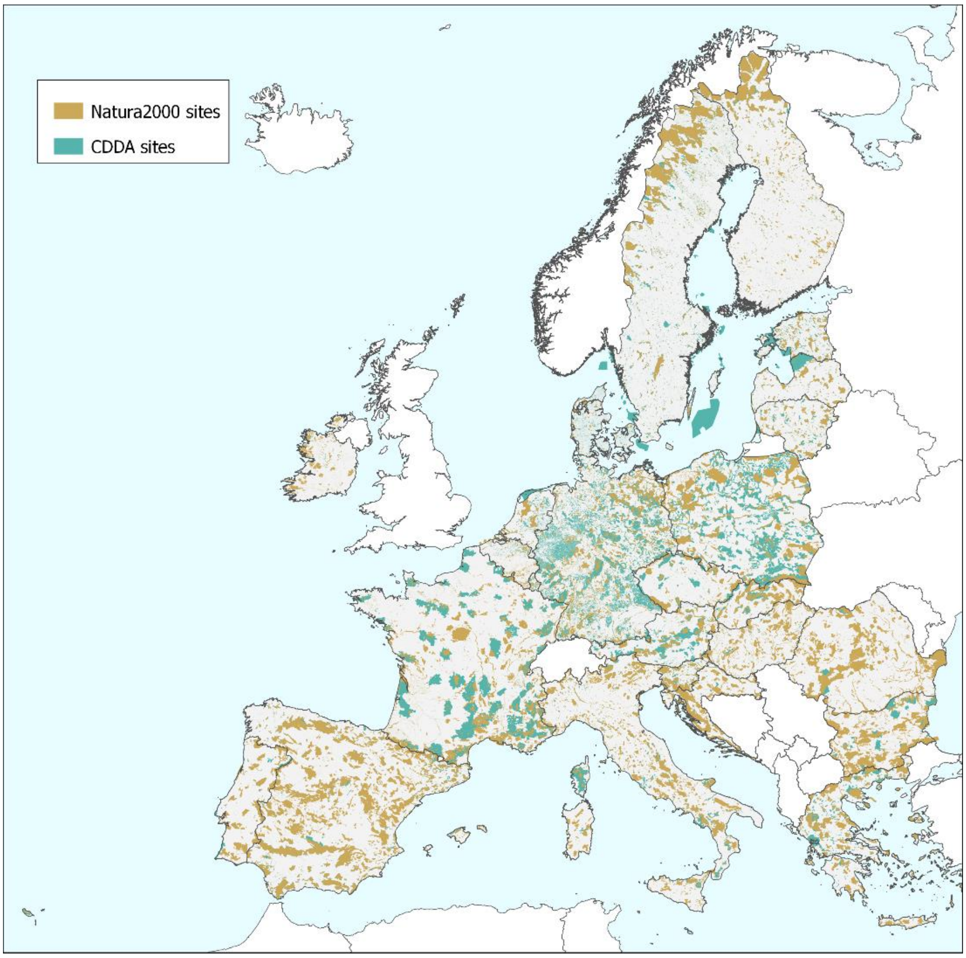

Figure 2.1: Distribution of Natura 2000 sites and nationally designated protected areas in the European Union, covering approx. 26% of the land surface. Data source: European Environmental Agency, 2023.

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However, **the current network of protected areas alone is insufficient to safeguard biodiversity**. First, the location of historically designated protected areas is often biased towards least productive and least threatened areas, leaving several types of ecosystems under-represented (Joppa and Pfaff, 2009). Second, climate change can alter temperature and precipitation patterns, and cause changes in the distribution of ecosystems, habitats and species. Many species will require shifting their distribution ranges to more suitable climatic conditions to persist, and therefore the current distribution of protected areas may not be sufficient to protect these species (Dobrowski et al., 2021). Third, many protected areas are too small (Monaco and Genovesi, 2014) and they are insufficently connected to be effective (Santini et al., 2016; Ward et al., 2020). **According to recent estimates, only 9.7% of Earth's terrestrial protected network can be considered structurally connected** (Ward et al. 2020). In the European Union's Natura 2000 network, connectivity estimates seem to be more optimistic. Approximately 80% of Natura 2000 sites dominated by woodland and forest are considered connected by natural and semi-natural features in the wider landscape (outside of the Natura 2000 sites) across the 27 EU Member States. Among these sites, over 50% are linked by continuous patches of unprotected forest and woodland ecosystems (Carrao et al., 2020).

Creating ecological corridors between protected areas is of the utmost importance. Corridors work as a pathway for the movement of plants, animals, and other organisms, allowing them to migrate, disperse, and interact. Ecological corridors are usually defined as strips of natural habitat that connect two or more areas of similar habitat that are surrounded by a nonhabitat matrix (Beier and Noss, 1998) and that are managed over the long term to maintain or restore connectivity (Hilty et al., 2019). Corridors may include landscape features such as hedgerows, tree lines, riparian strips, or managed agricultural land, offering a blend of open space and more sheltered passageways for species (Travers et al., 2021). However, corridors do not need to be narrow strips of habitat. They can also consist of a combination of natural and semi-natural habitats able to increase the permeability to dispersal and other movements of organisms (Eggers et al., 2010; Travers et al., 2021). This is particularly relevant in highly transformed landscapes, where protected areas often include heterogeneous mixtures of different ecosystem types under different management regimes and intensity. In Europe, many protected areas are surrounded by a matrix of intensive land use with low natural connectivity potential (EEA, 2024).

The **main purpose of ecological corridors is to maintain connectivity** (Hilty et al., 2020). They may also contribute to conserve in situ biodiversity but this is not a strict requirement. In contrast, the main objective of protected areas is in situ conservation, although they may conserve connectivity as well. Each corridor should be designed with specific objectives in mind and be managed accordingly. Regardless of the types of areas that compose them, ecological corridors should always be distinguishable from non-designated areas based on the specific activities that are permitted or prohibited within them (Hilty et al., 2019, 2020).

2.2 Structural and functional connectivity

The concept of ecological connectivity encompasses both structural connectivity and functional connectivity (Hilty et al., 2019; Taylor et al., 2006).

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Structural connectivity focuses on the physical arrangement and configuration of habitat patches and corridors. It primarily considers the spatial contiguity of species habitats, ecosystem types, etc., and how this contiguity is affected by fragmenting features. When applied to specific species, structural connectivity captures the spatial arrangement and configuration of habitat patches within a landscape, hence, it depends on the size, shape, and location of habitat patches (Fahrig, 2003). Different species perceive the landscape differently (in terms of seeing distinct land covers as resources) and possess distinct habitat requirements, movement behaviours, dispersal propensity and distances. Therefore, a given level of structural connectivity is likely to translate into different levels of functional connectivity for different species (Taylor et al., 2006). Structural species connectivity can be seen as a simplified alternative (compared to functional approaches) that focuses solely on the spatial arrangement and configuration of species habitats within a landscape, where one ignores, on a first approach, the details of individual species biology. Examples include classifying different land cover types in term of suitable habitats for species movement of (e.g. forests, wetlands, extensive agriculture) or reducing these movements (e.g. urban areas, infrastructures, intensive agriculture). Assessments based exclusively on structural landscape analyses can provide a cost-effective means of assessing connectivity for conservation purposes, although at the cost of ecological detail (Saura et al., 2011). Structural connectivity approaches can also integrate multiple ecological features when assessing the spatial contiguity of focal patches, such as land use types, species composition, and human pressures, therefore providing more holistic perspectives on the ecological connectivity of natural habitats (e.g., Fernández et al. 2020).

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Functional connectivity, on the other hand, emphasises the demographic, genetic, and community processes affected by dispersal and movement. **Functional connectivity quantifies the (potential) movement of genes, gametes, propagules or individuals move through landscapes, and their ecological function**. Naturally, the two concepts are interconnected, as functional connectivity often depends on the presence and configuration of structurally connected habitat patches.

The functional connectivity of a landscape for a particular species (or a group of species) is assumed to be determined by both movement potential through different habitat patches and local subpopulation dynamics including demographic effects (Doerr et al., 2011). **Assessments of the functional connectivity of populations inform on the effects of dispersal across the landscape on the distribution, abundance, dynamics, and genetics of populations** (Fernández et al. 2016; Bruggeman et al. 2010).

Functional connectivity is therefore specific for a given species or community assemblage occurring in a given region. In fact, species are predicted to change their behaviour and experience variations in their fitness based on the type, shape, and spatial arrangement of habitat patches and ecotones (Bélisle, 2005). The pattern of movements of a given species can be strongly influenced by biological characteristics such as sex, age, and individual behaviour (Maiorano et al., 2017).

Functional connectivity has been often measured at the level of a single species. However, the idea of finding functional corridors for multiple species is certainly appealing. Two possible approaches are commonly considered:

1. the use of **"connectivity umbrella"** or indicator species: a species that has a large body size, home range, charisma and conservation status, and habitat requirements that overlap with other species. These are typically large and mobile, with large requirements of space and resources. The postulate is that a landscape that ensures connectivity for an umbrella species can potentially serve also other (smaller or less mobile) organisms (Dutta et al., 2023). However, the umbrella species approach is limited by the ecological similarity and the level of interactions with co-occurring species (Natsukawa & Sergio 2022).
2. Consider **multiple species** explicitly, measuring functional connectivity for all of them and obtaining integrated or consensus connectivity maps. This should allow for the identification of critical areas for facilitating the movement of multiple focal species accounting for their specific ecological requirements, such as for multiple threatened species, community guilds, or particular interacting species.

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Theoretically, multispecies strategies should provide positive conservation outcomes more effectively than single-species strategies. However, they have a potential downside for single species spatial planning (Brodie et al., 2015). Several studies have explored and compared the two options (e.g., Meurant et al., 2018; Wang et al., 2018) highlighting how the use of a multi-species approach could be more effective in the development of conservation actions, such as the creation of corridors, because it allows for the protection of a wide range of different habitat types and also to meet the different spatial and structural requirements of the several species considered (Cushman and Landguth, 2012).

There is still a third approach, based on identifying archetypal species. **Archetypical species are stylized "virtual species" obtained by the combination of species with similar ecological and physiological traits**. Theoretically, if properly selected, an archetypal species may be representative of groups of species that are expected to have fairly similar characteristics in the context of connectivity, sharing similar spatial requirements and habitat selection and perception.

2.3 Connectivity in the context of Green and Blue Infrastructure

In 2013, the European Commission (EC) adopted a strategy to develop green and blue infrastructure (GBI) in the EU (see Section 3.4) in the scope of the Action Plan for Nature, People and the Economy. GBI is broadly defined as a network of natural and semi-natural areas, together with other environmental features designed to deliver a wide range of ecosystem services to people, while enhancing biodiversity. GBI, with its green (terrestrial) and blue (if aquatic systems are concerned) components, is a promising approach for land-use planning (Houet et al., 2022) as it is multi-functional to incorporate both biodiversity (although not related to specific targets or species) and ecosystem services targets.

Connectivity is one of the principles of GBI design, along with multi-functionality and spatial planning (Estreguil et al., 2019). The social and ecological benefits of GBI depend to a large degree on connectivity (Benedict and MacMahon, 2002; Ignatieva et al., 2011; Petrisor et al., 2021).

The multi-functional perspective of GBI spans many policy sectors and raises some challenges to connectivity design, namely through defining the relative weight of the biodiversity *versus* ecosystem services objectives. As an example, when designing connectivity corridors, the fact that vegetation is native or exotic may make no difference for some specific ecosystem services (e.g., carbon sequestration), but it might have strong implications for biodiversity potential as non-native vegetation may not serve as suitable habitat for many species. However, the prevalent view is that **there should be a complementary perspective assuming that GBI is composed of biodiversity-rich areas that also provide multiple ecosystem services to people** (Estreguil et al., 2019). In any case, the involvement of stakeholders from different sectors is crucial to determining priorities, costs, and benefits for GBI, and consequently how to approach connectivity to deliver benefits for specific species but also to society.

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Approaches for using GBI in spatial planning are based on two components: (1) the mapping of existing GBI components (protected areas and ecological networks), focusing on the identification and physical delineation of landscape features consisting of green and blue elements; and (2) an ecosystem service-based mapping, based on assessing the capacity of the current land cover to provide ecosystem services. In contrast to the physical mapping approach, which refers to the delineation of physical landscape elements, the ecosystem service-based mapping approach further adds a function to the physical element by expressing the ecosystem services they deliver (Estreguil et al., 2019), for example the potential for increased pollination supply due to existing hedgerows.

2.4 Spatial scale issues and dispersal

Projects addressing the restoration and protection of connectivity may be implemented at various spatial scales, ranging from local to regional or even continental, depending on the specific objectives and the species being considered. For example, migratory birds may be extremely philopatric (return to the same locations) in their breeding ranges while migrating for thousands of kilometres (from Europe to south Saharan Africa) twice a year (e.g., the dunlin *Calidris alpina* has a natal dispersal distance below 5 km and a migratory distance which can be over 4,000 km, with peaks of 1,200 km per day during migration. On the opposite extreme, saproxylic beetles (e.g., the hermit beetle *Osmoderma eremita*) never move from their natal tree (Ranius 2006) and cave salamanders (e.g., *Speleomantes strinatii*) do not move more than 20 metres, being sedentary throughout their entire life. Large carnivores are somewhat in the middle, although with variability, even at the species level. For example, female bears are extremely philopatric (with females often taking over part of their mother's home range) while male bears make relatively long dispersal movements (Maiorano et al., 2017). Migratory fish species, particularly susceptible to fragmentation, include endangered medium-distance migrants (e.g., *Acipenser ruthenus*, *Hucho hucho*) and large-distance migratory species (e.g., *Acipenser stellatus*, *Huso huso*) which became extinct in the upper Danube catchment as a consequence of the closure of the Iron Gate dams (Jungwirthh et al., 2003).

These differences must be considered in any management and/or conservation planning with each scale of approach having different requirements and challenges. Both habitat selection and connectivity are very sensitive to the spatial (and temporal) scale of analysis (Ashrafzadeh et al., 2020). An incorrect scale can result in incorrect inferences that may lead to inefficient conservation actions. The optimal scale for planning and managing habitat connectivity

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therefore depends on the system under consideration and on the goal of the conservation strategy.

At the **local scale** (Noss, 1991), several studies have demonstrated the value of field margins and other small, linear patches of natural habitats in agricultural landscapes. Fencerows may act as local corridors between woodlots, allowing for metapopulation persistence in micromammals (Fahrig and Merriam, 1985), antipredator strategies in birds (Ausprey et al., 2023), and movement in reptiles and amphibians (Noss, 1991). A hedgerow approach focusing on local connectivity in a human-dominated landscape (e.g., agriculture conservation) can be extremely important for animals and plants with limited dispersal capabilities (most herptiles, many small mammals, non-flying invertebrates, etc.). A clear disadvantage of hedgerows (and of linear corridors in general) is that they are often narrow strips of habitat and therefore not all species can use them (e.g., forest interior species will not, and edge effects will increase exposure to threats).

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At the **scale of a landscape**, we often deal with landscape mosaics, including habitat patches and corridors. At this scale, any wide-ranging mammals (e.g., a bear) require corridors to move from one habitat patch to the other to meet their daily needs for food, water, and shelter, often spanning tens of kilometres in a single day. At the same scale, but on a different time frame, ungulates use landscape connectivity for seasonal movements, while amphibians migrate between wintering grounds and breeding ponds.

At the **regional to continental scale**, in many parts of the world, there is an ambitious strategy to connect nature reserves into regional networks (e.g., the Natura 2000 network in Europe or the Yukon to Yellowstone National Parks in North America). This strategy is particularly important when we enlarge our temporal view up to centuries and millennia. In the past, huge biogeographical corridors have been critical in permitting the shift of floras and faunas in response to global changes (e.g., the Bering land bridge, and the isthmus of Panama). Future climate changes, probably occurring over the next few decades, also require a large-scale vision. In this framework, human-related habitat fragmentation has greatly increased the number of barriers for most native species and at a large scale, therefore regional networks of nature reserves will play a fundamental role. A Europe-wide approach (focusing on transboundary conservation/management) is potentially vital for species having large-scale requirements and long dispersal distances, for example for the Italian/French wolf population (Ciucci et al., 2009), for most large carnivores in western Europe (Chapron and Arlettaz, 2006), or anadromous sturgeons (Friedrichs et al., 2018). Focusing particularly on the large scale of analyses, connectivity is central to many global change analyses, in which the response of

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single species or entire communities is related to ongoing and future climate changes (Tesson and Edelaar, 2013). For example, many Mediterranean species will relocate their distributions to temperate or boreal regions (Maiorano et al., 2011).

The scale of analyses must be linked to the ecological traits of the species being considered, focusing particularly on dispersal capacity, and its commonly used proxies such as body size and home range size. Dispersal, or better natal dispersal, can be defined as the movement of an organism (animal or plant) from its natal place to the place where it will reproduce. In some cases, natal dispersal information is not necessarily useful for connectivity projects. Take long distance migratory birds as an example, where the distance between natal and breeding locations are in reality separated by thousands of kilometres spent in autumn and spring migration. In this case, using natal dispersal as an indicator of dispersal capacity is not useful.

The effects of dispersal can be seen at all spatial scales, from intraspecific genetic diversity (Suárez et al., 2022) to species geographic ranges (Gaston, 2003). Furthermore, there is a growing understanding of its importance in a global change context (Anderson et al., 2012). Dispersal plays a central role in the response of populations and species to global changes, including climate change, habitat loss and fragmentation, as well as invasive species (Tesson and Edelaar, 2013). Distance between patches of suitable habitat, or distance among protected areas must consider the dispersal capability of the species. In general, spatial requirements may help define stepping stones both in their size and in their distance (e.g., Parks et al., 2023).

However, **data availability on dispersal is limited in many taxonomic groups** (Nathan, 2001). The reasons for this gap of knowledge go from inconsistencies in both the measurement and the definition of dispersal to difficulties in collecting field data, and the existence of unpredictable long-distance dispersal events (Bowman et al., 2002). Furthermore, a dispersal event can take many forms, going from a gradual shift (e.g., typical of philopatric mammals like brown bears) to a one-way movement over great distance (Sarkar et al., 2021).

Often dispersal distances have been estimated using correlative models with ecological and physiological traits as covariates. Multiple traits have been demonstrated as important correlates for dispersal. For example, gestation length and maximum life span have been identified as important to explaining the distance moved by species ranges during the North American glacial/interglacial cycles (Lyons et al., 2010). A suite of demographic traits (e.g. fecundity) has been correlated with dispersal abilities in butterflies (Stevens et al., 2012). Although no single model outperformed all others in the literature (Whitmee and Orme, 2013), body mass and home range consistently emerged as important predictors of dispersal ability (see also Section 6.3).

2.5 Corridors and stepping stone design

Corridors and stepping stones are the two main landscape designs targeting the conservation or restoration of ecological connectivity. **Corridors** are more traditionally utilised in connectivity conservation as they are continuous linear connections between two or more habitat patches. **Stepping-stones** are a network of smaller habitat patches between large

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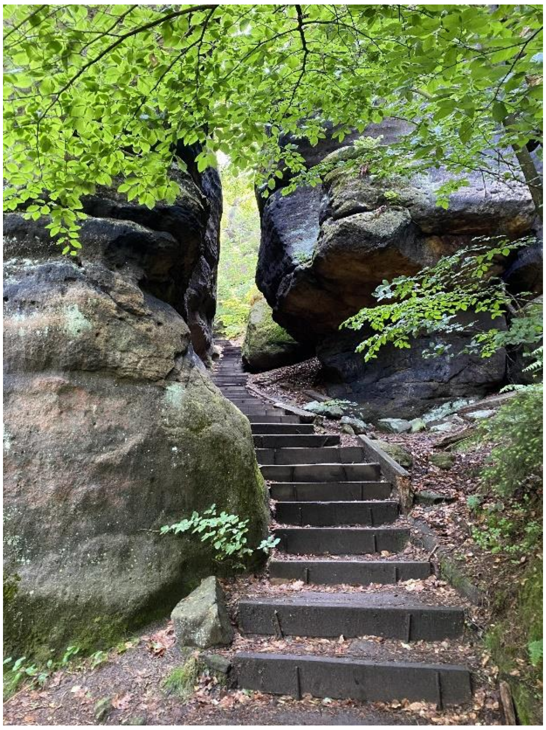
protected areas that act as refugia for species to maintain genetic connections and move between the protected areas. Quite often **a complex connectivity design will contain a combination of corridors and stepping stones to connect dozens of protected areas across a broad region, and including across borders** (e.g., multi-country).

Corridors are more heavily relied upon as they are intended to maintain an unbroken connection through a landscape that may already be heavily modified by humans. Examples of large landscape corridors include the connections of undeveloped habitat for mountain lions (*Puma concolor*) in heavily urbanised southern California, unbroken protected forests for the movement of tigers (*Panthera tigris*) between reserves in India, and the Mount Kenya Elephant Corridor for the migration of African savanna elephants (*Loxodonta africana*), or the initiative to set cross-border connectivity corridors in the Carpathians and Danube basin, in Europe.



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In the European context, intensive land management and the mixture of habitat types in and around protected areas bring added complexity to the placement and configuration of corridors. These complexities have implications that need to be considered when designing corridors, e.g.: (i) protected areas are often a mixture of habitats, raising the question of which habitat types should be included in the corridor; (ii) should we design different corridors among protected areas for each target group?; (iii) if two nearby Natura 2000 areas do not share any habitat type (e.g. one is a forest and the other is a wetland), is a corridor justified?; (iv) what are the socio-economic challenges of corridor management in these humanized landscapes?

Appropriate corridor width is important to ensure that species of concern will successfully move through the corridor and reduce the chances that wildlife will come into conflict with humans. If a corridor is too narrow, then the edge effects from human presence likely affect successful movement and the habitat may be too degraded for species movement. For example, forest birds are impacted 50-70 metres from human recreation and development, thus a corridor that is less than 150 metres wide contains very little core habitat that is not in some way influenced by human pressure. Large mammals are impacted at much greaterdistance thresholds, thus corridors that are greater than 1 km in width can reduce the impacts of humans while reducing the chances of human-wildlife interactions (Dertien et al., 2021).

Stepping stones facilitate the movement of species and help maintaining connection between two or more larger habitat areas without direct structural connection. Just like a chain of small islands between two large land masses, a stepping stone design can be seen as islands of

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habitat surrounded by an ocean of unprotected land. Stepping stone designs can be more feasible to implement in more highly populated areas where land protection for a fully connected corridor may be much more difficult to implement (Lynch 2019). Also, the protection of stepping stones can be the first step in the planning for the restoration of permanent corridors between stepping stones. While stepping stones are often considered secondary substitutes for corridors, studies have shown the importance that even small habitat patches can have on maintaining ecological connectivity for some species (Herrera et al., 2017). Birds, plants and aerial insects are known to benefit the most from stepping stones given their dispersal abilities, and in fact can be key to a species range expansion (for example Saura et al., 2014). For example, wetlands are important stepping stones along migratory flyways for aquatic birds (Merken et al., 2015).

To maximise connectivity through ecological stepping stones, several key principles should be considered in their design (Box 2.1):

Box 2.1 Key principles to consider when designing ecological stepping stones

1. Proximity and Alignment: Stepping stones should be strategically placed to minimise the distance between them and larger habitat areas. They should form a series of rest stops that align with the natural movement patterns of species (e.g. North-South migrations) (Bennet, 2003, Saura et al., 2014).

2. Habitat Quality and Diversity: Each stepping stone should offer a variety of microhabitats and resources (such as food, water, and shelter) to cater to the needs of different species. The quality of these habitats is just as important as their presence (Bennet, 2003)

3. Landscape Context: The surrounding landscape should be considered in the design of stepping stones. This includes understanding the matrix of agricultural, urban, and natural areas to optimise the placement and composition of stepping stones for the target species (Bennet, 2003, Hilty et al., 2006).

4. Size and Shape: While stepping stones are inherently smaller than core habitats, their size and shape should be optimised for the species of interest. Larger stepping stones can support more species and provide more extended stays, while the shape can influence the edge effects and the internal microclimate of the habitat (Saura et al., 2014).

5. Target Species Needs: The specific needs of target species or groups of species should guide the design of stepping stones. This includes considerations of the species' dispersal abilities, habitat preferences, and threats they face (Bennet, 2003).

6. Monitoring and Management: Once established, stepping stones require monitoring and management to ensure they continue to serve their intended function. This might include measures to control invasive species, maintain habitat structures, and adapt to changing conditions or new scientific knowledge (Bennet, 2003, Hilty et al., 2006, Saura et al., 2014).

In urban settings, the difficulties of land acquisition and city design may require a stepping-stone approach (Lynch, 2019), though there is evidence that corridors rather than stepping stones are more effective at supporting urban biodiversity (Beninde et al., 2015). In the rural or peri-urban (exurban) landscape, stepping stones may be forest patches, riparian

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zones, or highly heterogeneous agricultural areas. Moving into the urban matrix these stepping stones can become even more human-dominated such as parks, brownfields, greenways and even rooftop gardens. As the urban matrix becomes more developed and difficult to traverse, stepping stones must be closer together to maintain linkages. However, if the urban matrix becomes entirely too hostile to the movement of wild species (e.g., urban centres), stepping stones are not effective and a continuous protected corridor is the only option to maintain ecological connectivity. Difficulties may also persist with planning and managing stepping stones since many are available opportunistically (rather than pre-planned) and may be owned privately rather than publicly.

Ultimately, the use of corridors or stepping stones as features for maintaining connectivity is reliant on the geographic situation, the species or ecological processes that one is trying to conserve, and the political will for the creation of a connectivity network.

2.6 Freshwater and cross-realm connectivity

Connectivity analyses of terrestrial habitats have often included rivers as two-dimensional elements but neglected their internal structure and heterogeneity that in turn represent a ‘riverscape’ (Wiens, 2002). Although knowledge and approaches from terrestrial assessments can also be transferred to aquatic ecosystems, **rivers exhibit certain characteristics, which should grant them a special position in connectivity conservation** e.g., (1) rivers represent both a habitat and migration corridor (Ward, 1989; Wiens, 2002), (2) connectivity acts on four (one temporal and three spatial) dimensions, whereby the importance of each dimension changes along the river course (Vannote et al., 1980; Ward and Stanford, 1995), (3) hydrologic connectivity allows the passive downstream transport of matter and energy (Pringle, 2006; Ward and Stanford, 1995), but enables a multidimensional dispersal of organisms (Branco et al., 2014; Ward and Stanford, 1995), and (4) while terrestrial analyses often focus on the connectivity of specific habitat types (e.g. grasslands or forests), the connection of different habitats may be more important in the freshwater realm where certain species and life stages require diverse habitat patches to complete their life cycle, e.g. sturgeons of salmons (Jungwirth et al., 2003).

Freshwater ecosystems host remarkable biodiversity and provide substantial ecosystem services such as flood retention, water purification or recreation (Hanna et al., 2018; Kaval, 2019; Tickner et al., 2020). However, the decline of freshwater species populations is happening globally faster than declines in marine and terrestrial realms (Reid et al., 2019). This decline results from a set of threats, including fragmentation, and others such as flow regulation, pollution, habitat loss and overexploitation of biological resources, and invasive species (Dudgeon, 2019; Haase et al., 2023; Strayer and Dudgeon, 2010).

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Connectivity plays a key role in the conservation, restoration and management of freshwater ecosystems because of their connected nature, which facilitates the maintenance of ecological processes (including the movement of freshwater organisms, the hydrological transport of energy, solutes, pollutants and sediments), but also allows for the propagation of threats (such as pollution and invasive species) (Linke et al., 2011; Pringle, 2003; van Rees et al., 2021). However, human pressures constrain freshwater connectivity worldwide, particularly river fragmentation, water abstraction and flow regulation, sedimentation, water consumption, and urbanisation (Grill et al., 2019).

Due to limited migration opportunities, **fragmentation is particularly damaging in stream networks**, since it is more difficult or even impossible for fish to avoid disconnections (Fagan, 2002). Even though weirs represent the most obvious way of fragmentation in riverine habitats, dams may also be associated with other hydromorphological changes, which then alter the spatial and temporal patch composition and, consequently, connectivity patterns (Wiens, 2002). In this context, residual flow sections and impoundments may not only alter habitats but can also contribute to habitat fragmentation by preventing fish migrations through sections with limited water depths and flow velocities (Schmutz and Sendzimir, 2018).

2.6.1 Four dimensions of connectivity in rivers

Ward (1989) defined freshwater ecosystem connectivity across four dimensions: longitudinal, lateral, vertical, and temporal. Firstly, the **longitudinal dimension** refers to the connection between upstream and downstream regions, which facilitates the life cycle of migratory species and species dispersal (Vannote et al., 1980). Freshwater longitudinal connectivity is distinct from general terrestrial connectivity because it has a strong directional component (Moilanen et al., 2008). Some studies focused on maximising linear connectivity throughout the river catchment. For example, Moilanen et al. (2008) suggested measuring freshwater connectivity by considering its hierarchical network topology and creating functions to describe upstream and downstream connectivity, reflecting the water flow. These functions can be

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adjusted based on the ecological needs of different species. Hermoso et al. (2011) modified the hierarchically based approach by measuring longitudinal connectivity between each sub-catchment and each upstream sub-catchment as the inverse of the distance (measured through the river) between them.

Secondly, the **lateral dimension** plays a key role too in maintaining the flow of matter and energy and the daily routine of semi-aquatic species by connecting freshwater ecosystems with nearby floodplains and wetlands. This connection can be established through river floods during the wet season, or by dispersal of semi-aquatic organisms, such as some insects, turtles, birds and mammals. The lateral dimension and connectivity to riparian areas play a vital role in connecting aquatic and terrestrial habitats. Hermoso et al. (2012a) and Reis et al. (2019) proposed a set of new inter-sub-catchment metrics to account for connectivity between the river network and adjacent wetlands not connected by the river network. The aim was to account for the ecological requirements of species that move across drainage divides, such as waterbirds.

Thirdly, the **vertical dimension** includes interactions between the surface and groundwater, comprising gradients in habitat stratification, temperature, light and oxygen levels, which together condition the vertical migrations of species. This dimension of connectivity has received less attention than the others. Notably, Nel et al. (2011) measured vertical connectivity by developing a predictive model to map the probability of groundwater interacting with surface water. This method was used to identify areas most critical to maintaining seasonal refuge pools.

The fourth dimension is **time**, which affects freshwater ecosystems through changes in river flow (conditioning drought and floods), climatic conditions and life cycle dynamics. Freshwater connectivity is limited by water flow, which seasonally fluctuates in permanent rivers and is even not permanent in a high proportion of rivers (known as temporary or intermittent rivers). Freshwater habitats in these systems may become restricted to a reduced and disconnected set of pools, which become ecological refugia, vital to recolonization after the dry period. These types of rivers are more likely to occur in climatic regions with pronounced wet-to-dry seasonality, such as the Mediterranean, which is predicted to become increasingly subjected to droughts (Estrela-Segrelles et al., 2023; Naumann et al., 2018), and in arid regions where in most of the year the water is restricted to water pools. In addition, water availability can also fluctuate inter-annually, given that extreme drought events are predicted with global climate warming (Naumann et al., 2018). Examples to address temporal connectivity include Hermoso et al., 2012a), who used water residency time as a proxy.

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2.6.2 Connectivity between freshwater and other realms

In addition to addressing the four dimensions of connectivity in rivers, **there has been increased attention to considering connectivity among terrestrial, freshwater and marine ecosystems** (Adams et al., 2014; Alvarez-Romero et al., 2011; Álvarez-Romero et al., 2015; Beger et al., 2010a). The interactions between these ecosystems are necessary for species persistence and for the maintenance of ecosystem services through the flows of energy, materials and organisms (Giakoumi et al., 2019; Hermoso et al., 2021a; Soininen et al., 2015). Hermoso et al. (2021b). However, there are several approaches to assess connectivity: Tsang et al. (2019) measured the connectivity between inland and marine habitats as a function of distance. Leontiou et al. (2022) measured connectivity for species that breed inland but forage on the sea as the inverse distance between these areas. Tulloch et al. (2021) used models of land-sea runoff and ocean dispersal to estimate threats to the marine ecosystem and Devlin et al. (2012) identified inshore ecosystems exposed to surface plume pollutants.

However, an increase in connectivity within and between realms may foster the propagation of threats (see Section 6.7), such as the dispersion of pollutants, the spread of invasive species, and exposure to diseases (Adams et al., 2014; Alvarez-Romero et al., 2011; Tulloch et al., 2021). Identifying, measuring and actively managing these connections is vital, but such practice is complex, given the broad spectrum of connectivity concepts, particularly when focusing on realms and accounting for spatial-temporal dynamics (Beger et al., 2022). These complexities require integrative planning that assesses the co-benefits and trade-offs of various links to make cross-realm connectivity more informative and to highlight advantages and disadvantages (Álvarez-Romero et al., 2015).

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2.6.3 Tools and approaches to assess connectivity across realms

Although connections between the different realms may be difficult to measure, some tools are available to examine proxies for connectivity patterns from large to short spatial and temporal scales (Beger et al., 2022). A common approach is to identify connections between important conservation areas in the different realms. For instance, Naia et al. (2021) measured connectivity between desert water pools (gueltas) and their upstream contributing sub-catchments based Euclidean distances between them. This connectivity can be very important to relict populations which use gueltas as refugia during dry periods and disperse during the wet season, such as the *Crocodylus niloticus* in Mauritania (Brito et al., 2011; Vale et al., 2015). For large spatial scales, remotely sensed metrics such as the Normalised Difference Vegetation Index (NDVI) provide proxies for carbon, nitrogen and phosphorus eventually entering the freshwater ecosystems (Dahlin et al., 2021; Soininen et al., 2015). This information can be used to approximate biodiversity-ecosystem functioning linkages, particularly interactions, feedback, and synergies between terrestrial and freshwater ecosystems, and across trophic levels. Remote sensing can also aid in assessing types of vegetation that function as freshwater corridors, such as riparian vegetation and floodplain seasonality (Reis et al., 2019). Riparian corridors provide and regulate a wide range of ecosystem services (Atkinson and Lake, 2020), including contributing to functional connectivity. For instance, they enable the connection of forest fragments widespread over the landscapes and allow movement and dispersal of several species (Keten et al., 2020; Larsen-Gray and Loehle, 2022). Remote sensing techniques can also track the propagation of some pollutants (Gholizadeh et al., 2016), which is important to assess the potential impacts on biodiversity patterns and processes to which they are connected through water flow (Álvarez-Romero et al., 2015).

Investigating aquatic animal movements has become widespread and popular with the use of radio or acoustic telemetry as well as Passive Integrated Transponder (PIT) tags (Burnett et al., 2021). This technology can aid in assessing connectivity directly for anadromous and catadromous fishes based on their migration pathways including the assessment of the effectiveness of fish passages that aim to restore functional connectivity for fish. Furthermore, genetic tools and landscape genetics have also been used to assess connectivity indirectly, as barriers and fragmentation affect gene flows between populations (Keller et al., 2015). This can be important to species with terrestrial and aquatic habitat requirements such as the Eurasian otter (Leoncini et al., 2023), or for wetland-breeding amphibians (Gutiérrez-Rodríguez et al., 2017; Watts et al., 2015).

2.7 Integration of connectivity in the process of area-based planning

Spatial conservation prioritisation is a process concerned with the identification of priority areas accounting for quantitative or qualitative conservation targets to achieve specified benefits for biodiversity, while allowing to account for social, economic and political constraints (Margules and Pressey, 2000; Moilanen et al., 2009). Conservation prioritisation can optimize and integrate multiple conservation features - e.g. ecosystems, species, populations, genetic lineages, multiple facets of biodiversity or targeting multiple objectives (Carvalho et al., 2017; Jung et al., 2021; Margules and Sarkar, 2007; Pollock et al., 2017), over space and time. **Connectivity can be an important aspect in deciding where to allocate future**

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conservation efforts and the inclusion of connectivity in conservation prioritisations can bring advantages in the long term. However, it can also facilitate the propagation of threats, such as diseases, pollution, invasive species and fires.

One common approach for incorporating connectivity in the prioritization process is that more connected areas should have a higher priority, e.g. are more likely to be selected as candidates for expanding a network of sites. However, benefits for species will likely rely on a set of trade-offs considering size, shape and habitat quality of sites, and connectivity between sites. Previous research shows that spatial priorities differ significantly when connectivity is not integrated into the conservation optimization (Hanson et al., 2022; Makino et al., 2013), with conventional methods approximating connectivity often fail reflect functional connectivity that supports greater gene flow between sites (Hanson et al. 2019).

There has been a proliferation of mathematical and analytical methods to solve complex decision-making problems in various aspects of conservation efforts, from heuristic algorithms to more sophisticated optimization methods using operation research (Alagador and Cerdeira, 2022; Pressey, 2002). These include identifying priority conservation areas space (Allan et al., 2022; Montesino Pouzols et al., 2014; Pollock et al., 2017; Ward et al., 2020), optimising surveys and monitoring networks (Carvalho et al., 2016; Hanson et al., 2023), and allocating management actions (Adams et al., 2014; Cattarino et al., 2015).

Different algorithms and tools have been developed to support decision-making in spatial conservation prioritisation optimization, including Marxan (Ball and Possingham, 2000), Marxan Connect (Daigle et al., 2020), Zonation (Moilanen et al., 2014), and the *prioritizr* R package (Hanson et al., 2019). These tools vary in their algorithms, optimization approaches, flexibility in objectives and constraints, and output types. For instance, Marxan uses a minimum-set approach to heuristically identify near-optimal sets of planning units that achieve a set of conservation targets at a near-minimal cost, while Zonation uses a Maximum coverage approach, aiming at ranking gridded planning units for their biodiversity benefits and considering a specified cost. *Prioritizr*, on the other hand, allows the use of multiple problem formulations (including both minimum set, minimum shortfall and maximum coverage formulations) and relies on exact algorithm that guarantees optimality, e.g. the areas selected are the best possible given supplied data (Beyer et al., 2016). All these algorithms enable the consideration of connectivity between chosen priority conservation areas. However, different tools vary in the connectivity concepts used and respective methodologies.

In mathematical terms, connectivity can be integrated in the prioritization problem as a goal or as a constraint (Daigle et al., 2020). Traditionally, the consideration of connectivity in spatial planning focused on preferring compact and contiguous configurations. To achieve larger conservation areas and a less fragmented network, connectivity is used as a constraint in the objective function, which penalises solutions with a higher total length of edges between selected areas, thus preferring areas in the ranking that are more compact and contiguous rather than isolated in space. The data required for this procedure is a relation table specifying the shared edges between each planning unit and its direct neighbours. However, connectivity concepts go beyond achieving network compactness and, in many cases, it may require an extended relational table specifying a connectivity measure between each pair of planning units. This relation matrix can be obtained with different methods, for instance, using Euclidean distances, least cost paths, resistance matrices attained with circuit theory, biophysical models, etc. (see Chapter 4). This is the case, for example, when the goal is

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facilitating movement or migrations of a particular species (Mazor et al., 2016), account for directional connectivity within and across freshwater and marine ecosystems (Beger et al., 2010b; Bode et al., 2008; Hermoso et al., 2021a), optimise gene flow (Hanson et al., 2019), deal with horizontally and vertically connectivity in a three-dimensional space (Venegas-Li et al., 2018) and when accounting for species' migratory needs derived from ongoing and future climate change (Sonntag and Fourcade, 2022).

In general, available algorithms are restricted to a single connectivity constraint, making it difficult to address multiple connectivity objectives. An alternative is to use a composite index of connectivity, which can combine multiple connectivity metrics (Magris et al., 2014) and provide a quantitative estimate of how each planning unit contributes to maintaining or enhancing connectivity. In this case, connectivity can be treated as a conservation feature in the optimization algorithm, rather than as a constraint (D'Aloia et al., 2017). While this approach can be computationally practical, it can have the caveat that through aggregation it becomes impossible to differentiate which connectivity aspect is driving the solution. Additionally, **another challenge in planning for connectivity in a network of protected areas is the assumption that all connections between protected areas (and the areas themselves) will persist through time once they are established**, but it is likely that land use, habitats and species ranges will shift and change under climate change, which can disrupt the functionality of the network (Nuñez et al., 2013).

2.8 Caveats of corridor design

Corridors design must also consider possible drawbacks which, under some circumstances, might entail unexpected or negative consequences for biodiversity conservation.

Ecological corridors are often planned with long and narrow shapes, which create extensive boundaries. Edge effects along these boundaries can negatively influence the corridor effectiveness. Furthermore, abrupt transitions between corridors and surrounding habitats may alter the microclimatic conditions (Bernaschini et al., 2019; Hofmeister et al., 2019; Laurance et al., 2002) and the distribution and behaviour of species within the corridor.

Research also indicates that edge effects can cause certain species to perceive corridors as unfavourable habitats or ecological traps and avoid them. Ecological corridors may also increase predation rates, as they create a narrow pathway that predators can exploit. By connecting populations or habitats that were previously isolated, corridors may also increase the likelihood of disease dispersal and facilitate the spread of invasive species (Resasco et al., 2014). Similarly, increased connectivity might induce gene flow interfering with population distinctiveness between formerly isolated populations.

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Ecological corridors can also entail conservation conflicts. The consequences of species dispersal through corridors include potential damages to agriculture, e.g., ungulate species can cause damage to crops during raids. Corridor use by large carnivores can also result in attacks to livestock (Hilty et al., 2012).

Wild Wonders of Europe. © Cornelia Doerr/WWF

However, scientific evidence does not support widespread negative corridor effects. An analysis of thirty-three corridor studies found no evidence that corridors increase species invasions or disturbances; edge effects can have either positive or negative impact on species abundances; and effects on antagonistic species effects or population synchrony were mixed. Whether or not the potential negative effects counteract the benefit of increasing connectivity strongly depends on the local ecological context and therefore no generalization should be made. Therefore, connectivity planning should acknowledge, identify, anticipate and monitor the potential these potential unwanted effects.

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Five major factors have been proposed as potential negative ecological consequences of corridors (Haddad et al. 2014):

1. Edge effects particularly affecting of long and narrow corridors
2. Colonization or population reinforcement of species that are antagonistic to conservation targets, such as pathogen hosts or competitor species
3. Proliferation and increased abundance of invasive species
4. Propagation of disturbances like fires
5. Synchronisation of population dynamics between connected habitats

2.9 Do ecological corridors work?

Ecological corridors play a crucial role in conserving biodiversity. However, their implementation can be costly and may have significant economic and social implications. Therefore, it is essential to assess their effectiveness in promoting connectivity between habitats.

The effectiveness of ecological corridors has been assessed in two large meta-analyses. In 2010, Gilbert-Norton et al. (2010) conducted a meta-analysis of 78 experiments from 35 studies conducted between 1985 and 2008 to investigate the impact of corridors on increasing movement between habitat patches. The results showed that corridors had a significant effect on movement, increasing it by approximately 50% compared to patches that were not connected with corridors. The study also found that corridors were particularly important for the movement of invertebrates, non-avian vertebrates, and plants, rather than birds. **These findings suggest that corridors can be an effective strategy for enhancing movement between habitat patches, which in turn can help maintain and restore populations of plants and animals in fragmented landscapes.** In 2019, Resasco (2019) conducted a meta-analysis involving 32 additional studies conducted between 2008 and 2018, utilizing the selection criteria established by Gilbert-Norton et al. (2010), and arrived at comparable conclusions.

Overall, **the effectiveness of ecological corridors is well founded on scientific evidence**. However, the effectiveness of corridors will vary depending on factors including the species involved, the characteristics and quality of the corridor, the landscape context, and the pressures.

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3. Global and EU policy instruments addressing connectivity

Connectivity is addressed in different policy instruments related to biodiversity conservation, with different approaches and targets. A short overview is made below for the key biodiversity policy instruments in the EU.

3.1 Connectivity in the post-2020 Global Biodiversity Framework

In the post-2020 Global Biodiversity Framework (GBF) (CBD, 2022a), the overall aim of maintaining, enhancing or restoring natural ecosystem connectivity is mentioned in its first goal (Goal A). Global targets for 2030 also include connectivity objectives in the scope of **restoration** of degraded areas (target 2), implementing a **well-connected system of protected areas** (target 3), and improving ecological **connectivity in green and blue spaces in urban and densely populated areas** (target 12). Proposed headline connectivity indicators for the GBF (CBD, 2022b) include a Protected Area Connectedness index, a dendritic connectivity index, and a Convention on Migratory Species (CMS) connectivity index. These are expected to be discussed and operationalized by an ad hoc technical expert group on indicators, with a time-bound mandate until the sixteenth meeting of the Conference of the Parties.

3.2 Connectivity in the EU Biodiversity Strategy

The EU Biodiversity Strategy for 2030 (EC, 2020) includes the desing of a coherent Trans-European Nature Network including **ecological corridors "to prevent genetic isolation, allow for species migration, and maintain and enhance healthy ecosystems"**. In this context, the protection and restoration of ecological corridors, investments in green and blue infrastructure, and cooperation between Member States across borders is promoted. Preserving and restoring habitat connectivity is also key for **bringing back at least 10% of farmland under high-diversity landscape features** (including e.g. buffer strips hedges, terrace walls, fallow land). Within the scope of **urban greening plans**, connections between green spaces should also be promoted. Lastly, the Strategy sets out a pledge to **plant at least three billion additional trees** by 2030 in full respect of ecological principles. The respective Commission staff working document (EC, 2021b) acknowledges the need to **ensure connectivity benefits of afforestation at the landscape level**, including in forests, agricultural landscapes and in actions related to the impact of infrastructures on habitat fragmentation. Such actions must combine large-scale conservation and restoration planning with the creation of new connecting infrastructures, i.e., from the creation of corridor habitats to strategically placed green bridges and tunnels for wildlife movement.

The goals and targets of the **Nature Restoration Regulation** proposed by the European Commission is central to the implementation of the EU Biodiversity Strategy (EC, 2022). The regulation places special regard to the connectivity between the habitats of species listed under the Habitats Directive and the Birds Directive. It also requires improving the connectivity

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of the habitats listed in Annex I to the Habitats Directive. These provisions require that nature restoration measures contribute with ecological corridors and other measures enhancing connectivity, with the aim of improving the habitat quality and conservation status of species and the ecological condition of habitats. In freshwater ecosystems, restoration measures should include the removal of artificial barriers in rivers, lakes and alluvial habitats to achieve significant increases in the longitudinal, vertical and lateral connectivity (such as restoring the natural functions of floodplains). Specific emphasis is also placed in restoring the connectivity of forest ecosystems. Other obligations will similarly require increasing connectivity to restore pollinator populations, such as implementing “buzz lines” where insect pollinators could move across landscapes, and harshening high-diversity landscape features with great potential to increase connectivity for species and habitats across agricultural ecosystems.

3.3 Connectivity in the EU Forest Strategy

In the EU Forest Strategy for 2030 (EC, 2021a) connectivity is not a central topic. However, there is a mention of **establishing ecological corridors in agricultural areas, as an expected outcome of reforestation or afforestation of biodiverse forests**.

3.4 Connectivity in the Green and Blue infrastructure strategy

In parallel to the strictly biodiversity-focused approach, the EC drafted a strategy to develop green and blue infrastructure (GBI) in the EU (EC, 2013, 2019), in the scope of the Action Plan for Nature, People and the Economy. Here, **green infrastructure (GI) is broadly defined as a network of natural and semi-natural areas, together with other environmental features designed to deliver a wide range of ecosystem services**. The blue component (BI) includes freshwater and marine realms. The EC encourages the preservation, restoration and enhancement of green infrastructure to halt the loss of biodiversity and enable the provision of ecosystem services. So, although GI is assumed as a tool for biodiversity objectives (Natura 2000 is assumed as the backbone of the EU GI), it includes a strong component of ecosystem service delivery objectives (it is assumed as “services-oriented”), therefore aiming for ecological, economic and social benefits through natural solutions (assumed as more sustainable than conventional civil engineering solutions, the so-called “grey infrastructure”). GI has a strong focus on urban settings and includes a wide range of objectives including climate change, health and disaster risk management.

Green and blue infrastructure is expected to positively contribute to the sustainability of several EU policies, including regional development, social cohesion, agriculture, transport, energy production and transmission, disaster risk management, fisheries and maritime policies. **Because of the multifunctional perspective of GBI, projects may have very different scopes,** including increasing landscape permeability for wildlife through better road and railway planning (e.g., TRANSGREEN project), large-scale corridors for large mammals, using power lines rights-of-way as ecological corridors, river and dune restoration, green infrastructure in cities, or setting regional networks of protected areas.

The EC drafted a guidance document focused on supporting tools and instruments to support investment, as well as good practices for GBI (EC, 2019). EU-level GI should cumulatively

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comply with the following criteria: (i) contribute to the conservation and/or enhancement of multiple ecosystem services at a significant scale, (ii) contribute to the goals of Nature Directives, (iii) have a strategic approach with EU-level impact, with at least a national or regional level approach. An overview of scientific and technical tools for GI mapping, including the European Mapping and Assessment of Ecosystems and their Services (MAES) initiative; and geospatial methods, data and tools (e.g., CORINE, LUCAS, Copernicus), are detailed in a technical report (Estreguil et al., 2019).

3.5 Connectivity in the Water Framework Directive

The EU Water Framework Directive (WFD) targets connectivity indirectly by recognizing the interconnected nature of water bodies and emphasizing the need to maintain and enhance connectivity within and between them. The directive aims to achieve "good ecological status" for all European water bodies and acknowledges that the ecological health and functioning of aquatic ecosystems depend on the free movement of water, sediment, and biota across different habitats. **The WFD identifies threats to connectivity, such as dams, weirs, and other physical obstacles in its River Basin Management Plans** (RBMPs). For at least 20% of EU river water bodies, barriers are considered a significant pressure under the WFD, contributing to the non-achievement of a good ecological status (EEA, 2021) and a decline of 93% in migratory freshwater fish in Europe since 1970 (Deinet et al., 2020). Consequently, **Member States are encouraged to adopt measures that promote connectivity and integrated water management approaches.** However, no direct measures to improve connectivity are foreseen in the EU Water Framework Directive.

3.6 Connectivity in the EU Pollinators Initiative

Connectivity is addressed in the EU Pollinators Initiative (EC, 2023) through **the promotion of well-connected, high-quality habitats for pollinators**. These ecological corridors (named “buzz lines”) are expected to enable species movement in search of food, shelter, and nesting and breeding sites, as well as acting as migration routes for species impacted by climate change. Connectivity for pollinators is particularly important in farmland, but also in urban areas, with the expectation that GI expansion can result in benefits for pollinators in those environments as well. By 2027, the Commission and Member States should devise a blueprint for a **network of ecological corridors for pollinators** and develop a plan of measures for implementing it.

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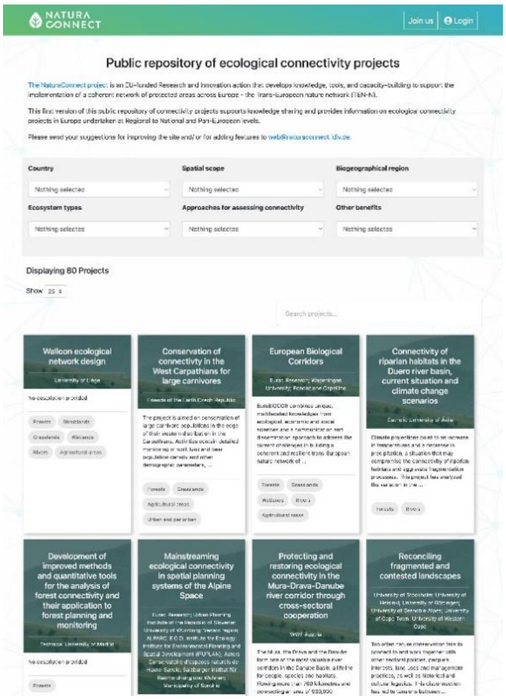
4. Connectivity projects in Europe and information needs

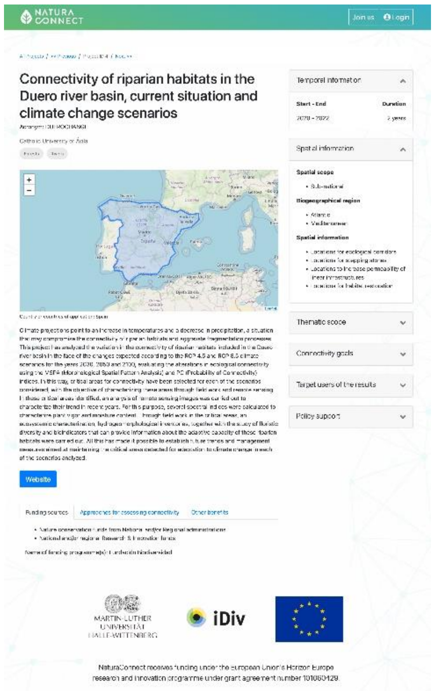
4.1 Survey of connectivity projects in Europe

To obtain a comprehensive, pan-European snapshot of connectivity initiatives taking place across Europe, an online survey was developed and disseminated, gathering information on ecological connectivity projects being implemented by actors at regional, national, and pan-European levels. The breadth of projects submitted included public and private conservation action plans and strategies, connectivity conservation projects, restoration projects, and research and innovation projects. The survey consisted of 27 questions covering project information, scope, participants, and selected approaches (see Annex S1.1). The survey was conducted between May 2023 and January 2024, using Google Forms and distributed via email and social media to project stakeholders and members of the wider conservation community and public. For more information on survey design, dissemination and response processing please see Annex S1.2.

This Section presents key results and findings from the survey, which help to build a more complete picture of ecological connectivity efforts across Europe. The insights derived from this exercise contributed to developing the framework for connectivity conservation and planning outlined in Section 6.

A companion online database has also been developed for public use, which contains all the projects included in the survey (80 projects). Its aim is to serve as a dynamic resource for researchers, policymakers, conservationists and members of the public interested in connectivity conservation projects conducted in Europe. To utilize this database, users can





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navigate through a user-friendly interface to access detailed information on a project, including its scope, participants, and methodologies. The results are systematically organized to enable intuitive exploration and comparison of projects at regional, national, and Pan-European levels. The database is accessible at https://naturaconnect.idiv.de/projects/:

4.1.1 Project information, location and duration

The final project list comprised 80 projects conducted in 35 European countries, along with Russia. The top five countries where connectivity projects were most frequently reported were Spain, France, Italy, Germany, and Austria (Fig. 4.1). Most (~75%) of the projects were completed within two to six years.

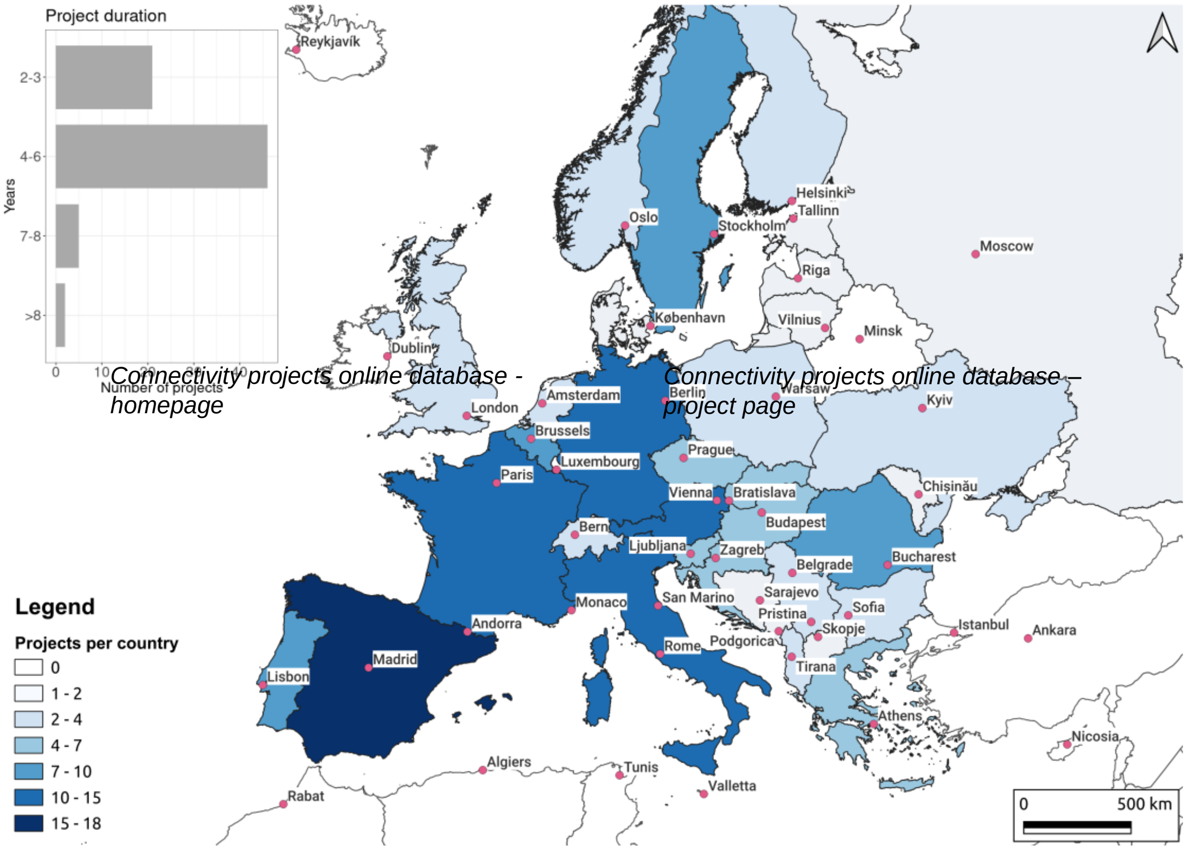

Figure 4.1: Number of projects per country and reported project duration (inset, top left).

4.1.2 Goals and scope

In reference to the connectivity goals of projects, the three most frequently stated goals were “Connectivity between protected areas", "Connectivity between specific habitat types", and "Protection of multiple species", which represented 72% of all responses (Fig. 4.2).

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Regarding the thematic scope of the projects, which refers to what they aim to enhance, "Ecological corridors (continuous corridors or stepping stones)" and "Ecosystem restoration" accounted for 54% of the responses.

Respondents were also asked to identify other benefits their projects may deliver, in addition to promoting biodiversity conservation. The three most frequently mentioned benefits were "None", "Recreation", and "Climate regulation", which comprised 52% of all replies.

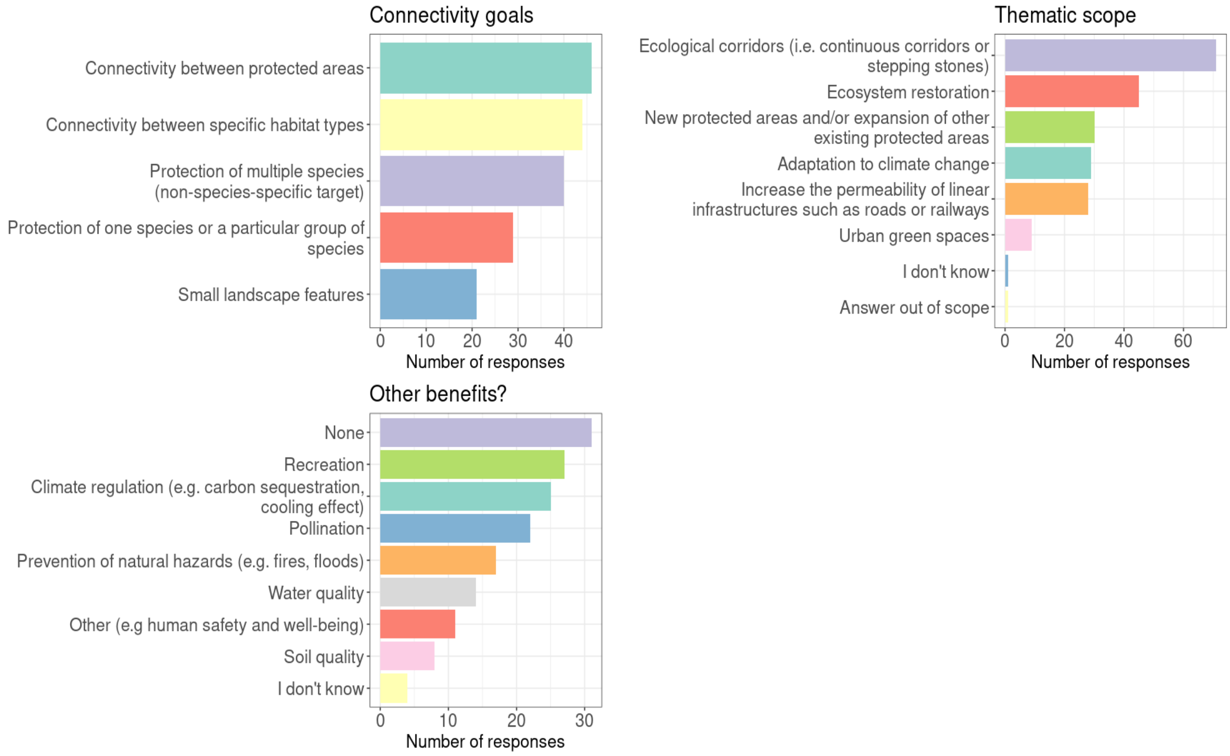

Figure 4.2: Response frequencies for stated connectivity goals, thematic scope and other benefits that a project may bring

4.1.3 Taxa and ecosystems

Respondents were asked to identify the taxonomic groups that their project focused on. The results showed that large carnivores make up 30% of the reported taxa, while arthropods and birds make up 19% and 13%, respectively. In terms of ecosystem types, forests account for 20% of the responses, grasslands 17% and agricultural areas 15% (Fig. 4.3).

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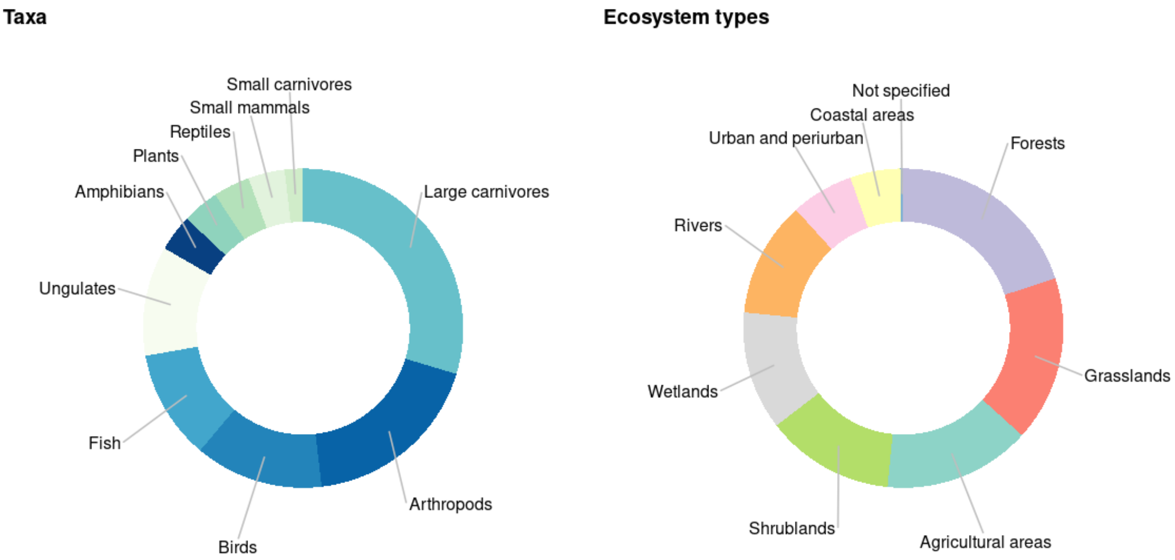

Figure 4.3: Response rates for taxonomic groups and ecosystem types.

4.1.4 Policy context, target users and funding

To evaluate the policy context of the projects, respondents were asked to indicate if their project was commissioned by an administration. We found that this was the case for only 38% of projects (Fig. 4.4).

In terms of the target users of the projects, "Regional and/or local administration(s)" and "National administration" accounted for 50% of reported target users. Regarding the policies that the projects aim to support, the most common responses were "Biodiversity conservation policy and strategies", "Spatial planning of protected areas", and "Green and Blue Infrastructure policies", which together accounted for 64% of the replies.

Finally, in relation to projects' funding sources, “Nature conservation funds from National and/or Regional administrations", “European funds associated with sustainability policies" and “Private funds" were identified as funding sources most frequently, accounting for 58% of answers.

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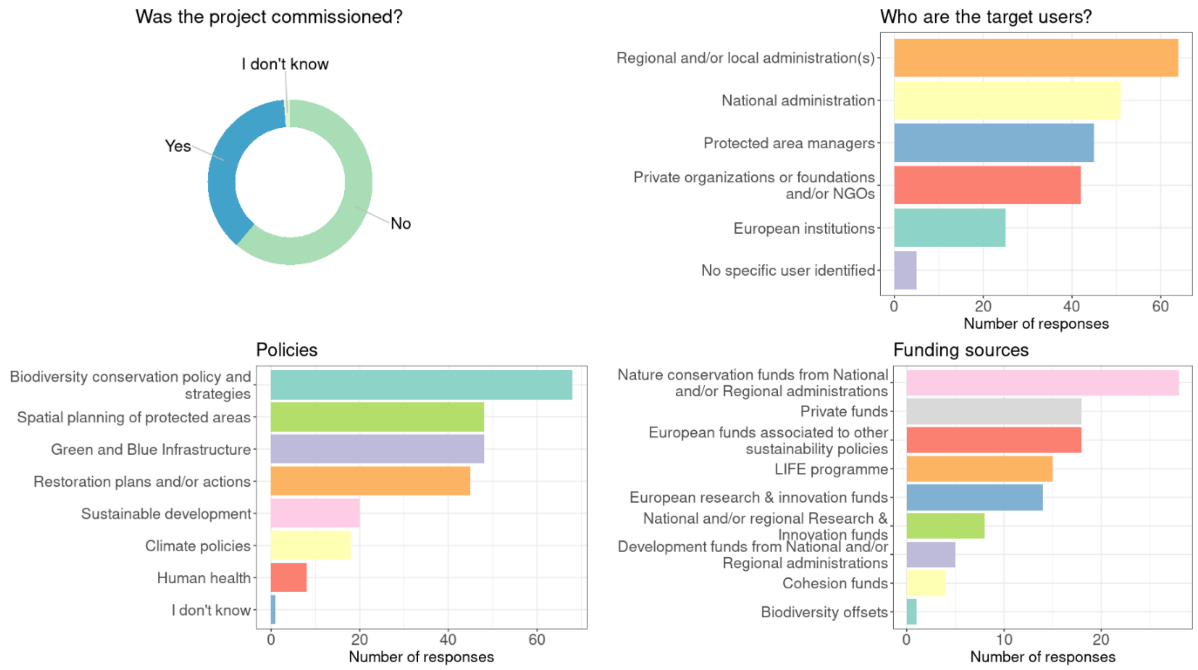

Figure 4.4: Response frequencies for the questions concerning policy context, target users and funding sources.

4.1.5 Spatial scope

With regards to the spatial scope of projects, “Sub-national (spatially comprehensive for one or several administrative regions)", “Transboundary (connecting across 2 or more countries)" and “Local (e.g., covering one or several municipalities or a specific infrastructure)" accounted for 73% of responses (Fig. 4.5).

For the biogeographical region where projects took place, the continental region was reported most frequently and accounted for 23% of the reported regions, while the alpine and Mediterranean regions accounted for 20% and 18%, respectively.

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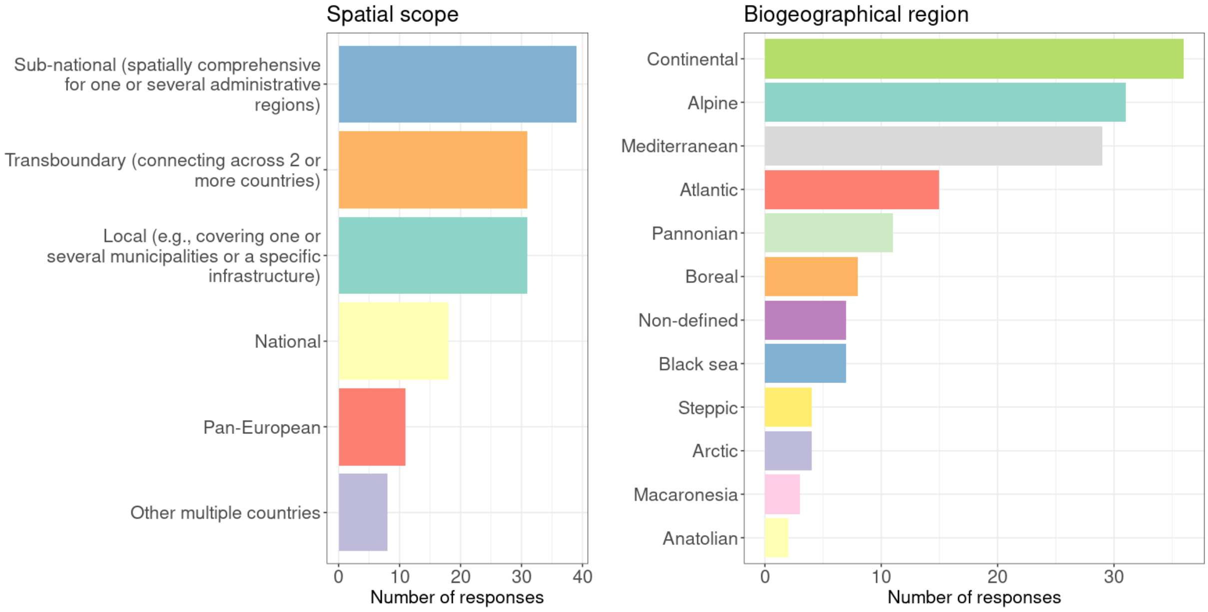

Figure 4.5: Response frequencies for questions related to projects' spatial scope and the biogeographical regions where they took place.

4.1.6 Selected approaches and outputs

For approaches used in projects for assessing connectivity, "Land cover and land use analyses", "Expert-based" and "Analysis of infrastructures (e.g., roads and railway) and urban sprawl" were the most frequent answers, accounting for 55% of the reported approaches. Regarding the kinds of spatially explicit information projects produced, "Locations for ecological corridors" and "Locations for stepping stones" accounted for 49% of the responses (Fig. 4.6).

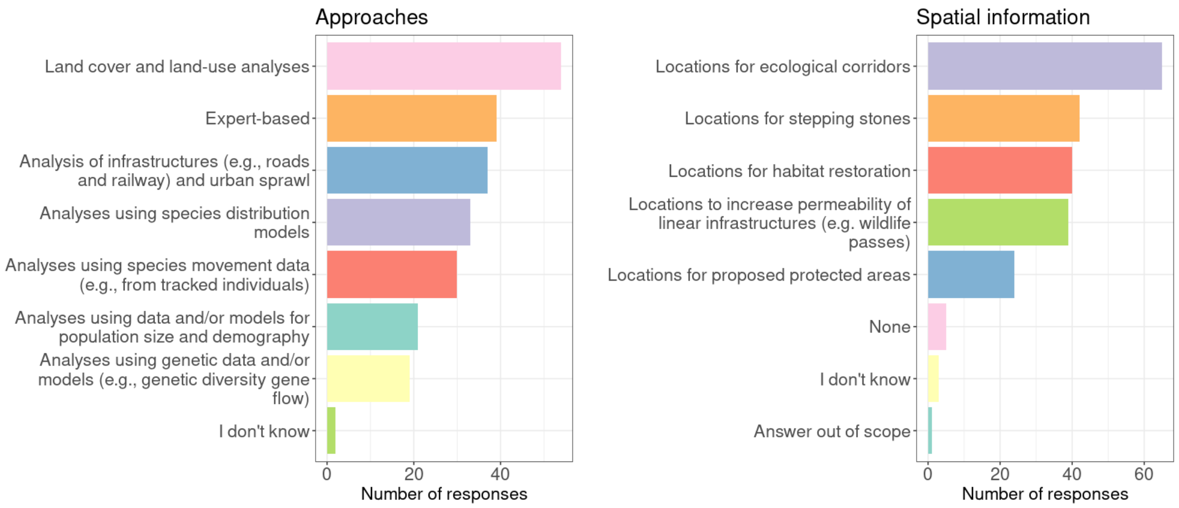

Figure 4.6: Response frequencies for questions concerning selected approaches and what kind of spatially explicit information projects produced.

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4.1.7 Assessing project effectiveness

Respondents were asked to determine if their projects included connectivity monitoring. Only 28% of projects reported implementing monitoring (Fig. 4.7), which suggests two possibilities. The first is that many projects did not propose testable approaches for enhancing connectivity. The second is that they did not consider or had insufficient funding for conducting monitoring.

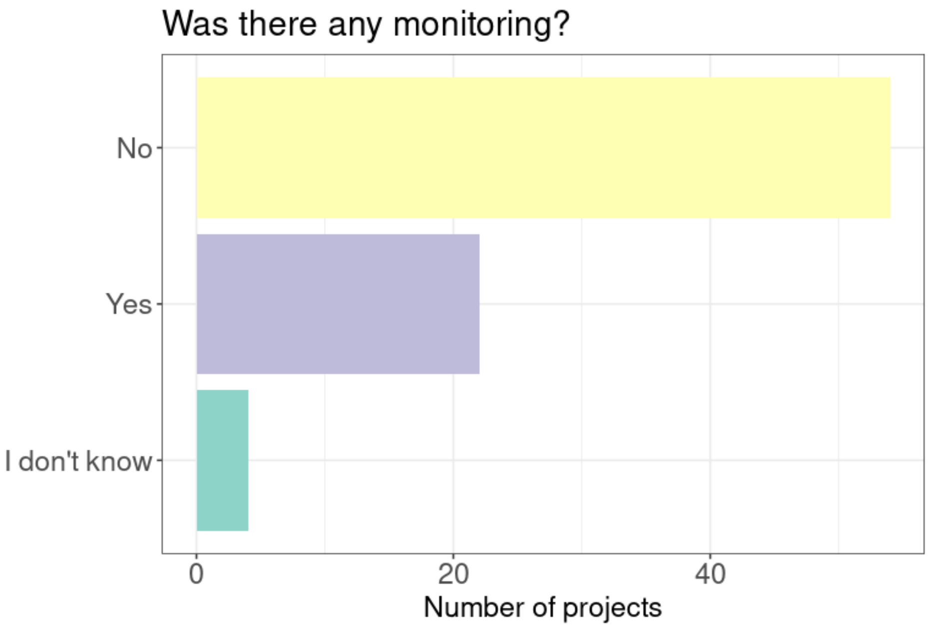

Figure 4.7: Number of projects that did and did not implement monitoring.

4.1.8 Potential negative effects

Regarding any potential negative impacts associated with increased connectivity, the most common response, accounting for 41% of the answers, was “None" (Fig. 4.8). The answers “Increased human-wildlife conflicts” and “Increased spread of invasive species” accounted for 17% and 14% of the responses, respectively.

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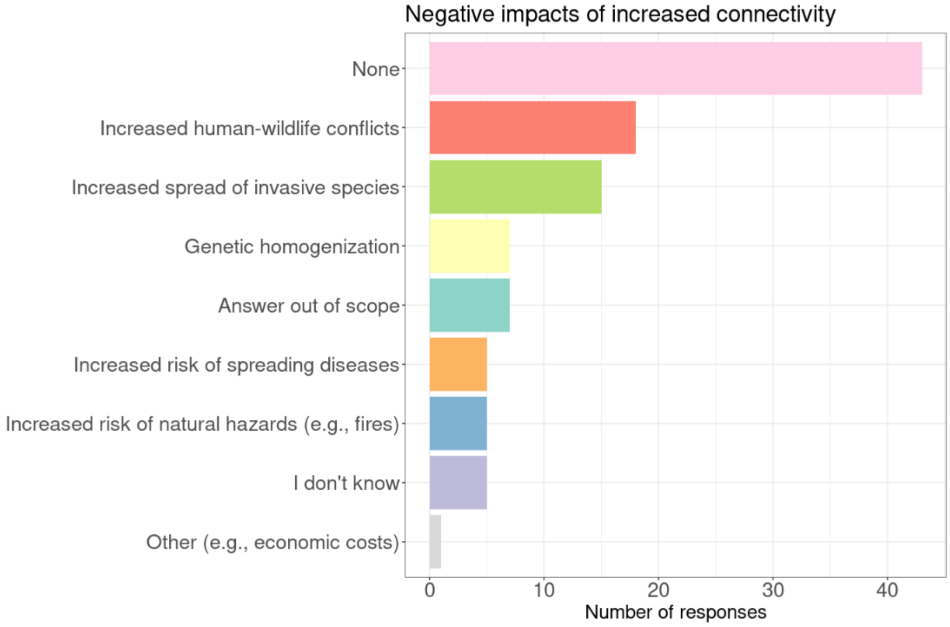

Figure 4.8: Response frequencies for potential negative effects caused by increasing ecological connectivity.

4.2 Priorities, gaps, and challenges in European connectivity planning

Maintaining and enhancing connectivity requires careful design, implementation, monitoring and the involvement of different stakeholder groups, including experts and practitioners from multiple sectors. Following the past and current state of European connectivity projects through the online survey, further insights on stakeholder priorities and challenges for future multi-scale connectivity planning across the continent were gathered via an online workshop. Overcoming gaps and challenges is critical for meeting the long-term success of a resilient ecological network across Europe for nature and people, and the online workshop served a crucial role in collecting stakeholders about the difficulties they face with connectivity planning, and potential actions that can help with remediating those challenges.

The two-day online workshop was organised in October 2023 and titled “Assessing Ecological Connectivity in Europe: Conservation goals and information gaps”. It gathered ~70 experts and stakeholders across the two days, from multiple sectors including EU/EC institutions, national and sub-national governmental administration and authorities, non-governmental organisations (NGOs), the private sector, and research institutes and universities (Fig. 4.9).

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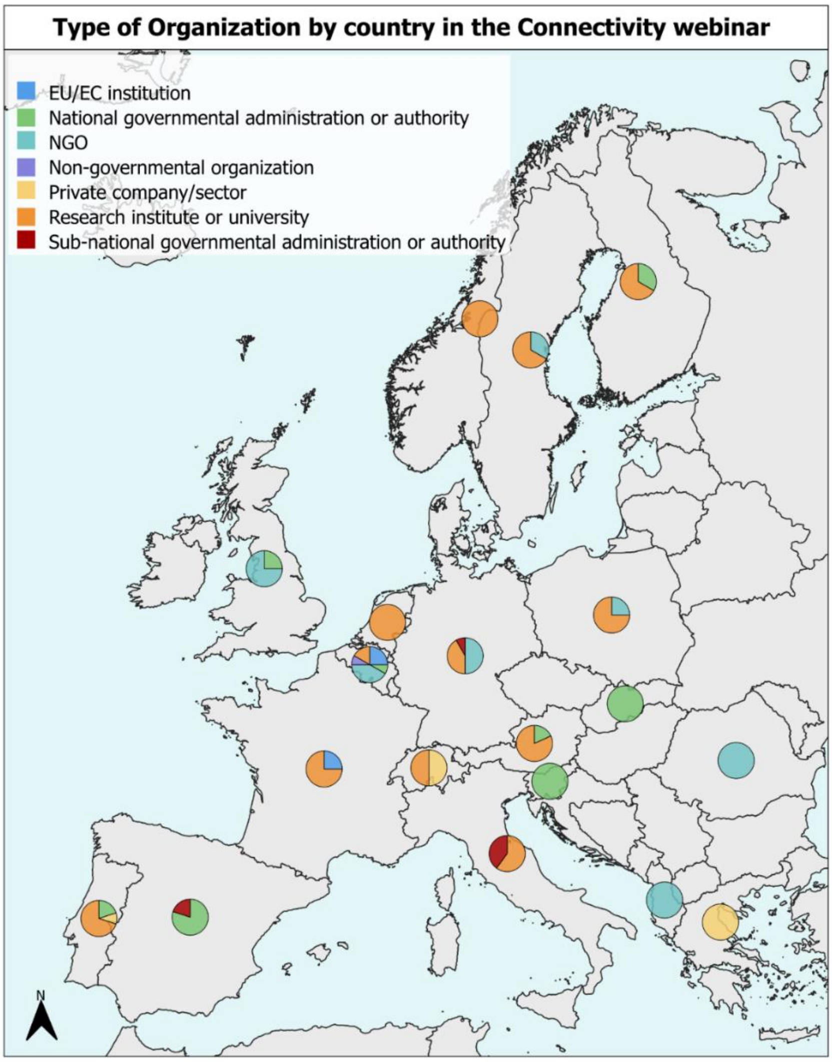

Figure 4.9: Type of organisation and distribution (% of total) by country of the participants in the online workshop "Assessing Ecological Connectivity in Europe: Conservation goals and information gaps".

The workshop consisted of two sessions, each divided into several breakout groups and aimed at answering a set of questions provided at the beginning of the sessions for guidance. Within both sessions participants were divided into different thematic breakout group discussions (Table 4.1); each discussion centred on a virtual whiteboard ("Miro Board") with multiple prompts where participants could leave responses (Fig. 4.10). The first day focused on identifying priorities for connectivity planning in Europe from five different subjects. The questions tackled ranged from the desired outcomes of connectivity across scales, to which areas should be better connected, where to establish corridors, and what measures have been, or should be, implemented to maintain and enhance connectivity. The second day focused on the technical challenges, data needs and potential solutions for connectivity planning. The questions addressed related to the data needed to implement connectivity projects, critical information gaps perceived, technical challenges and guidance constraining

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connectivity design, how to plan for connectivity in the face of climate change, and other challenges, needs, or solutions for connectivity planning and corridor design (Fig. 4.10; see Annex S2 for additional examples).

All responses from the Miro Boards were gathered, and a two-stage qualitative thematic analysis was conducted across all the groups. This form of analysis aims to synthesise responses into major groups to classify and categorise survey or discussion responses. There were multiple repeating themes in the responses provided by the participants for both priorities (Day 1) and challenges and solutions (Day 2) (see breakout group themes in Table 4.1), which are summarised in the following Sections.

Table 4.1: Breakout group themes for the two days of the "Assessing Ecological Connectivity in Europe: Conservation goals and information gaps" workshop. Stakeholders participating in the workshop self-selected their group and then interactively added responses to prompts derived from their general theme.

Day 1: "Identifying priorities for connectivity planning in Europe"	Day 2: "Technical challenges and gaps for connectivity analyses and planning"
Ecosystem Processes & Services	Enhancing Connectivity for Endangered Species & Habitats
Protected Areas & Natura2000	Human Infrastructure & Land Use Impacts
Species Conservation	Planning & Management of Multifunctional Corridors
Terrestrial & Freshwater Habitat	Socio-Cultural Barriers & Opportunities
Urban & Peri-urban Biodiversity	

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Figure 4.10: Miro board produced in the breakout group on "Enhancing Connectivity for Endangered Species and Habitats" from the workshop "Assessing Ecological Connectivity in Europe: Conservation goals and information gaps". The red circles indicate the issues that participants identified during the session as the most pressing ones and the arrows indicate some connections between the questions being addressed.

4.2.1 Stakeholders' priorities for connectivity planning

4.2.1.1 Long-term ecological resilience

Overarching all the priorities identified by stakeholders across Europe who participated in the online workshop, was the need for ecological connectivity to maintain ecosystem resilience into the future. Given the impacts of fragmentation on the landscape and ongoing climate change, the increased and efficient planning of connections for species and ecosystem services is of paramount concern. Multi-functional areas with high redundancies in species communities and in ecosystem services and multi-scale planning to incorporate different species needs at different scales were specific needs repeatedly highlighted. So was the need for stepping stones (in addition to corridors), especially as stopover sites for migratory species such as waterbirds.

A high level of future uncertainty also requires the identification of probable climate and evolutionary refugia in multiple locations to create redundancies in the system. This will aid in the relative short-term for resilience of species sub-populations and for the maintenance of extant populations of the species in the long-term.

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4.2.1.2 Connecting across realms and patch sizes

Connectivity planning across major ecological realms (e.g., terrestrial and freshwater) has been historically less of a focus in connectivity planning, however, stakeholders view it as very important for creating a truly holistic network of protected areas. Determining how to best create connections across ecosystem types as well as including smaller potentially suboptimal patches within the highly fragmented European landscape was seen as a high priority. There was some disagreement on whether to prioritise connections of the big intact habitats or a broader system of connections between a mixture of larger "source" patches and smaller potentially "sink" patches. This extended to the need for creating connections for ecosystem services especially between patches of "surplus" services to those with increased "demand" or deficit for those services.

4.2.1.3 On the health and wellbeing of humans

Increased ecological connectivity can have multiple benefits for human health and wellbeing. Stakeholders included considerations of human wellbeing as one of the many facets in the planning of multi-functional corridors with a focus on recreation, prioritising those ecosystem services that ultimately benefit humans, such as provisioning services that promote clean air and water, carbon sequestration, aid for organic farming, etc. Such multi-functional corridors can benefit the local economy through recreation and ecotourism and can preserve cultural services within the region, maintaining or building a 'sense-of-place' for the residents. A better sense-of-place then has the potential to aid in the maintenance of conservation initiatives within that area. These principles are particularly relevant in urban and peri-urban settings, where connectivity should deliver ecosystem services in addition to bringing biodiversity into the city (rather than aiming to have major ecological corridors crossing urban areas). Peri-urban agricultural areas and nature parks are particularly important to link to important biodiversity (protected) areas surrounding cities.

4.2.1.4 Freshwater and coastal areas

Freshwater and coastal ecosystems connectivity is often overlooked in many connectivity studies, but is key for the conservation of biodiversity, the movement of nutrients, and for a plethora of other ecosystem services. Existing knowledge within freshwater and coastal systems is sparse compared to larger terrestrial systems. Connectivity planning that is inclusive of riverscapes and in coastal systems was often noted as a priority concern for stakeholders as they have seen little research and guidance concerning the connectivity management of these ecosystems. Rivers, in particular, were considered as backbones of connectivity planning in several contexts, recognising their critical role as linear habitats.

4.2.1.5 Policies and actions that support enhanced connectivity

There were a wide assortment of policies and actions suggested as priorities for connectivity, from the local to continental scale. Promoting the creation of more natural and artificial connections on public and private lands, increased funding, and a common EU to local level policy framework were frequently cited as overarching priorities for connectivity conservation. Policies that assist landowners/managers to maintain connectivity through their property, such as forest grants and agricultural subsidies for farmers to maintain small-scale landscape

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elements, should be supported and expanded upon, according to workshop participants. In addition, legal actions are needed to expand the size of current protected areas and assign Other Effective area-based Conservation Measures (OECMs) to corridors that may not receive traditional protected area status. Additionally, some comments focused on the need to increase legal protection for specific habitat types and features such as creating effective measures to protect riparian galleries or incentives to protect unique wetland pockets that could act as stopover locations for migrating waterbirds.

Management actions should target mainly the local level, where they could potentially have the greatest impact. Actions such as the creation of fish ladders, dam removal and the restoration of natural rivers, and remodelling existing bridges to include a parallel “green strip”, were some of the ideas given as priority actions. Other priorities included temporal actions that reduce landscape resistance and wildlife mortality, such as the promotion of “dark passages” for bat movement and halting wind turbines during bird migrations. The need to increase permeability of linear infrastructures (roads and railway) featured as an acknowledged priority.

4.2.2 Technical challenges for connectivity planning

4.2.2.1 Data gaps for implementing connectivity projects

Data availability gaps were a definitive challenge identified by most participants in the workshop. Data needs varied from the fine-scale species data to land cover and socioeconomics. The availability of species data was particularly a prominent concern (Fig. 4.11) with movement and dispersal data, for all taxa, appearing to be the most in-demand given its utility in models to identify corridors and stepping-stones. There is also the need for information on species requirements during migrations and the magnitude of impact from different anthropogenic barriers. In addition, the stakeholders identified population demography, abundance, habitat use and the relationship between habitat suitability and demographics as important data needs.

Without accurate land-use / land-cover (LULC) data, projections of potential movement pathways and the spatial configuration of connectivity networks could be wildly inaccurate. Having accurate LULC data that are continually updated at fine resolution (<100m) can assist with reducing error in predicted relationships with all species and processes of connectivity concern. Historical land cover photos and rasters would also assist in understanding current land dynamics and, perhaps more importantly, could be used to parameterize LULC models and contribute to better predict future land system configurations under human global change. Finally, data on current habitat management information such as timber management and sales, would be in the next level of land use detail beyond just categorical information on the land class. Incorporating finer land management detail would add a needed temporal component to predictions and assist in large landscapes that appear homogeneous from satellite derived LULC layers but are in fact temporally dynamic in their structure (e.g., forests of central and northern Finland).

Another major data gap is spatial and non-spatial social and socio-economic data. Items such as peoples’ perceptions of environmental management actions, values or socio-economic interests are lacking according to workshop participants. Information on perceptions and

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knowledge of ecosystem services and valuation of protected areas or for recreation opportunities would assist in planning multi-functional corridors.

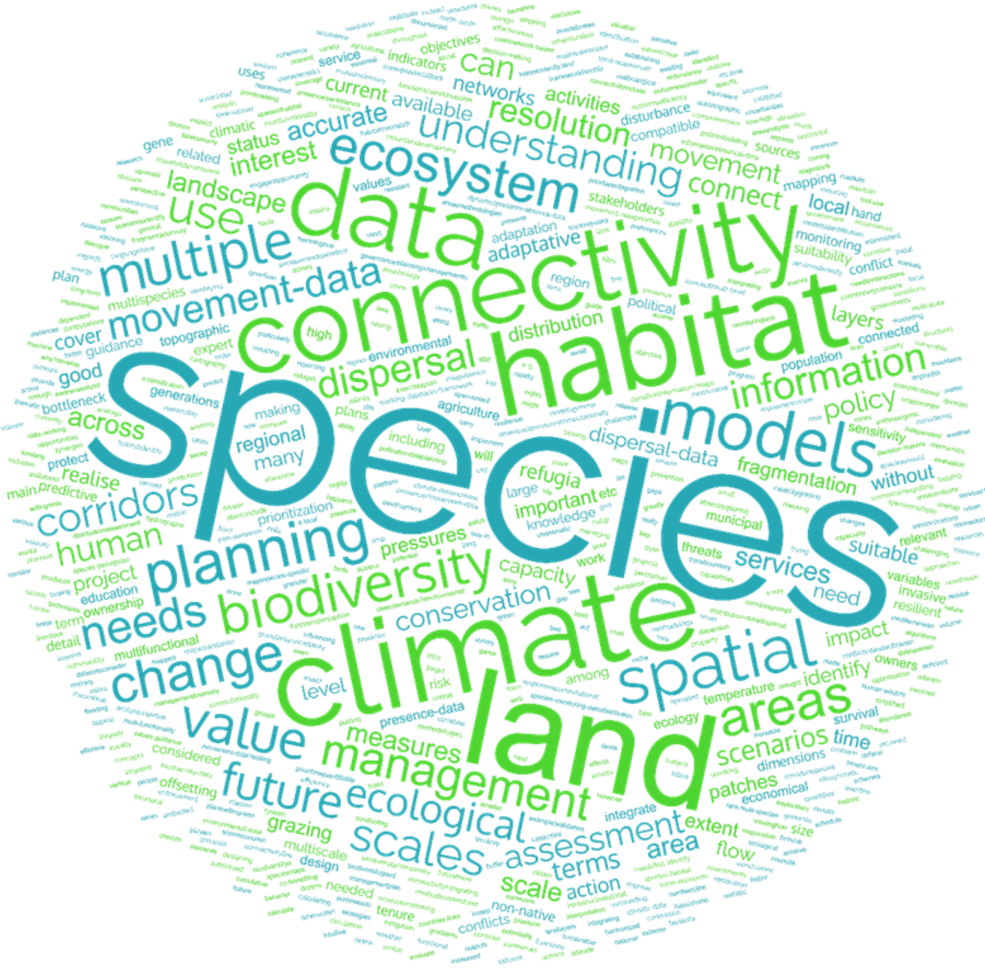

Figure 4.11: Word response frequency retrieved from the Miro boards for Day Two of the "Assessing Ecological Connectivity in Europe" workshop. Day Two was concerned with identifying the technical challenges, data needs, and solutions for connectivity planning in Europe. Data on species spatial distribution, abundance and movement was the most highly discussed response.

4.2.2.2 Critical information gaps

Compared to data gaps, information gaps included those guidance and rules needed for future connectivity modelling and on-the-ground implementation. Primarily, this included aspects of the correct parameters of corridor configuration and overall connectivity network design. Among these parameters, minimum corridor width is often discussed especially in areas of high human development. While there is no one simple answer, participants noted the need for clear guidance on how much land needs to be protected to enable free movement of wildlife through a corridor, or the maximum distance between connectivity stepping-stones (see Section 6.5). There is also the need for better guidance on what situations warrant the use of

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multiple corridors to add redundancies into the protected areas network or when one corridor will likely suffice.

Designing and implementing multifunctional corridors was seen as a means for stacking multiple goals into one conservation action (e.g., integrating biodiversity conservation, human recreation, and provisioning ecosystem services - amongst other goals - into one coherent design). However, the existing frameworks for complex problems and multiple objectives and constraints have not been widely applied yet to connectivity related problems.

Other challenges to implement connectivity projects relate to land ownership issues; creating corridors on private land requires working closely with landowners, and setting participatory approaches where they have the required knowledge and are involved in decision making. Finally, the issue of assigning economic value for connectivity was also raised to better argue for the need for restoration/connectivity planning, namely compensation schemes for conservation actions including features that increase connectivity.

4.2.2.3 Technology and capacity constraints

Connectivity analyses rely heavily on geographic information systems (GIS) to capture landscape dynamics. However, the resolution of the data (i.e., grain size) may not be fine enough to realistically capture many of the ecological dynamics of the system, if at all. Therefore, many participants in the workshop noted that there is a mismatch between the grain size and smaller scale dynamics which may lead to the wrong predictions in modelling species preferences and likely movement patterns, amongst other conclusions. In addition, there is still difficulty and lack of guidance, in the opinion of many of the participants, on the complexities of integrating social, economic, and political factors into spatial planning. While some frameworks have been introduced (Ogletree et al. 2019), some data is difficult to represent in a spatial manner and even, when possible, how do you relate that to its impacts on the ecological dynamics?

Another major challenge is the need to simultaneously account for horizontal (i.e., across space) and vertical (i.e., through time) connectivity. This challenge is due in part to the static nature of most GIS data, the difficulties of integrating the management of species with different life histories, and the complexities of creating multi-functional corridors with multiple, often competing, goals. Furthermore, these difficulties will likely only increase with the predicted volatility in climatic patterns and the increase in extreme stochastic weather events.

Many workshop participants also focused on the multitude of other capacity deficiencies that can hinder effective connectivity planning. Planning and management of connectivity networks require the organisation of a multi-level governance structure which is, first, difficult to construct and second, difficult to maintain given the perceived lack of funding and time for its maintenance. There is also often the lack of capacity to implement a participatory spatial planning process, given deficiencies in funding, staff time, and other resources necessary for proper communication with multiple landowners. Built into this is the need for better coordination between public and private organisations to increase engagement across user groups and regions. Increased technical training opportunities are also required.

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4.2.3 Solutions to overcome challenges and needs

4.2.3.1 Repositories for data and capacity building resources

Building upon many of the challenges identified by participants, there were also many potential solutions. Participants saw better availability of relevant data and capacity building resources as a paramount solution to several of the challenges. A more centralised repository of the different data types identified in Section 4.2.2 could allow for more efficient and accurate connectivity modelling and planning. In addition, well documented case studies and methodologies that can be used as examples for further planning and management as well as a harmonisation of methods across scales would promote and streamline other connectivity planning projects. Capacity building resources should include technical training for different connectivity tools, training materials for the facilitation of stakeholder engagements, and education materials aimed at teaching the general public about the importance of connectivity for the conservation of nature.

4.2.3.2 Collaboration and engagement at the forefront

Connectivity planning is inherently a multidisciplinary endeavour; early, continual collaboration and engagement across public and private stakeholders was seen as one of the most important aspects of a successful connectivity planning exercise. Engaging with decision makers could help "mainstream" the importance of connectivity measures and cement it as a factor in local and regional spatial planning. Continual engagement with NGOs and community stakeholders will assist in identifying the multitude of goals from different community groups and assist in garnering support for the implementation of the project's final recommendations.

4.2.3.3 Policies, regulations, and funding streams

As noted in the priorities above, a unified set of policies and regulations that can be implemented from the EU to the local level would be a major step in improving and promoting connectivity planning projects. Incentives for private landowners to increase permeability on their lands and regulations that can reduce wildlife mortality are both general solutions that can have large landscape impacts. There should also be a focus on establishing basic requirements for ecological corridor protection including expanded use of legal land protections, including OECMs, for corridors and stepping stones. Other important factors highlighted by participants included providing resources for connectivity planning best practices, exhibiting the importance of connectivity planning to policymakers, and finally lobbying for higher funding availability from multiple levels of government agencies.

One of the key findings from the survey of connectivity projects (see Section 4.1) is that only 38% of the projects were commissioned by an administration, suggesting that promoting ecological connectivity has not been a priority for government agencies. Another significant finding was that only 26.8% of the projects reported conducting any monitoring or evaluation of effectiveness. This suggests two possibilities. The first is that many projects did not propose testable approaches for enhancing connectivity. The second is that they did not consider or had insufficient funding for conducting monitoring.

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4.2.3.4 Planning for global change

Further connectivity planning needs to be inclusive of shifting landscapes due to global change. A focus on the temporal aspects of connectivity is increasingly important given the increasing changes to climatic and habitat patterns altering nutrient cycling and species distributions. Identifying habitat sensitivities to these changes, then projecting species distributions through time will assist in the accuracy of connectivity planning outcomes. Going further, including adaptive planning that contains multifunctionality and corridor or stepping stone redundancies can fortify a network against increasing unexpected weather events. One must be careful though when considering public opinion, as some workshop participants noted, to balance both reactive approaches such as those to decreasing species abundance or improving water connectivity and proactive approaches such as rewildling corridors for species that do not currently occupy an area. Finally, the workshop participants came back to the need for environmental education for key stakeholders (landowners, city councils, agricultural associations, etc.) to explain how climate change will alter historical patterns and why the need to fortify the connections across a fragmented landscape is now more important than ever given an increasingly dynamic system.

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Part II: Tools and guidelines for implementation of connectivity projects in Europe

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5. Tools and data sources for modelling connectivity

5.1 Introduction

Connectivity analyses are being used for a broad array of subjects from water conservation to megafauna movement. However, what currently works best, for example, to identify key corridors to conserve European bison (*Bison bonasus*) movement likely is not the best model to predict structural connectivity for dead wood beetles (Rocca et al., 2017). Therefore, understanding the strengths and appropriate applications of different connectivity modelling approaches is vital to producing the most accurate results to address your problem.

Modelling connectivity is an important step in the design and implementation of a connectivity project, and should take place after initial steps of scoping and problem assessment, and setting of connectivity objectives (see the connectivity network design framework in Chapter 6 for more details).

In the following subsections, different frameworks as families of models are introduced, and the applications of these methods, and their strengths and weaknesses are discussed.

A summary of modelling families

Data inputs can vary across the different types of connectivity analyses. Central to nearly all connectivity modelling families, however, is some form of information on the habitat patches or "focal nodes" where species or processes of interest occur and where movement is expected to originate and/or terminate (Table 5.1).

Table 5.1: Outline of the most common modelling families for functional and structural connectivity. Lists of applications and software are not exhaustive but demonstrate some of the possibilities with these models. Resistance and source weight surfaces are rasters that are inputted typically in ASCII format or another raster format depending on the software package (see Dutta et al. 2022 for an extensive listing of software).

Model Family	Data Needs	Applications	Software & Packages
Least-cost Path & Resistant Kernels	Resistance surface, focal nodes, and species dispersal data (RK)	Focal species corridors, population dispersal potential, area of potential use, pollinator movement, probability of human movement	LCP: ArcGIS Tools, QGIS plugin, R packages ('gdistance', 'leastcostpath'); RK: UNICOR

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Graph Theory	Focal nodes & connection file of attributes between node pairs	Analysis of landscape structure and potential functionality, prioritisation of patches and connections, long-term population persistence	Conefor, ArcPro Network Analyst, R packages (‘iGraph’, ‘riverconn’)
Circuit Theory	Resistance surface & focal nodes (Circuitscape) or source weight surface (Omni)	Focal species connectivity and pinch points, water flow, pollinator movement, invasive species control	Circuitscape, GFlow, Omniscape, Linkage Mapper (multi-family)
Agent-based models	Model specific: Focal node and network data, survival rate, population growth rate, fecundity, node transition probabilities, resistance surface, etc.	Long-term population persistence, patch and connection importance, source-sink analysis	MetaIPM, HexSIM, NetLogo, R packages (‘p SiMRiv’)
Structural Connectivity Metrics	(*Will differ depending on the used metric(s)*) Number of patches, patch size(s), boundaries and perimeter, distance between patches, focal nodes, presence/absence of links, number of paths.	Assessing connectivity of select components in the physical landscape, e.g. protected areas, specific habitats and/or corridors. Both in relation to intra- and inter-patch connectivity.	Conefor, ArcPro Network Analyst, R packages (‘iGraph’, ‘riverconn’, 'gdistance')
Spatial prioritisation tools	Study area planning units layer, biodiversity distributions, land cover/land use, current protected areas, etc.	Identifying structural connectivity via prioritisation of landscape elements and systematic conservation planning	Marxan, Zonation, R packages (‘prioritizr’)

The habitat patches or “focal nodes” where species or processes of interest occur and where movement is expected to originate and/or terminate are often protected areas, but this depends on the research question as, for example, the analysis could revolve around the

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inclusion of hypothetical unidentified nodes that could improve ecological connectivity. This can be represented as single or clusters of pixels derived from a raster or polygon shapefiles. Data requirements on these nodes can vary from a simple text (i.e., ASCII (American Standard Code for Information Interchange) format), CSV (comma-separated values) file with the distances between pairs of pixels, to spatial data formats (e.g., shapefiles) that contain georeferenced characteristics about each patch.

Creating resistance surfaces

Also, central to the least-cost path, resistant kernels (Section 5.2), and circuit theory models (Section 5.4) is a measurement of resistance of movement between and possibly within habitat patches (Table 5.1). Resistance is generally defined as the inherent difficulty that an animal, plant or abiotic process will have while trying to cross a section of land or water. This resistance is input into the models as a resistance surface, a raster of spatial data where each pixel is the energetic cost, risk, or force exerted to move across that pixel. The cumulative resistance to movement can thus be calculated as the summation of all the pixels crossed on a path between two habitat patches. The easiest conceptualization of this cumulative resistance to movement may be the difficulties faced by a large mammal attempting to cross a landscape over hours or days. However, the temporal scale of this cumulative resistance can vary depending on the focal problem. Other examples could include the varying seasonal forces acting on the seed dispersal of particular plant species, the resistance met by subsequent generations of a grouse species as it expands its range, or the seasonal and anthropogenic forces acting on the flow of water in a regional watershed.

There are a variety of methods to create resistance surfaces, depending on the type of data available for the species of interest (Zeller et al., 2012). Species distribution models (SDM) that correlate environmental variables to species habitat use are currently the most common method for the creation of resistance surfaces. These models may use presence data (e.g., GLM, random forest, Maxent, etc.) or detection-nondetection data (e.g., occupancy models) to estimate habitat suitability. Results from the SDM are often then inverted so that the areas with the greatest habitat suitability values have the lowest values of resistance. A major assumption in this is that habitat suitability values are completely and inversely correlated with the resistance to movement that land cover exerts on that species (i.e., the same magnitude of force dictating habitat preference for an area dictates the ability to move across that area). Data transformations that decrease the level of resistance of moderately suitable habitats have been proposed and used in recent studies to compensate for a part of this distinction (Keeley et al., 2016). Other methods include the use of telemetry or GPS point and tracking data from collared wildlife individuals. Point data can be applied to resource selection functions to generate the relative probability of resource use and track data is used in path-selection functions, which generate a relative probability of movement raster (Zeller et al., 2018). Finally, resistance surfaces can be generated from landscape genetic data collected from across the study area. The genetics of a population differentiates with increasing distance between subpopulations and obstacles to individual movement, therefore, differences in the spatial patterns of pairwise genetics can be used as a proxy for the spatial distribution of resistance values. While this can be seen as a measure of functional connectivity, optimization of resistance surfaces using landscape genetic data is much more complex and requires running a genetic algorithm in conjunction with calculations of pairwise effective distances from

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connectivity models to determine an optimal resistance surface (Dutta et al., 2022; Peterman, 2018).

More complex modelling frameworks

Data types and needs change as we move further into more complex modelling frameworks that attempt to simulate individual movement or metapopulation dynamics (Table 5.1). Models in this family are especially useful for analysing population viability over time, therefore, inputs can include data on population survival rates, abundance and fecundity, probability of dispersal from patches, and multiple characteristics of the focal patches. Like graph theory (Section 5.3), one can use these models to prioritise focal patches, with the added benefit of determining long-term processes such as identifying potential sources and sinks amongst the different patches. Source-sink dynamics analyses how population growth is affected by variation in habitat quality (Pulliam 1988). In this approach, sources correspond to high quality habitat allowing populations to increase, while sinks correspond to low quality habitat that on its own would not support a population. However, sink populations may persist indefinitely if surplus individuals move from sources to the sinks. Thus, considering source-sink dynamics can inform conservation decisions.

Spatial prioritisation

Finally, spatial prioritisation software can serve as a means of identifying and prioritising structural connectivity between habitat patches (Beger et al., 2022; Daigle et al., 2020). Spatial prioritisation software is typically used within a broader systematic conservation planning (SCP) process to identify efficient means of conserving a broad suite of natural and cultural features (Table 5.1; see also Section 2.7). Generally, the user gives the program a spatial layer of the study area divided into "planning units", each unit serving as the base-level decision-making unit. The user also provides spatial features of interest such as endangered species presence, key biodiversity areas, culturally sensitive landscapes, important watersheds, etc. In addition, output from the other connectivity modelling families (e.g., least-cost corridors, high current density areas) that explicitly measure levels of structural or functional connectivity can then be used as a conservation feature in the spatial prioritisation software (Hanson et al., 2022). The program can then attempt to meet the conservation targets maximizing the occurrence of considered spatial features, while creating a connected and relatively compact protected area network. An advantage of including connectivity in prioritizations (see Section 2.7) is that any area selections (e.g., protected area expansions) are not considered in isolation from connectivity within a wider land- or seascape.

5.2 Least-cost path and Resistant Kernels

Least-cost path analysis is the form of connectivity modelling that has been applied the longest. These models find the most cost-effective path between two points across a resistance surface taking into consideration the distance travelled and the cumulative

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resistance. It is therefore considered the path that a hypothetical animal would most likely take as it would exert the least amount of energy. Given the methodology, the path it identifies is only one pixel-wide, leaving the user with theoretically the single most effective corridor for conservation between those two points. This method was extended to the factorial least cost path, which considers multiple source points or locations where an animal may be originating and ending its movement (Cushman et al., 2013, 2009). Factorial models predict all the possible combinations of source to endpoint paths cumulating the resulting paths together. This creates a quasi-prioritization of path areas, as the higher the cumulative weight on the landscape the more overlapping pathways you are conserving. This is somewhat more realistic, especially for larger protected areas where it is much more difficult to predict where on the PA border an animal is likely to enter or leave.

However, there are a couple of key assumptions and issues when relying on a least-cost path analysis. First, we are assuming an animal has the knowledge and foresight of the landscape matrix to choose the path that gives it the least resistance (Unnithan Kumar and Cushman, 2022). Depending on the situation this could be a troublesome assumption as most individuals will likely not have this foresight for the landscape, especially for dispersing individuals that have potentially never been in that area. Second, as with many of the connectivity analyses, we are assuming that the cost layer that we are using captures the true resistance that a species faces when it attempts to move through that land area. Third, we are identifying only one “best” corridor that is the width of a pixel, rather than multiple solutions that take into account a buffer area around the corridor. Highlighting the one best connection is only the starting point in determining if conserving that area is sufficient to ensure first structural and then functional connectivity. Most likely, a much wider corridor that possibly incorporates even wider stepping stones is necessary to achieve the functional connectivity needed for conservation success. Some of this can be solved by factorial least-cost path analysis, but there can still be heavy overlap in the identified paths leading to very narrow corridors.

Resistant kernels are the last member of this family. It is a unique adaptation of least-cost path analysis that seeks to broaden the interpreted area of the least resistant path by using a hull or moving window estimator and information on the dispersal potential of the animal. This moving window approach can assist in identifying the corridor buffer area needed by that species, especially when constrained to the output from a least-cost path analysis (Cushman et al., 2013). In addition, there is no information needed on the end point of movement, as the model does not assume that the focal species has prior or precise knowledge of its final destination, an assumption that must be made in least-cost path analyses.

Least-cost path and factorial least-cost path have been broadly applied in connectivity analyses but are primarily used for modelling the likely movement of a single wildlife species between protected areas including mammals, reptiles, amphibians and insects. There is also application in simulating possible downstream water flow and flooding routes and routes for pollinator movement (over short and long periods). The applications are the same for resistant kernels but with the added benefit of including the dispersal ability of the species. This can be expanded to include the scattered dispersal of insect or animal movements from hives or colonies. Given the functional connectivity aspects of resistant kernels, they could also hypothetically be used to simulate likely sediment flow and potential plant dispersal under climate change.

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Some of the software and programming packages that can implement least-cost path and resistant kernel analyses include (Table 5.2):

Table 5.2: Software and programming packages that can implement least-cost path and resistant kernel analyses.

Model Family	Software & Packages	Functions & tools	Details
Least-cost Path	ArcGIS toolbox	Distance Accumulation function (ArcPro:Spatial Analyst) (https://pro.arcgis.com/en/pro-app/latest/help/analysis/raster-functions/distance-accumulation-global-function.htm)	Beyond the basic functionality of calculating an individual least-cost path this tool can calculate the equivalent of factorial least-cost. The function also can consider true surface distance and a raster of landscape barriers as input. This function will automatically attempt to parallelize the analysis across half the available cores in your computer, which should increase processing time.
		Cost Path tool (ArcMap:Spatial Analyst) & Optimal Regions Connection (ArcPro) (https://pro.arcgis.com/en/pro-app/latest/tool-reference/spatial-analyst/optimal-region-connections.htm)	Can calculate least-cost paths between 2 or more sources, however, typically requires the output from one of the other weighted cost tools in the ArcGIS toolbox (e.g., Cost Distance) to create the cost distance raster. *Note: ArcMap will no longer be updated post-February 2024 and will lose technical support March 2026.*
	QGIS	Least-Cost Path plugin (https://plugins.qgis.org/plugins/leastcostpath/)	Capable of calculating the least cost path(s) when given a cost raster, start points, and end points as inputs. https://github.com/Gooong/LeastCostPath for more information.
	R packages	leastcostpath (https://cran.r-project.org/web/packages/leastcostpath/index.html)	Fully integrated package with functions to create different resistance/cost layers and then run least-cost path analysis. Includes functionality for different forms of least-cost path analyses, though primarily oriented to barriers and slope costs.
		gdistance (https://cran.r-project.org/web/packages/gdistance/index.html)	Greater functionality than 'leastcostpath' which makes it more complicated to operate. Includes abilities beyond least-cost path including constrained and non-constrained random walk functions with similarities to resistant kernels and circuit theory.

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Resistant kernels	UNICOR	Universal Corridor network simulator (https://github.com/ComputationalEcologyLab/UNICOR)	This is the primary software used for resistant kernels estimation. It was created by the developers of the resistant kernels methodology. It is a Python-based program and can be used through the Python command line or in a graphical user interface (GUI), which can be launched following the instructions in the UNICOR manual. Grid/raster input data is in ASCII format. Additional input information includes distance of movement thresholds and parameters of the kernel density estimator. An older but more in-depth manual can be found at this web address: https://www.fs.usda.gov/rm/pubs_other/rmrs_2011_landguth_e002.pdf

Ultimately, these methods are still used and in the case of least-cost path analysis is a simpler and quicker way to identify the potentially important movement corridors in a landscape. This is especially useful for large and high-resolution datasets given the heavy computing capacity needed for some of the other connectivity methods. However, while the more information and preparation may be required, resistant kernels can give a better and more realistic output as to the best overall areas to be conserved for connectivity (Sumar & Cushman, 2022). Also, with the addition of dispersal information into the model, resistant kernel output can be seen as measuring functional rather than just structural connectivity.

5.3 Graph Theory

Definitions and applicable situations

Graph Theory is a mathematical discipline that finds wide application in various fields, including computer science, linguistics, social network analysis, transportation network analysis, and ecological connectivity. Graph Theory focuses on structures known as graphs, which consist of vertices (nodes) and edges (connections).

In the context of ecological connectivity, graph theory models allow us to prioritise habitat patches and links between patches relative to one another. Vertices represent patches of habitat (or any other relevant features such as protected areas), while edges represent the connectivity between these patches (Bunn et al., 2000). Vertices can be assigned weights that influence their connectedness with neighbouring nodes and their overall importance in the network. In ecological connectivity analysis, the weight is typically based on some property of the habitat patch, such as its area, overall quality, population size, estimated number of propagules produced, etc. Similarly, edges can be modelled in different ways. In a simple binary representation, an edge indicates the presence of a connection between a pair of vertices, for example, when two vertices are closer than the species' dispersal distance. In

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more sophisticated versions, edges are represented as probabilities of connection between vertices, which can be a function of dispersal probability at a given distance, based on dispersal kernels.

The application of graph theory to connectivity analysis enables the examination of network connectivity, allow us to compare between different networks. It also allows for the analysis of adding or subtracting individual vertices or edges to the overall network connectivity (i.e., if habitat patch X is added how much better is the network connected). Various metrics have been developed to describe the degree of connectivity in a network, some of the more common metrics used in connectivity modelling is the Integral Index of Connectivity [IIC], Probability of Connectivity [PC], and Equivalent Connected Area [ECA] (Pascual-Hortal and Saura, 2006; Saura et al., 2011; Saura and Pascual-Hortal, 2007). For individual vertices metrics such as the generalised betweenness centrality metric measures how centralised or well-connected a node is within the network (Bodin and Saura, 2010).

To estimate the relative contribution (i.e., importance) and non-redundancy of vertices or edges to the network, these metrics can be applied to evaluate network connectivity with and without specific vertices or edges, leading to the above indices IIC and PC to be expressed as the percentage of variation: dIIC, dPC, respectively. This can be interpreted as the **importance** of the node or edge according to the index. The relative contribution of a patch can be further analysed by estimating its contribution in terms of habitat area (dIICintra, dPCintra), its connectivity to neighbouring patches (dIICflux, dPCflux), and its role as a stepping stone (e.g., dIICconnector, dPCconnector), resulting in (Saura and Rubio, 2010):

$$dIIC = dIICintra + dIICflux + dIICconnector$$

and

$$dPC = dPCintra + dPCflux + dPCconnector$$

Data inputs, packages and software

Ecological connectivity analyses using graph theory typically require two types of input data: a list of vertices with their attributes (typically a list of protected areas), and a list of edges with their attributes. The vertex dataset includes all vertices present in the network and generally consists of two columns: a vertex ID and its weight. The edge dataset represents realised connections in the network and is typically reported with three columns: two columns indicating the connected nodes and one column indicating the measure of connectivity between them.

Connectivity between patches can be expressed as a probability, which can be estimated based on the probability of dispersal to a given distance. To obtain such a probability, knowledge of the average or median dispersal distance of a species is necessary, along with information about the distribution of dispersal distances in a population. The commonly assumed distribution is a negative exponential distribution, but other distributions are also possible such as for instance Weibull for plants (García and Borda-de-Água, 2017). Additionally, the probability of connection between vertices can be influenced by the permeability of the landscape. While the simplest approach assumes Euclidean distance

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between vertices, more sophisticated methods can estimate distance as a least-cost path or similar approaches.

Connectivity analyses using graph theory have incorporated asymmetric connectivity, which considers differential probabilities of dispersal from one patch (e.g., patch A) to another (e.g., patch B) compared to the reverse direction (from B to A). This development has applications in source-sink dynamics or the modelling of passive dispersal, such as wind or water-mediated dispersal.

The R package "iGraph" is commonly used for computing graph theory analyses and visualising graphs (Csárdi et al., 2023). However, ecological connectivity analysis using graph theory is often performed using the software Conefor, which includes a wide array of metrics commonly used in connectivity analysis.

Conefor

Conefor (originally 'Conefor Sensinode') is an open-source software implemented in C, providing computational efficiency compared to R. It offers a user-friendly graphical user interface (GUI) and can also be run from the command line (Saura and Torné, 2009). Both versions of the software can be downloaded from the official Conefor website (http://www.conefor.org/index.html), which also provides a comprehensive manual and reference list. Several GIS software have also developed extensions to apply connectivity analyses using Conefor (e.g. QGIS: https://github.com/ricardogsilva/qgisconefor; ArcGIS: http://www.jennessent.com/arcgis/conefor_inputs.htm).

Conefor requires a node file and a connection file as inputs. The connection file can contain attributes represented as Booleans (0 or 1), distances (which are converted to probabilities of connection based on an average dispersal distance and assuming a negative exponential kernel for probabilistic metrics), or direct probabilities of connection. Users can select specific connectivity indices and define a maximum dispersal distance to limit connections between nodes beyond a certain biological threshold. The software also allows users to compute metrics for the overall network (faster) or for each vertex and edge (slower). Additionally, Conefor provides the capability to assess scenarios involving the addition of vertices to the network, as well as improvements or deteriorations in the existing connections between nodes.

For publications using Conefor on landscape planning and monitoring case studies see http://www.conefor.org/applications.html, which includes a map allowing to find publications for specific parts of the world, including Europe.

5.4 Circuit Theory

Circuit theory connectivity models are graph theoretical methods which use principles of electrical current to simulate the potential movement of an animal or other entity across a resistance surface. We know that electrical current will attempt to flow through areas of least resistance and that in those areas where there is high resistance current density can be compressed through lower resistance areas (Fig. 5.1; McRae et al., 2008). This becomes very useful as an allegory for the movement of living species as well as abiotic processes,

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especially when we are trying to identify corridors and pinch points (i.e., areas where the movement of species is highly concentrated into a very narrow path). This has similarities to factorial least-cost path analysis; however, circuit theory models can provide a continuous raster surface of "current densities" which can be viewed as an index depicting the likely concentration of species movement over each pixel (Fig. 5.1). The higher the current density the greater the electric current is being concentrated at that point.

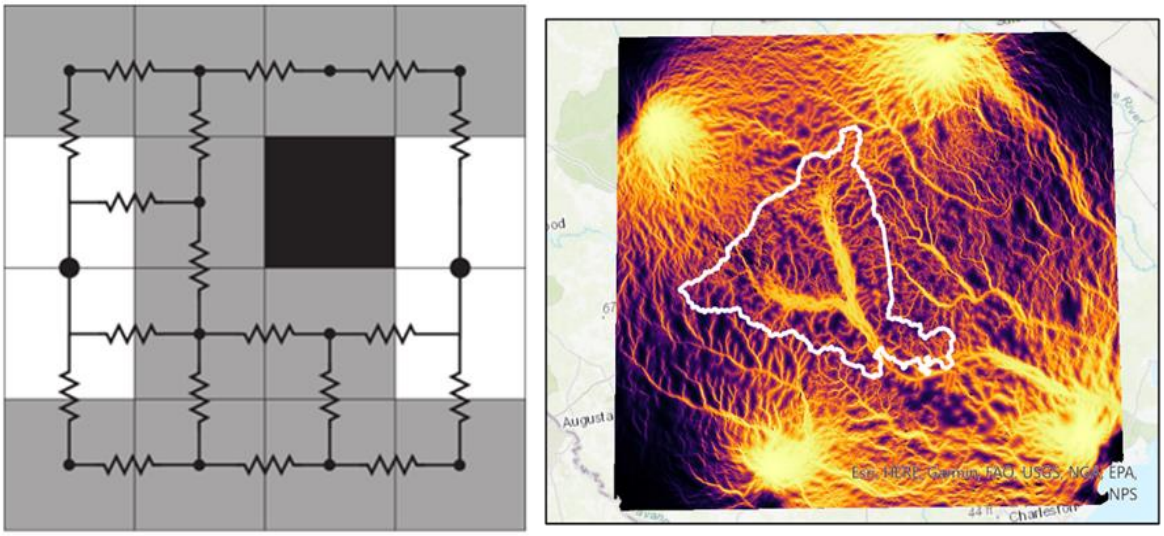

Figure 5.1: This simple illustration (left) shows nodes in the white pixels and the movement of electrical current through each "resistor" (i.e., pixel). The black pixel is a permanent barrier that blocks any current flow. Once applied to a real-world landscape (right) one can see how the current densities between the four focal nodes concentrate along certain paths or diffuse (northern border) when no clear paths are present. This example is of North American river otter connectivity through an agri/silviculture landscape surrounding forested wetlands. The model concentrated current flow into riparian areas and the forested wetlands in the centre of the map (Sources: McRae et al. 2013, Dertien and Baldwin 2023).

Models in the circuit theory family can be divided into directional and omnidirectional circuit models. Directional circuit models use focal nodes or patches similar to the least-cost path; however, in circuit theory, these node pairs are designated as either a source (origin of electrical current) or ground (termination of electrical current). Hence, your source node is the point where your species or process of interest is starting from, moving in the direction of and terminating at the ground node. You can model movement in both directions by switching these designations. The resulting raster output covers your entire study area and can present one or multiple options for the most important movement corridors. Directional circuit models are best applied to problems involving multiple patches, such as a system of separated protected areas surrounded by unprotected "matrix" habitats. Additionally, directional circuit theory may be applied to problems such as known migration routes or predicted directional movement under climate change.

Newer omnidirectional circuit models run through the program Omniscape allow you to model the connectivity potential of the landscape from all directions. Therefore, this model does not require the selection of focal nodes, but it does require a new form of data input, a source weight surface. The source weight surface depicts the potential for each pixel to, in essence,

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be a source node (Fig. 5.2). The model then uses a moving window calculation where the centre pixel at each stop of the moving window is considered the ground node (McRae et al., 2016). The model then calculates the connectivity from all the remaining pixels (i.e., source nodes) within the moving window to the central ground node. Given the limited use so far of this method there is little information on the correct moving window size, however, it should be in part informed by the process or wildlife species that you are trying to model and your computational resources.

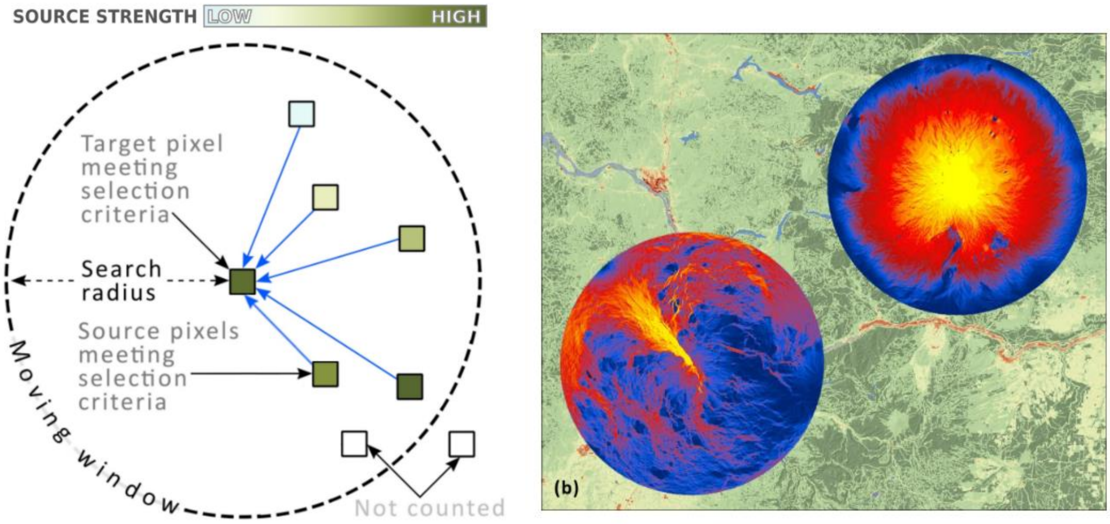

Figure 5.2: Illustration of the moving window (left) that moves over the source weight and resistance surfaces.The green pixels are coded as potential source pixels of varying strengths while the open white pixels are coded as not a potential source (e.g., urban core). Current movement is then calculated between all potential sources to the target (right). Cumulative current density for the landscape is calculated once all moving window calculations for the landscape are complete. Adapted from Landau et al. (2021) and McRae et al. (2016).

Omni-directional models have great potential to solve many of the pressing landscape conservation questions, especially for large landscapes where there are limited protected areas, where there is extensive use by wildlife in the unprotected matrix, or where it is not clear where wildlife or ecosystem processes may originate. However, given the cumulative moving window approach taken by the model, the computational demand is significantly higher than in directional models (i.e., Circuitscape). Running models for even smaller regions can take days if using a single computer and may not be possible without access to high-throughput computing or a supercomputer. Reducing the size of the moving window or instructing the model to create a multi-pixel target node in the centre of the moving window are two ways of reducing the computational demand for a model.

Like least-cost path analyses and resistant kernels, circuit theory models have been used for a plethora of different applications. Dickson et al. (2019) found hundreds of peer-reviewed studies over a ten-year period that applied circuit theory. These primarily focused on mammalian movement but also included studies on birds, amphibians, reptiles, arthropods, and fish. Additional applications have included the potential for wildfire movement, water flow, and ecosystem services (e.g., pollinators and seed dispersers). Other studies include

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mapping connectivity and conservation opportunities on agricultural landscapes (Suraci et al., 2023) and prioritizing multispecies habitat networks that are robust to climate and land-use change (Albert et al., 2017). Different circuit theory applications and versions developed are detailed in Table 5.3.

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Table 5.3: Circuit theory applications developed detailing needed data inputs and sources.

Application	Details	Inputs	URL
Circuitscape 5	The current version of Circuitscape is developed in the Julia programming language, allowing the program to run much faster and model much larger landscapes. The only coding needed is when loading the program and to input the needed data files (only 6-7 lines of code). Preparation of data inputs is however much more time-consuming.	Data inputs include ASCII text files for focal nodes and resistance surfaces, and a .ini file that gives the program instructions on how the model should calculate currents between the nodes, and what type of outputs the model should produce (see instructions and adaptable templates for the .ini file in the link provided).	https://github.com/Circuitscape/Circuitscape.jl
Circuitscape 4	This older version of circuitscape is restricted to smaller regional-scale landscapes and has a slower processing speed. However, it still uses an easily navigable GUI that is especially helpful for first-time users and contains many of the same advanced options.	Inputs for rasters layers are in ASCII format like Circuitscape 5	https://circuitscape.org/downloads/
Omniscape	Omniscape is written in Julia by the same developers as Circuitscape. Like Circuitscape 5 there are only a few lines of code necessary to run these models in Julia, and formatting the data correctly is much more time-consuming. Computational times can take days or weeks depending on landscape extent, data resolution, moving window size, and if target pixels are clumped in the moving window. It is advised to start with a much smaller extent to adjustments these options.	Data inputs include ASCII text files for the resistance and source weight surfaces, and a .ini file that gives the program instructions on moving window size, target pixel block size, what type of outputs you would like the model to produce, and several other advanced options.	https://github.com/Circuitscape/Omniscape.jl

5.5 Agent-based models

Agent-based models (ABM) or, for our purposes, more aptly called individual-based models, simulate the behaviour of individual agents, such as animals, in their environment. They provide a flexible approach by allowing the simulation of each agent as a distinct entity, with a set of rules and behaviours. They are powerful tools to understand and explore the emergent

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patterns and processes that arise from the interaction of the agents among themselves and with their environment. Not surprisingly, ABMs have found application in a wide variety of fields, such as social sciences (Silverman, 2018), in particular economics (Farmer and Foley, 2009; Hamill and Gilbert, 2015), and in biology and ecology (Grimm and Railsback, 2005; Railsback and Grimm, 2019; Zhang, 2018).

The main advantage of ABMs relative to other mathematical approaches, such as those with differential equations, is that the latter are restricted by mathematical tractability. This means that the only mathematical models that could be analytically developed were studied, but these were often too simplified, to the point that one could doubt whether the relevant characteristics of the system at hand were being properly modelled. Such doubts often arose when (i) nonlinearities were present, (ii) the inclusion of interaction among individuals, or these with the environments, were essential to understanding emergent patterns, (iii) modelling the space explicitly, and its heterogeneity was required, (iv) agents/individuals were different, and (v) agents/individuals exhibit complex and adaptive behaviour, such as learning (Zhang, 2018). Therefore, an important characteristic of an ABM, though necessarily a simplification of a real system, is that it still retains enough processes and interactions so that simulations include some of the most prominent processes of the real system that it attempts to model, and thus an ABM can more closely emulate natural systems. Moreover, experiments that cannot be feasibly carried out from a practical (or even ethical) perspective, e.g., the impact of fragmentation on the persistence of populations, can be simulated with ABMs and the consequences of different actions (and policies) evaluated.

The development of an ABM requires a multidisciplinary approach. At its core is the development of a model that describes the movement patterns of individuals and how they are affected by the environment, by the presence of other individuals, and eventually any other factors that are known to influence movement. This model, which is a set of mathematical rules that connect the movement properties (e.g. the distributions of step lengths and turning angles of different movement states) to all the factors that influence them, is characteristic of a species (or a species archetype) and can be developed either from expert knowledge alone, estimated from real movement location data, or a combination of the two (see Table 5.4 for examples of Software packages). Other, more complex or customised types of models may be developed by writing a specific computer program that accounts for all the processes of interest with no limitations, but in that case, there are no packages to allow estimating model parameters from real data, and the model must be parameterized from expert knowledge.

Table 5.4: Table 5.4. Examples of software packages commonly used to implement agent-based models.

Software packages	Details	Source
moveHMM	Based on Hidden Markov Models and Maximum Likelihood estimation. Allow fitting individual multistate movement models to real location data.	Michelot et al. (2016)
momentuHMM		McClintock and Michelot (2018)
SiMRiv	Uses optimization to fit a multistate model to location data.	Quaglietta and Porto (2019)

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	Can be used to simulate the movement of aquatic species and predict road mortality hotspots.	
samc	Connectivity modelling with spatial absorbing Markov chains.	Marx et al. (2020)
rangeShifter	Built using object-oriented C++ providing computationally efficient simulation of complex individual-based, eco-evolutionary models and species responses to environmental changes.	Bocedi et al. (2020)
NetLogo	Flexible, programmable simulation environments, greatly simplify the task of translating a movement model into a computer program and simulating the dynamics and analysing the outcomes of an entire system based on its agents	Wilenski (1999)
HexSim		Schumaker and Brookes (2018)

As said, there are two pathways to parameterize an individual-based model: either estimating the parameters from real location data or using expert knowledge. The first approach needs real tracking data (e.g., telemetry data) over a time series, and, depending on the complexity of the model, may have hard requirements as to the time resolution and period of the data. A complex movement model (e.g., multistate movement in a heterogeneous landscape) may require higher resolution data (e.g., location in every minute) and longer periods, to properly fit the model. Models that account for landscape heterogeneity additionally require the landscape structure to be provided as inputs. This can be in the form of a single landscape resistance raster, as in SiMRiv (Quaglietta and Porto, 2019), or in the form of spatial covariates that are known to influence movement, like forest cover, wind velocity, etc. (McClintock and Michelot, 2018). In the case of landscape resistance data, it usually requires expert knowledge about the species in question to score land cover types in terms of “resistance”, from the prism of that species.

momentuHMM (McClintock and Michelot, 2018) and SiMRiv (Quaglietta and Porto, 2019) are noteworthy models in that they allow integration of the influence of landscape structure in the movement model, and thus can be used to simulate realistic movements constrained by real or simulated landscapes, for example, as derived from scenarios of landscape change. rangeShifter (Bocedi et al., 2020) can be used to explore the concept of evolving connectivity in response to land-use modification, by examining how movement rules come under selection over landscapes of different structure and composition.

If real tracking data is not available, or not sufficiently detailed to allow estimating model parameters, these can be set manually from expert knowledge. For example, a given animal may be known to have two movement states, and to spend most of the time in “state one”. Then, the state transition matrix (i.e. the probabilities of changing from one state to another) may be parameterized manually to respect this known behaviour. Similarly, the type of movement in each state may also be set manually by defining basic movement properties like the step length distribution and the amount of correlation between successive step angles, in

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a trial-and-error process, to achieve a realistic movement pattern in light of what is known about the species. Although this manual approach may achieve reasonable results (Quaglietta and Porto, 2019), it is plagued by the typical problems raised by *a priori* and arbitrary decisions, and, naturally, should be avoided if there is real tracking data available. However, manual parameterization may be the only option when a complex or customised movement model is needed, as statistical estimation procedures are not available for all kinds of models and do not cover all particular cases.

After the user has a parameterized movement model (or models, if there are multiple species of interest), they can be used to simulate a large number of individuals in landscapes, for a given time frame. The emergent patterns of these simulations are of paramount utility in addressing questions of connectivity, landscape fragmentation, and landscape change. By combining all the simulated movements along the simulated years, it is possible to derive, for example, metrics of connectivity (Whittington et al., 2022) and infer the best location for corridors. For instance, areas that are more intensively used by the simulated individuals may be seen as areas that are important as corridors. Further, the impacts of changes in the landscape can be explicitly addressed, by simulating individuals in different landscape configurations, that may be dynamic according to different scenarios, and assessing the differences in connectivity that result (Whittington et al., 2022). This ultimately allows assessing the consequences and effectiveness of different planning and management approaches on population spread (migration) or persistence (extinction). In theory, there are no limitations to the potential applications of such models in landscape connectivity problems, the foremost practical limitation is that the higher the model complexity, the more difficult it is to parameterize it in an ecologically meaningful way. Validating the outputs of such models will always require expert knowledge of the system at hand.

5.6 Structural Connectivity Metrics and moving window-analysis

When assessing the structural connectivity of landscapes, applying one or more of a larger collection of connectivity metrics, all varying in complexity can often be a direct and straightforward methodology. Connectivity metrics are formulas that use various components and/or characteristics of the landscape, to provide the user with distinct values of connectivity estimations. The values can either be between different patches of habitats or across larger landscapes (Keeley et al., 2021). Different metrics can vary a lot both in terms of input data and parameters needed for their implementation as well as in their resulting estimation and interpretation. Most structural connectivity metrics (Table 5.5) use physical components of the study area to provide its assessment, this could include characteristics such as but not limited to: the area-size of focal patches, the distance between patches, the threshold distance or perimeter of patches (Yang et al., 2024). Other metrics can require graph components based on graph theory, such as nodes/centroids or links and path (see Section 5.3).

Table 5.5: Table 5.5 Examples of various structural connectivity metrics, including references, all varying in complexity, with explanation of what the respective metrics measures. "" indicates metrics requiring only physical components. "**" indicates metrics requiring both physical and graph components.*

Metric	Explanation	Reference

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*Distance to nearest neighbour**	Edge distance to the nearest neighbouring patch.	*Prugh, 2009*
*Effective mesh size**	The probability of two randomly placed points in the landscape being connected, converted to area.	*Jaeger, 2000*
*Habitat within buffer**	A measure of how isolated or aggregated focal patches are in the landscape	*Prugh, 2009*
*Patch cohesion index**	Standardized area-weighted mean of ratio between the perimeter and area	*Schumaker, 1996*
*Mean radius of gyration**	A measure of how far-reaching a patch is across the landscape.	*McGarigal, 1995*
*Area-weighted mean radius of gyration**	An Area-weighted summarization of the mean radius of gyration	*McGarigal, 1995*
*Proximity index**	A measure of the size and proximity of all focal areas within a user-defined buffer around focal patch	*McGarigal, 1995*
*Betweenness centrality***	The degree for which a patch can serve as a stepping inside a network.	*Albert et al. 2017*
*Clustering coefficient***	The average fraction of a node's neighbours that are also neighbours with each other.	*Jordán et al. 2003*
*Compartmentalization***	The relationship between the degree of focal nodes and the average degree of neighbouring nodes.	*Minor et al. 2008*
*Integral index of connectivity***	The connectivity of focal areas based on habitat size and the number of stepping stone patches separating focal areas.	*Pascual-Hortal and Saura, 2006*

The advantages of using structural connectivity metrics are that they are often easier to apply since the input data needed are often more widely available or can be acquired computationally since most metrics do not require any ecological of species-specific data. The downside of these metrics is the sometimes lack of spatial explicitness. Some metrics only result in a single value of connectivity for the focal area, and they are therefore most useful for quicker assessments of connectivity in smaller areas or for comparisons of regions/countries. However, on larger spatial scales structural connectivity metrics can become less informative, as some metrics do not take the geographical placement of areas into account in the final results.

An approach to attempt to make structural connectivity metrics more spatially explicit, could be the implementation of a moving window analysis, also referred to as focal analysis or neighbourhood analysis. This type of analysis is a common technique when it comes to data analysis, image processing and feature extraction, particularly in relation to multi-scale data

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(Hagen-Zanker 2016). This method consists of a window, with a fixed size, moving sequentially along a dataset, where computations are then performed within each window, with the result often applied to the focal area or individual raster pixels. By combining a structural connectivity metric into a moving window approach, the metric is effectively to applied to the individual pixels and the whole study area at the same time, rather than providing the user with only a single connectivity value. This results in a gradient map of connectivity values; this provides more spatial explicitness to the metric as changes in connectivity across the landscape can be observed both at the local scale as well as a larger country-wide or even continental scale (Fig. 5.3).

It is worth noting that with the implementation of this moving window approach, the resulting ranges for which some connectivity metrics operate, will change, due to the metrics now being confined to a pre-determined size of the moving window. This is only applicable for metrics where the results can range from [0, + ∞) (e.g. Distance to nearest neighbour, Effective mesh size, Habitat within buffer, Mean radius of gyration, Area-weighted mean radius of gyration, Proximity index, etc.) (Yang et al., 2024). However, as mentioned, this approach allows for structural connectivity metrics to provide a better overview of connectivity in the landscape by being more spatially informative on larger and more local scales at the same time.

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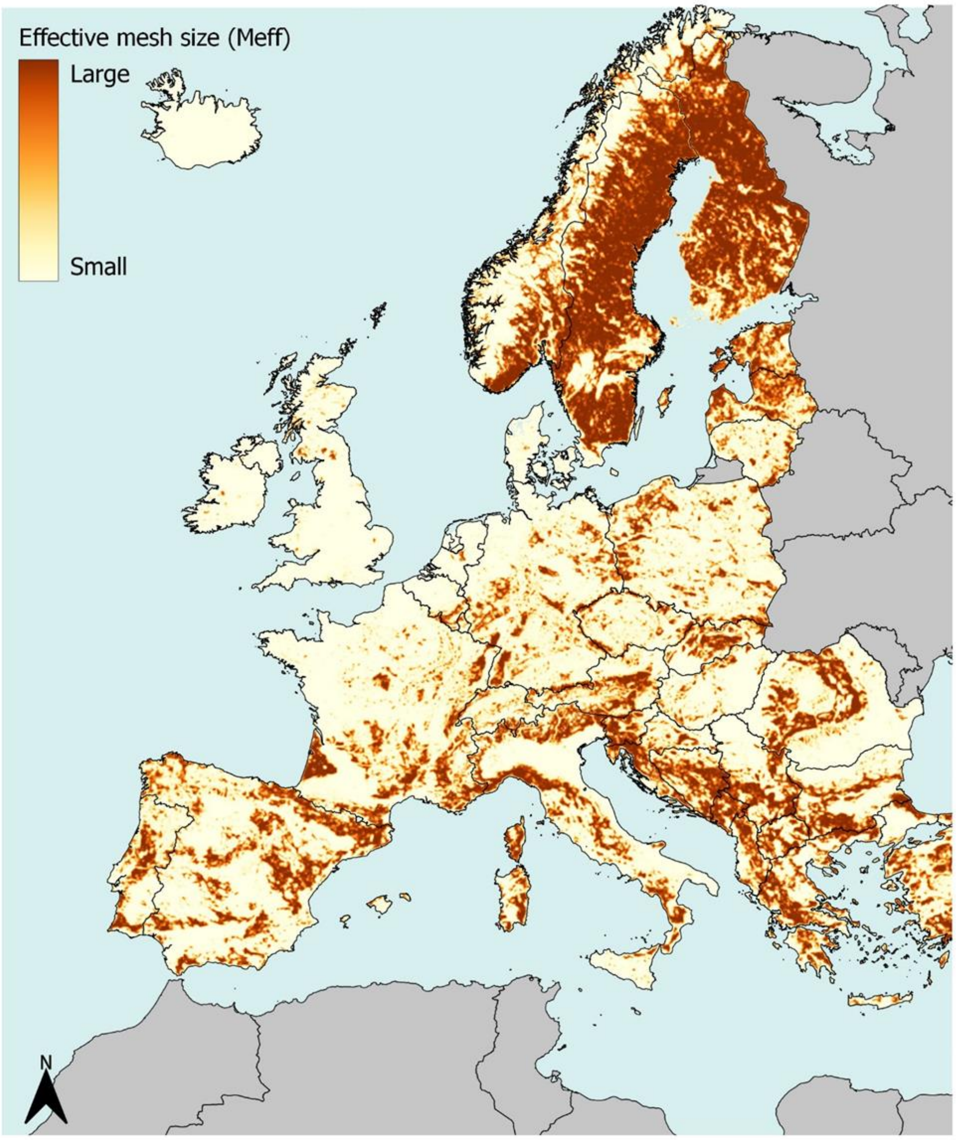

Figure 5.3: Map of Europe showing the result of using the moving window approach in conjunction with the Effective mesh size structural connectivity metric. In this case the connectivity metrics was applied to all forest patches extracted from the CORINE Land Cover. Darker brown colours indicate a larger effective mesh size value, further indicating higher connectivity.

5.7 Assessing ecosystem services

There are several approaches and tools to map ecosystem supply service and demand. For details, Burkhard and Maes (2017) provide a relevant overview and source of information. Most of these tools are openly available and are constantly evolving. The selection of an appropriate tool depends on multiple factors including the questions to be addressed, the spatial scale, data availability and so on.

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Ecosystem Services (ES) mapping approaches can broadly be classified into five categories (Burkhard and Maes, 2017; Honeck et al., 2020; Martínez-Harms and Balvanera, 2012).

The "lookup table" approach is a commonly employed and straightforward method connecting ES with geographic information, predominantly relying on land cover data. In this method, land cover data serves as proxies representing the supply or demand of various ES. The lookup table incorporates ES information often derived from statistics like crop yield in the context of agricultural production.

1. “Expert knowledge approaches” mainly rely on specialists to rank land cover classes based on their potential to provide services; experts estimate ES values in lookup tables but also use other methods such as Delphi surveys.
2. The "causal relationship" approach involves estimating ES by leveraging established connections between ES and spatial information extracted from literature or statistical sources. As an illustration, the estimation of timber production utilises harvesting statistics specific to various areas, elevations, and forest types as documented in a national forest inventory.
3. The “extrapolation of primary data” method associates weighted field data with land cover and other cartographical data; Approaches that estimate ES extrapolated from primary data such as field surveys linked to spatial information.
4. The “Regression models” method combines biophysical information from field data and the literature into a quantitative ecological system model.

The use of GIS in ES mapping can take three general approaches: (1) analysis tools built into GIS software packages; (2) disciplinary biophysical models for ES assessment (e.g., hydrological models such as the Soil and Water Assessment Tool or Variable Infiltration Capacity model for water-related ES); and (3) integrated modelling tools designed specifically for ES assessment (e.g., InVEST, ARIES) (Burkhard and Maes 2017). The initial method is suitable for straightforward analyses based on land cover and indicator mapping of Ecosystem Services (ES), as demonstrated, for instance, in Mapping and Assessment of Ecosystems and their Services (MAES). The second approach is suited for intricate model-based analyses of services, integrating expertise from distinct disciplines (e.g., ecology for crop pollination or hydrology for flood regulation mapping). The third approach builds upon the second by employing modelling tools capable of evaluating trade-offs and scenarios for multiple services (Burkhard and Maes 2017).

An overview of scientific and technical tools for GI mapping, including the European Mapping and Assessment of Ecosystems and their Services (MAES) initiative; and geospatial methods, data and tools (e.g. CORINE, LUCAS, Copernicus), are detailed in Estreguil et al. (2019). Relevant maps and data have been produced by the European Environment Agency and the Joint Research Centre (https://data.jrc.ec.europa.eu/collection/MAES).

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6. A framework for connectivity conservation and planning

6.1 Introduction to the framework

Designing and implementing an ecological connectivity network either at the local, regional, or continental scale involves considering several fundamental steps to ensure its effectiveness in promoting ecological connectivity. In this Chapter we present a general framework for planning and implementing a connectivity project (Fig. 6.1) and walk through five major steps. While the framework is presented linearly, it is often a very iterative process in part due to the continuous need to engage and collaborate with area stakeholders to ensure the production of the most accurate and useful plan possible. The framework covers these five steps:

(1) Scoping and Problem Assessment: Conduct a comprehensive analysis of the entire landscape to identify potential threats, connectivity actions, and impact of those actions, identify all relevant stakeholders and build an interdisciplinary collaboration team for connectivity analysis, communication, and implementation. Establish the general spatial extent at which your study will take place;

(2) Setting of Objectives: Use the assessment of the connectivity problem to establish spatial and temporally explicit objectives and targets that will help mitigate the identified problem. Determine the appropriate width and characteristics of corridors and stepping stones based on the target species and landscape characteristics. Finalize the spatial extent and needed data resolution;

(3) Analysis Selection & Data Preparation: Determine the correct model or models to analyse ecological connectivity. Given the model and your objectives collect and produce all the necessary data and spatial layers necessary to run the spatial analysis;

(4) Assessment of connectivity: Use connectivity metrics and models to determine the most effective design for a connectivity network that integrates with the current network of protected areas. Present draft results to stakeholders, iterate new models, and prioritize corridors and stepping stones;

(5) Implementation, Monitoring & Evaluation: Develop a comprehensive management and monitoring plan for the ecological corridor and/or stepping stones. This includes activities such as habitat restoration, invasive species control, monitoring of species movement, and assessing the corridor's effectiveness in achieving the connectivity objectives.

While the landscape characteristics, focal species or conservation objectives of each connectivity project can be different, these steps, in conjunction with the information provided thus far, provide a foundation for designing a connectivity network that may effectively facilitate ecological connectivity.

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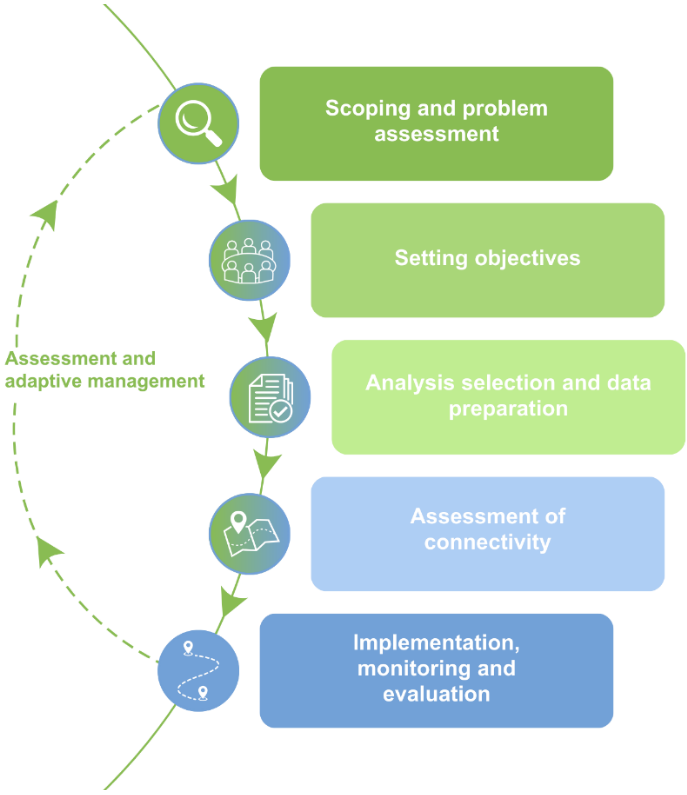

Figure 6.1: A schematic representation of a framework for connectivity network design.

6.2 Scoping and problem assessment

Assessing and developing a clear understanding of the connectivity problem is the first critical step in a connectivity planning exercise. In the context of connectivity such issues could include declining species population numbers, decreased migratory movement, or habitat loss due to climate change. Scoping the problem at this stage includes i) assessing the **threats** in the system (e.g., road mortality, encroaching development, dams), the possible **actions** that can be taken to mitigate these threats (e.g., protected corridors, underpasses, seasonal closures), and the likely **impact** from such actions. When assessing the likely impacts of any action, it would also be appropriate to consider how they will be evaluated.

A part of scoping will involve identifying all the key **stakeholders** involved with the problem and with the targeted region. Identifying as many stakeholders as possible and involving key individuals in the decision process from the beginning is vitally important to produce the best possible outcome. This steady involvement from the beginning will produce a more accurate pre-implementation plan, increase the chances of the plan being implemented, and lay the groundwork for management and monitoring post-implementation. Decades of collaborative

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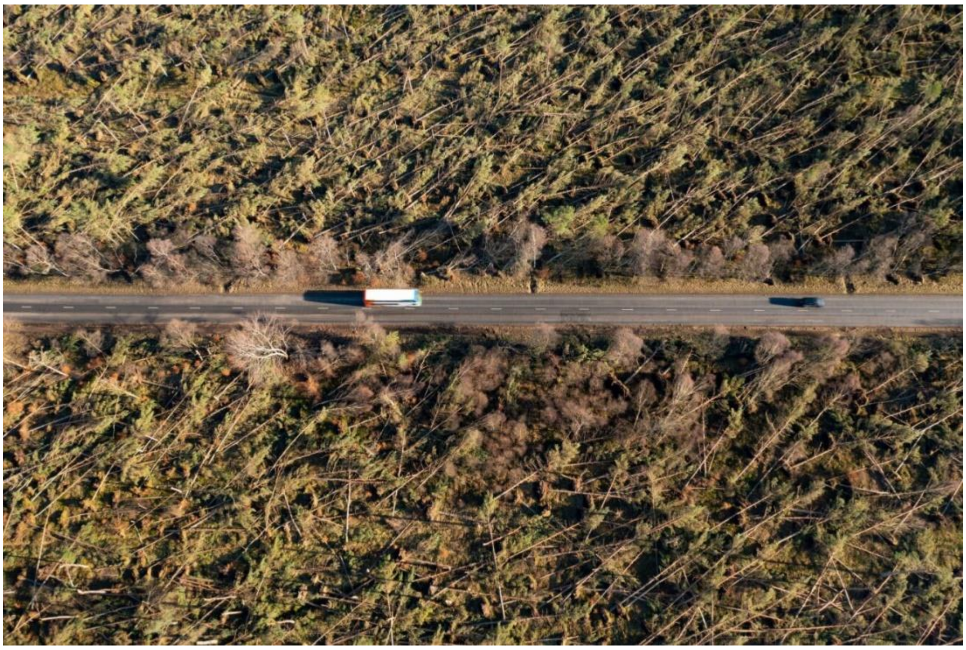
conservation projects have shown the importance of such sustained stakeholder involvement, and this was confirmed in our stakeholder webinar (Section 4.2) where participants frequently identified the need for comprehensive stakeholder engagement from the beginning of any conservation action or initiative. If producing deliverables informing landscape-scale planning is an ultimate goal, one should think about what products need to be produced to inform private citizens and public decision-makers about the important areas for corridor conservation.

Before determining the final objectives of the study and while still assessing the overall problem a **collaborative team** should be set. Given the ecological and socio-political complexities of these projects an interdisciplinary team should include natural resources practitioners, communication specialists, scientists, policymakers and ideally project administrators. This will assist in producing robust scientific results which are more representative of the on-the-ground situation and increase the chances that such a plan will garner support for implementation.

Defining the scope of the connectivity planning study will also include identifying the study's basic **ecological realm** (e.g., terrestrial, freshwater, etc.) and general **spatial extent** (i.e., total study area). The most effective spatial extent for successful implementation of connectivity and conservation planning is often context dependent; however, the spatial extents should ideally be informed by an intersection of the biologically relevant area and the socio-political conditions that support the implementation. Therefore, it is important to consider if the project is operating at a spatial extent that captures important ecological and abiotic processes while also being contained within a governance structure that can maintain support for the implementation of project aims.



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A focus on species' natural history and especially dispersal capabilities is important when deciding upon the spatial scale of your study (see Ch. 2.4). This is especially true for certain

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groups such as semi-aquatic species including river otters, salamanders, and turtles, which are cross-realm species especially threatened by linear infrastructure either blocking movement or causing mortality during dispersal (e.g., roadkill). Connectivity assessments in **riverine ecosystems** should ideally take place at large spatial extents (e.g., catchment or sub-catchment). Especially for long-distance migratory species, large-scale assessments can support the identification of bottlenecks and priority areas for restoration. For potamodromous species (i.e., species limited to freshwater ecosystems), smaller scales covering the distribution range of respective species might be sufficient. At the least, the selected spatial scale should include all required habitats for the target species to complete their life cycle (i.e., habitats for spawning, feeding, and wintering).

A final consideration while scoping the project is the potential impact improving ecological connectivity could have on the provisioning of **ecosystem services**. Connectivity can directly or indirectly affect ecosystem service provisioning, making these services valuable targets themselves. Furthermore, many ecosystem services are strictly linked to the movement of certain species. Examples are seed dispersal, pollination, nutrient cycling, and cultural and recreational activities. However, priority areas that improve connectivity to increase ecosystem services supply might not be the same as for the aim to mitigate threats for specific species to improve their conservation status. Aiming to increase ecosystem services is particularly important in locations near urban areas, where the multifunctionality of the green infrastructure is more relevant. By enhancing the connectivity for the species or functional groups that provide these services, connectivity interventions indirectly contribute to the provision of ecosystem services.

Once full scoping of the problem is complete and it appears that an action taken to promote the creation or restoration of a connectivity network will help mitigate the problem, the project team should decide on specific project objective

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6.3 Setting of Objectives

The planning of connectivity requires careful consideration of various factors, and it is essential to define the specific goals and beneficiaries of these efforts. Connectivity can focus on whole ecosystems, specific habitat types, species, functional groups or ecosystem services. This choice entails trade-offs between generality and specificity. Taking the findings from project scoping in step 1, it is then essential to establish one or more **clear and achievable objectives** that will guide the analysis and actions taken by the project (Table 6.1). Objectives can be customized towards the conservation of one species or wide-ranging to include multiple overlapping ecological functions that would benefit from connectivity conservation.

Objectives can include conserving the daily movement of a species, maintaining seasonal migratory pathways, increasing genetic exchange between populations, dispersal of seeds or pollen, or movement of nutrients (Hilty et al., 2019). Spatial and temporal scale are most important to consider when developing objectives and indicators as the planning decisions made henceforth will vary dramatically if, for example, you are interested in the dispersal capability of an individual animal or plant *versus* the long-term population viability of those species. Examples for general objectives could include: i) **biodiversity conservation** (e.g., daily movement of species; multi-species movement over decades; yearly fish migrations; wildlife and plant dispersal corridors due to climate change; invertebrate connectivity across intensive farmland or forestry); ii) **ecosystem services** (e.g., sediment capture and reduction of erosion; pollinator connectivity; water filtration; nutrient cycling and carbon sequestration; recreation); iii) reduction of **impacts from infrastructure** (e.g., locations for green bridges or underpasses; prioritisation of dam or road removal; establishment of best land zoning regulations); iv) connectivity planning in **urban/peri-urban areas** (e.g., placement of greenbelts; restoring water flow between urban wetlands; v) **multi-functional corridors** (e.g., combination of objectives for species conservation, ecosystem services, human recreation, and/or other goals).

Depending on the connectivity project certain objectives may also include specific **quantitative targets** to be met to achieve that objective. For example, while the objective may be to establish a corridor to an isolated protected area to conserve movement of brown bears, a target could include a quantitative measure of the number of individuals or breeding females desired to disperse via the corridor (Table 6.1).

Table 6.1: Four potential connectivity problems with an example objective, target and action. Note that actions are not always just implementing and restoring a protected area (PA) or corridor but can include seasonal changes of human disturbance or alterations in permissible land use.

Problem	Objective	Target	Action

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Low genetic diversity and a decreasing abundance of brown bear in an isolated PA	Increase brown bear movement to isolated PA	Four or more breeding females establish new territories in the isolated PA	Implement the protection of a forested corridor >1km wide between a source population of brown bears and the isolated PA.
Rapidly declining pollinator presence in grassland habitat	Ensure spatial and temporal connectivity between grassland patches for pollinators	Return pollinator capture numbers to 110% of baseline before rapid decline	Seasonal ban on mowing of key stepping stone grasslands and fields
Increasing instances of livestock mortality due to wolf dispersal	Identify and restore new corridors to decrease human-wolf conflict	Reduce livestock mortality by 40% within 5 years	Restrict grazing within and expand the minimum width of two corridors prioritized by connectivity models
Increasing mortality of waterbirds during migration	Define new stepping stone habitats for migrating waterbirds	Establish 5 new migratory stopover areas AND increase annual waterbird survival by 3%	Work with local environmental ministries to implement other effective area-based conservation measures on identified wetlands.

6.3.1. Focal & archetype species for assessing connectivity in Europe

Connectivity studies often focus on a single or small suite of **focal species** to represent other species or the broader ecosystem. Historically, these were charismatic species threatened by habitat fragmentation and were thought of as an umbrella species whose conservation would hopefully benefit a broad suite of species and ecosystem processes. These focal species approaches are still frequently used given the special attention still paid to large charismatic mammals, the scarcity of presence or movement data for many species, and the relative complexity of attempting to model the connectivity of dozens of different species at the same time.

While the focal species approach can be effective in promoting and protecting some areas for connectivity, identifying a small grouping of species with differing habitat preferences has been shown to be more effective at capturing the needs of a broader species pool for a given habitat type (Meurant et al., 2018). Similarly, projects may target **groups of species** sharing some fundamental traits and with similar conservation needs. A typical example is large carnivores, which have large area requirements and might be particularly vulnerable to fragmentation. In these cases, a possible approach is focusing on **species archetypes**, i.e. generic sets of traits representing groups of species that are functionally similar from a connectivity perspective (see Box 6.1 for plant and vertebrate species archetypes in Europe).

Box 6.1 Description of archetype tetrapods.

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When projects target groups of species sharing some fundamental traits and with similar conservation needs, a possible approach is focusing on species archetypes, i.e. generic sets of traits representing groups of species that are functionally similar from a connectivity perspective. Connectivity between populations results from a combination of their physical distance, landscape resistance to movements, species reproductive potential (timing and output), and dispersal ability. Among species traits, reproductive potential determines the number of propagules that are produced over time, whereas dispersal determines the ability of each propagule to reach a given distance.

This approach has been explored for European plants by Lososová and colleagues (2023), while for terrestrial vertebrates no similar analysis has been published up to now. Following an approach like that published for plants, it has been identified a total of 27 archetypes in European tetrapods (see below) considering reproductive traits and other variables that can relate to spatial requirements and energy consumption (e.g., body mass, home range size; detailed methods are reported in Annex S3). Median trait values are reported in Annex S3 (Tables S3.2-S3.9).

- Non-volant mammals were divided in (1) large mammals with long life span and long dispersal distances, (2) large mammals with long life span and medium dispersal distances, (3) medium mammals with long life span and medium dispersal distances, (4) small-medium mammals with medium life span and short dispersal distances, (5) small mammals with short life span and short dispersal distances.

- Bats were divided in (1) bats with small home ranges and short dispersal distances, (2) bats with large home ranges and long dispersal distances, (3) bats with medium home ranges and short dispersal distances.

- Birds were represented by (1) large birds with long lifespan, medium dispersal and wide home range, (2) medium-sized birds with medium longevity, medium dispersal and medium home range, (3) small-medium birds with medium-short lifespan, long dispersal and small home range, (4) small birds, with short lifespan, short dispersal and small home range.

- Frogs were divided in (1) large frogs with a high clutch size, (2) small-medium toads with a low clutch size, and (3) small frogs with a medium clutch size.

- Salamanders was represented by three archetypes: (1) medium-sized newts with high clutch size and presence of larval stages, (2) big-sized viviparous salamanders with high clutch size, and (3) small- to medium-sized salamanders with low clutch size and presence of direct development.

- Turtles were divided in two archetypes: (1) small-medium turtles with high clutch size, and (2) large tortoises with medium clutch size.

- Snakes were characterised by three archetypes: (1) big-size snakes with high clutch size, (2) small-medium snakes with high clutch size, and (3) small-size snakes with low clutch size.

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- Lizards were represented by three archetypes: (1) big-size terrestrial lizards, (2) small-medium size saxicolous lizards, and (3) small-medium size terrestrial lizards.

Understanding species habitat preferences (Fig. 6.2) is crucial to establish a connection between archetypes and a specific environmental context highlighting the critical role of landscape resistance in conducting effective connectivity analyses. However, most species have species-specific combinations of habitat requirements (Figs. S3.1 and S3.2 in Annex S3), which prevents generalizations, even considering coarse habitat classes. In this context, a major challenge in connectivity modelling is represented by the consideration of geographic barriers. The modification of landscapes through the development of roads, railways, fences, and canals increases habitat fragmentation by reducing species movement and increasing mortality (Bastianelli et al., 2021). For example, birds that live on the boundary between roads and forest or pastureland are more susceptible to being injured or killed by vehicles or noise barriers; similarly, birds in anthropogenic environments have been reported to collide with wind turbines, power lines, and building windows (Medrano-Vizcaíno et al., 2022). In addition, traffic and roadkill represent a main threat for mammals across Europe, because of their movement ecology and the large amount of space that they require for dispersal and home range (Klar et al., 2009). In the European scenario, overcoming or eliminating geographical barriers could be crucial to enhance spatial connectivity for species of conservation concern. However, when analysing species-specific connectivity, it is essential to account for the resistance posed by such infrastructures to prevent overestimating or underestimating the species’ movement abilities in connectivity modelling.

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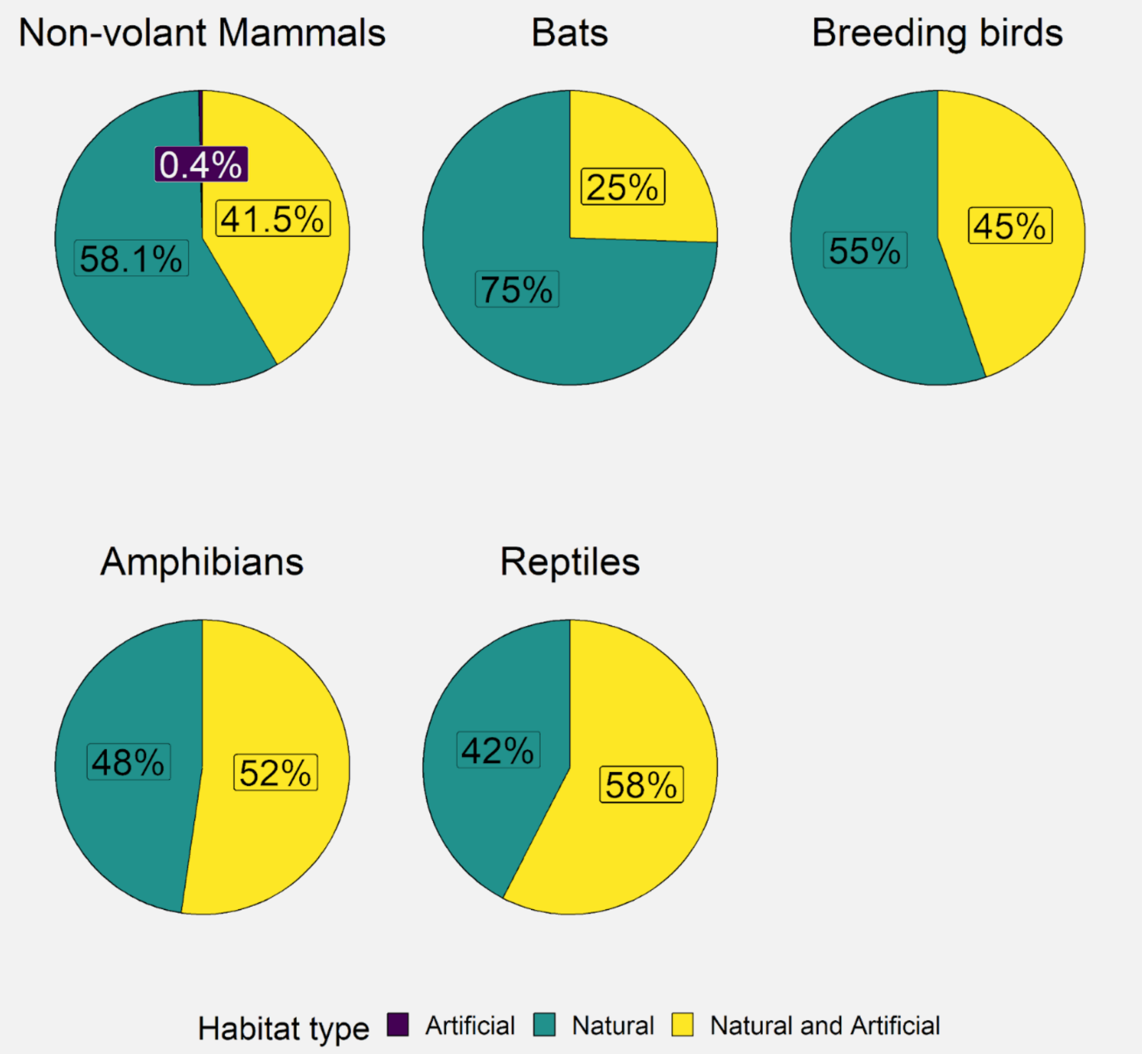

Figure 6.2: Habitat preferences (percentage of species) of European tetrapods using three coarse classes.

6.3.2 Corridor width

The width of ecological corridors is a critical factor for determining their effectiveness. Narrow corridors may not provide sufficient habitat or protection for wildlife, especially for species with wide-ranging territories. Conversely, overly wide corridors may be impractical or economically unfeasible, especially in densely populated or agriculturally intensive regions. **Corridor width** should be sufficient to accommodate two general groups of species based on their mobility, **passage species** and **corridor dwellers**. Passage species refer to those species in which an individual animal can traverse the length of the corridor in a single event, typically in a few hours or days. Corridor dwellers require more than a generation to move individuals and/or genes across the corridor (Beier and Loe, 1992). For corridor dwellers, it is important that the corridor is sufficiently wide to allow for overlapping home ranges allowing animals to live, find mates and reproduce in the corridor (Beier and Loe, 1992).

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Corridor design should also consider **edge effects** and the zone of influence of human activities which changes ecological processes inside corridors and reduces their effective width (Boulanger et al., 2012), that is, the residual space that occurs beyond the zone of influence of human activity. For instance, if a 400 m wide ecological corridor is adjacent to a residential area and the influence from that development is 100 m, then the effective corridor width is reduced to 300 m.

The current body of scientific research does not provide fully comprehensive evidence to determine how wide ecological corridors should be to attain all conservation goals (Gilbert-Norton et al., 2010; Haddad et al., 2011; Sawyer et al., 2011). Given the complexity, confounding effects, and time-consuming nature of assessing the effectiveness of ecological corridors and determining the optimal width (Beier, 2019; Gregory and Beier, 2014), the available evidence is relatively scattered (Beier, 2019); however, there are some key resources that provide valuable recommendations (Box 6.2).

Box 6.2 Debate and Guidance on Corridor Width

Beier's rule of thumb

Beier (2019) suggests that ecological corridors connecting habitat patches that are 8–80 km apart should have a minimum width of 2 kilometres, except for unavoidable bottlenecks such as highway crossings. This recommendation is based on the notion that a width of this magnitude would be sufficient to accommodate home ranges of up to approximately 8 km^2. This coverage would meet the needs of 345 species of mammals that are probable corridor dwellers, selected from a list of 429 terrestrial mammals provided by Tucker et al. (2014). Concerning edge effects, Beier (2019) notes that in North America negative edge effects were considered biologically significant at distances of up to 300 m (Kennedy et al., 2003), therefore a corridor that is 2 km wide would have at least 1700 m free of edge effects.

Ford's et al. approach

Ford et al. (2020) proposal is based on the concepts of zone of influence (Boulanger et al., 2012) and flight initiation distance (FID), that is, the distance at which animals flee from an approaching person. Specifically, their approach is based on determining how both these distances reduce effective corridor widths and use that knowledge to make recommendations on corridor width in different landscape settings. The authors searched the literature for case studies documenting the zone of influence and the FID from recreational trails and residential development for four North American carnivore species, black bears, grizzly bears, grey wolves, and cougars. From this analysis, they concluded that the effective corridor width should vary from 3000 to 6000 m close to residential areas and 400 to 1000 m in areas containing recreational trails, depending on the species.

USDA's recommendations

The United States Department of Agriculture (USDA) conducted an extensive review of 66 studies, including movement ecology studies, observational studies, and habitat management studies conducted in North America, encompassing a diverse range of species groups that are also present in Europe (Bentrup, 2008). While the USDA acknowledged that many of the studies did not encompass a wide enough range of corridor widths to definitively determine optimal sizes, they did provide general recommendations.

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Concerning the general recommendations, they suggest that 1) larger species need wider corridors to facilitate movement and provide potential habitat, 2) longer corridors should be wider than shorter corridors and 3) shorter corridors are more likely to provide connectivity than longer corridors.

As for the specific recommendations, they proposed minimum corridor widths and recommended corridor widths for several groups of species ranging from plants to large predator mammals (Table 6.2).

Table 6.2: Minimum and recommended corridor widths based on the review of 66 scientific studies (Bentrup, 2008).

Group	Minimum corridor width (m)	Upper end of recommended width (m)
Plants	30	101
Invertebrates	30	61
Aquatic species	30	61
Reptiles & Amphibians	30	183
Birds: interior species	61	1609
Birds: edge species	30	101
Small mammals	101	101
Large mammals	101	2414
Large predator mammals	101	> 4828

6.3.3 Final Spatial Extent and Resolution

During the scoping process a general spatial extent was identified at which the project will be operating. Now at this step once specific objectives are defined and potentially the targets associated with those objectives, there can be greater concentration on the precise spatial extent and resolution of an analysis that will assist decision makers in an impactful conservation outcome.

Two main factors should be of focus when determining the spatial extent (i.e., total study area) and resolution (i.e., grain) of your connectivity analysis. First, what is the extent and resolution that will most accurately represent and capture the **ecological process** which you are attempting to model and conserve? Second, what is the extent and resolution that will be effective for practitioners and policymakers to **implement** the findings? For example, attempting to model the corridors that are important for a seasonally migratory large ungulate will likely require a spatial extent that is orders of magnitude larger than that for the connectivity for a local ground beetle.

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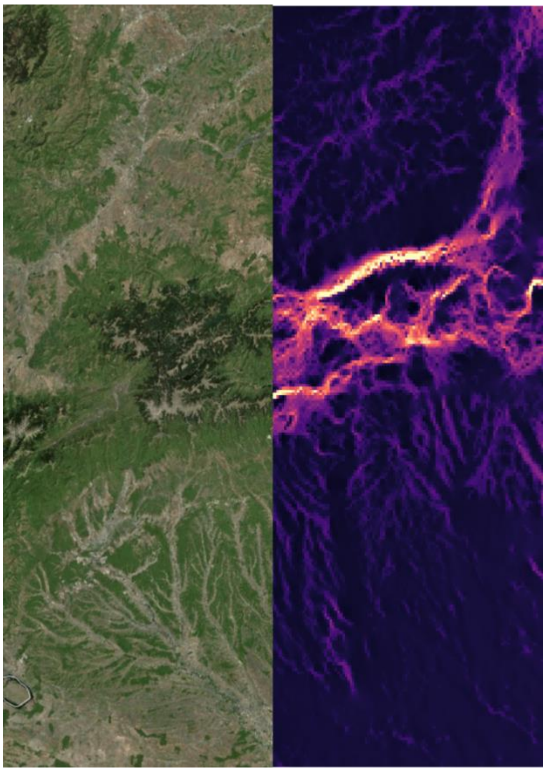
Likewise, data resolution must be much finer (i.e., smaller pixel size) for an analysis of ground beetle connectivity (<10 m) compared to the ungulate population (30 m - 1 km) given the differing scales at which the species respond to their environment. Local and regional scales of assessment are frequently the scale management actions are implemented at to increase connectivity and thus require fine-grained, accurate and detailed data. The large-scale (transborder or continental) mapping of corridors needs less detail and is adequate for projects related to the planning of transportation infrastructure or trans-boundary coherence for the connectivity of protected areas.

The primary concern is to produce analysis products that are at fine enough resolution to give meaningful and operational information for practitioners and decision-makers, at a spatial extent which will be implementable. Producing coarse grain connectivity assessments may not necessarily provide any new information to local resource managers to aid them in conservation decision-making.

In addition, to produce more accurate results, the impacts of study area boundaries on different models should be considered when determining the entire spatial extent to conduct the connectivity analysis. This is true for circuity theory models (see Section 5.4) and other models influenced by boundary edge effects where results near boundaries can be significantly biased and are less trustworthy (Koen et al., 2010). Therefore, depending on the model, analyses should include buffer areas beyond the agreed-upon study area to negate any boundary impacts within the area of interest. These buffer areas can be simply clipped off from the final connectivity results and deliverables.



Overlay of satellite imagery and Circuitscape results

Finally, a third factor to consider for large-scale projects is the computational power needed to run analyses as they approach large extents and finer spatial resolutions. This may not be a factor for relatively simpler analyses such as least-cost path, but with analyses such as resistant kernels, circuit theory models and certain movement models fine spatial resolution at large spatial extents may require access to a high-throughput computing cluster or supercomputer to complete analyses over multiple days.

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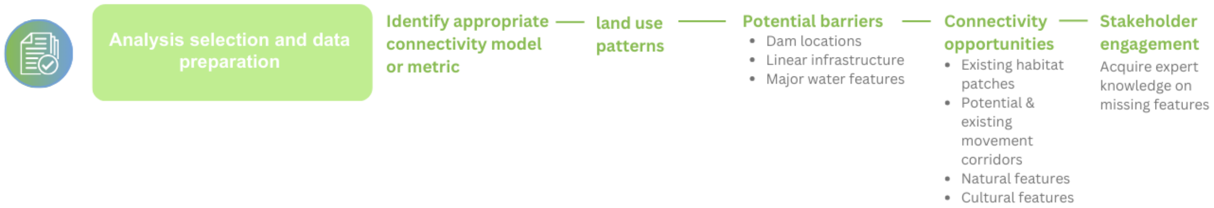
6.4 Analysis Selection & Data Preparation



Having established your objectives and before extensive data collection, it is important to **determine the analysis** that will achieve them. As was introduced, there are many tools to choose from to address the project question or objective (Chapter 4). When the objective is connectivity of habitat types (e.g., connectivity of forests) or to enhance the connectivity of particularly intact natural ecosystem systems, structural connectivity metrics or graph theory models that only consider the basic structure of the landscape could suffice (e.g., iGraph, riverconn, Conefor; see Table 4.1). Conversely, functional connectivity (e.g., agent-based, circuit theory, and resistant kernels models) should be prioritised when project objectives centre on a focal species or a specific group of species.

Structural connectivity analysis via graph theory (e.g., Bunn et al., 2000) has been applied for analysing landscape structure and functionality, prioritising patches and connections, and for assessing long-term population persistence. Applying graph theory to connectivity analysis allows for examining network connectivity as a whole, which facilitates comparative analyses among different networks. Data needs include focal nodes and connection attributes between node pairs. The emphasis is put on the configuration of a network, including the isolation, size, and shape of the patches, connecting elements (e.g. corridors, stepping stones), and elements that can act as barriers (e.g. anthropogenic such as roads or natural such as rivers). Such simplified assessments are likely to be easier to communicate to stakeholders and policymakers (Saura et al., 2011).

If structural connectivity is being used as an index for multiple species, this approach assumes that enhancing connectivity at a structural level can facilitate the movement of various species, reducing the risk of population isolation and contributing to genetic diversity. This might be particularly sensible when species of these systems face similar connectivity challenges (e.g. riverine ecosystems where species face similar movement barriers). For instance, interventions to enhance connectivity in river networks, despite hosting diverse species, can equally benefit numerous freshwater species. Overall, enhancing the structural connectivity of certain habitat types is expected to yield benefits to plant and animal species dependent on these habitats.

Targeting **functional connectivity** must consider species-specific characteristics such as dispersal propensity and abilities, area requirements, permeability of different landscape elements to the species movement, behavioural response to infrastructures, etc. Movement models or some agent-based models that can use GPS or radio-tracked animals locations provide some of the closest information we have to true functional connectivity (Table 4.1). Circuitscape, Omniscape and Linkage Mapper can provide quasi-functional connectivity model estimates, especially when resistance surfaces are generated using either spatially-explicit

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genetics data of a species (i.e., allele variation between subpopulations of one species) or from detection/non-detection wildlife data.

Resistance to movement between and within habitat patches is central to least-cost path, resistant kernels, and circuit theory models. There are several methods to create resistance surfaces, depending on the type of data available for the species of interest (Zeller et al., 2012). The most common method is to invert habitat suitability values obtained with species distribution models so that the areas with higher habitat suitability values have the lowest values of resistance. Other methods include using telemetry, GPS point and track data.

In contrast, spatial prioritisation tools commonly used for systematic conservation planning can be useful to identify structural connectivity, by prioritising landscape elements (Hanson et al., 2022). Needed data inputs include a conservation planning units file, the spatial distribution of biodiversity, land use, or protected areas. Available tools include Marxan, Zonation, or the R package prioritizr (see Table 4.1 and Section 2.7 for details).

There are several approaches and tools to map ecosystem services (see Burkhard and Maes, 2017 and Estreguil et al., 2019 for details), whose selection depends as well on multiple factors including the questions to be addressed, the spatial scale, and data availability (Section 4.6). Graph theory or circuit theory models are best for problems surrounding water quality, sediment capture, nutrient cycling, and fire. Circuitscape especially is utilised for attempts to simulate potential fire spread. Seed dispersal and pollination services can be modelled with resistant kernels if there is data on dispersal distances for the species or using circuit theory models even without dispersal data. Finally, finding the best movement pathways for recreation can be accomplished using least-cost path methods or Circuitscape.

Data requirements for many of the models are very similar (Fig. 6.3). Most require some representation of the landscape via a **land cover** dataset and/or elevation model. Understanding the current protected area network including the georeferenced boundaries of each protected area is vital for any of the connectivity models. Spatial data should be acquired for all the **threats and potential barriers** identified in step 1, such as dams, border walls, motorways, or major water bodies. If the creation of a resistance surface is necessary, climate data could also be important for generating species distribution models. Gathering data on the dispersal capability of the species of interest is also important for resistant kernels, particularly. The checklist on the proceeding page covers some of the more common data needs but is not fully inclusive of all connectivity modelling contexts and Annex S4 provides a basic listing of geospatial data sources for the European continent.

Finally, before conducting the connectivity analysis, stakeholders should be engaged again (if they haven't been continually) to inquire if there are any data pieces missing or if there are unforeseen gaps in the data. For example, information on the protected areas network may have been downloaded from the World Database of Protected Areas. While the coverage of this database is quite extensive, it may not be comprehensive, especially at the local and regional level where several parks and protected areas or OCEMs may be excluded. So too is information on green bridges/wildlife passages whose locations may not be published or well-advertised.

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Checklist of Spatial Data:

Data layers frequently needed during a connectivity analysis with some more specific features.

- ▢ Protected Area Boundaries
- ▢ Political Boundaries
- ▢ Land Cover/Land Use
  - ▢ Land use projections
  - ▢ Land management practices
- ▢ Elevation Data
- ▢ Rivers & Lakes
  - ▢ Hydrologic features (vector data)
  - ▢ Wetness level* (raster data)
- ▢ Linear Infrastructure
  - ▢ Roads & Trails
  - ▢ Border Walls & Fences
  - ▢ Dams
  - ▢ Wildlife passages
- ▢ Species Presence Data
- ▢ Climate Data
  - ▢ Historical trends
  - ▢ Future climate scenarios

** Includes information on permanent vs. temporary wet areas, snow, etc.*

Figure 6.3: Checklist of common spatial data needs for connectivity analyses. Data needs will vary between the different models and research problems, so this should not be seen as an exhaustive list of what may be required.

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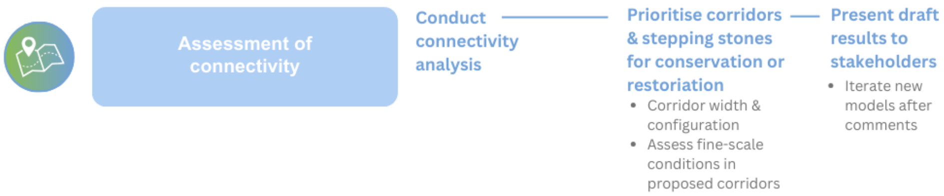
6.5 Assessment of Connectivity



Having determined the analysis framework you will be using, collected all the necessary data, and consulted with stakeholders about any gaps in the data, **connectivity analysis** can be conducted. This should be a cyclic process with the collaboration team generating draft model results and then gathering input from key stakeholders on the draft results, before running the models again. This aids in the effectiveness of the final plans and the realistic possibilities of it being implemented.

Depending upon the chosen approach, time for such assessments could take weeks or months to fully process and run the models. Typically, much more time is spent processing and preparing the data for input into the model, rather than the actual construction of code or runtime of the model. Graph theory models with simple input information on node and link characteristics or smaller-scale least cost path analyses can be run in minutes. Conversely, movement models that are processing tens of thousands of GPS locations or circuit theory models such as Omniscape can take days or weeks to complete the analysis for a single species. The online resources highlighted in Chapter 4 can provide guidance on what to expect in terms of runtimes and assistance in troubleshooting modelling problems.

Once you have draft results, they can either be **presented to stakeholders** (e.g., regional councils, land management agencies, conservation organizations, private landowners, etc.) for review or further analyses can be conducted to **prioritise** the corridors and/or stepping stone locations before stakeholder consultation (see Section below). Prioritisation may not always be necessary, depending on the project, or you may wish to seek stakeholder input on draft results to assist with the ultimate prioritisation.

Stakeholder reviews can be done **in-person** or via **webinar**. In either setting, members of the collaboration team should present the workflow followed in the project and the specific methods used to generate the connectivity maps. Like public regional planning meetings, initial results and maps from such assessments should be presented so stakeholders can provide expert opinions on the preliminary results.

In-person meetings should allow stakeholders to engage in open discussion and to draw and leave sticky notes on the maps. Ideally this will assist in identifying impractical or potentially spurious results coming from the models, missing information not uncovered during step 3, and opinions on prioritization of the proposed corridors or stepping stones. Online webinar formats should follow a similar flow, but with online mapping resources provided for stakeholders to leave georeferenced comments. Platforms that can support **public participatory GIS** (PPGIS) such as ArcGIS Experience, the Google Maps interface, and the R package 'PPGISr' allow stakeholders to draw points or polygon features on the map and add comments as attribute information for the feature. In addition, online PPGIS platforms allow participants to easily toggle between geospatial layers such as species distribution

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models or alternative connectivity scenarios, which may give the stakeholders a better understanding of the workflow that arrived at the proposed connectivity map. A combination of in-person and online meetings may give the most equitable coverage of stakeholders and concerned citizens as some people may not be able to attend in-person meetings but can leave comments remotely on a PPGIS interface.

Members of the collaborative team should synthesize all the comments and determine those recurring or major issues that should be addressed in the next round of the connectivity analysis. This may mean returning to previous steps in the connectivity design framework if, for example, there were missed landscape threats or if objectives need to be altered. Once connectivity model results are finalized, either at this round or after further consultation with stakeholders, then there can be the final determinations of management actions and prioritisation of corridors and stepping stones.

6.5.1 Prioritisation and restoration for connectivity objectives

Not all corridors or stepping stones are equally important to maintain the overall connectivity of the system. Beyond identifying potential corridors or stepping stones, connectivity analysis can be used as a decision tool to prioritise those identified areas, either to improve existing ones or to establish new ones through restoration activities, by helping to identify areas that hold the greatest potential for overall connectivity in the region (Rudnick et al., 2012). One way of getting this information is to evaluate the importance of removing each of the corridors (linkages) in the overall connectivity of the region, using different methods such as program Conefor or Linkage Mapper (see Chapter 4). For example, de la Fuente et al. (2018) used a graph-based approach to identify the conservation importance and the restoration importance of the corridors linking Natura 2000 sites across Spain. The latter was quantified as the increase in the connectivity of the network of Natura 2000 sites that would occur if the current conditions in each corridor were improved so that the land cover was fully composed of the most favourable habitat for species movements.

In the process of conservation area selection, there is a tendency to select areas with better conditions for movement by animals and plants and therefore higher connectivity. However, if these corridors are not maintained, e.g. due to land use changes, their function might be lost. This is an important aspect to consider when using connectivity information in spatial conservation planning (e.g., Daigle et al., 2018; see also Section 2.7), as the optimization algorithm will influence protected area selection assuming a priori connectivity estimates that might be changed in the future if the land cover types responsible for the high values are changed.

Restoration for connectivity is not restricted to habitat restoration but can include interventions on human infrastructures that act as barriers to movement. In the terrestrial realm, underpasses or overpasses in roads and railways have proved effective, though evaluating their effectiveness is still not a common practice and needs to be generalized (Soanes et al., 2024). Mitigating the impacts of such linear infrastructure on wildlife populations also includes preventing mortality due to wildlife-vehicle collisions. Under that perspective, methods to prioritise the placement of mitigation measures such as under or overpasses in roads or railways can include the use of connectivity models to identify crossing areas (Lee et al., 2023) and the identification of road mortality hotspots based on carcass surveys. The implementation

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of mitigation measures such as crossing structures should consider species-specific ecological requirements and follow best-practice guidelines (Soanes et al., 2024). For example, Gurrutxaga and Saura (2014) used habitat network analysis to evaluate how the location of road permeabilization measures for highway defragmentation would restore landscape connectivity in a forest-protected area network in the Basque country in Spain. More recently, Lee et al. (2023) used a combination of connectivity modelling (based on empirical data of migratory routes and using least-cost pathways and corridor prioritisation) and road mortality hotspot identification together with citizen science data to prioritise road mitigation opportunities for pronghorn in Canada.

In the freshwater realm and especially in rivers, dams and weirs as well as other obstacles represent significant impacts on connectivity thus affecting biodiversity. While large dams inherently create barriers, even smaller infrastructural elements, like small dams, act as (micro-)barriers. These smaller barriers, although often overlooked, can cumulatively affect larger areas and hence are seen as priority zones for restoration to enhance connectivity.

Although possibilities exist to enhance partial connectivity in rivers, such as migration facilities for fish, full connectivity (i.e. enabling not only the movement of fish but also a free flow of water and materials such as sediments) can only be established in rivers by removing the barrier. Dam removal has gained considerable importance through the last years and will gain further importance as the EU Nature Restoration Law aims for at least 25 000 km of free-flowing rivers, compared to 2020. Thus, approaches to prioritise the removal of dams and barriers can help to efficiently reach this target. The prioritisation of barrier removal should first increase the connectivity of habitats that are relevant for species to fulfil their life cycle (e.g. habitats for spawning, juveniles, adults for migratory fish). However, trade-offs between costs (e.g. reduced energy production) and conservation benefits must be considered too (ideally this should first be identified during step 1 of the decision framework) (McKay et al., 2017). Overall, the connectivity of the river network can be optimised in regard of different aspects (Branco et al., 2014; Hermoso et al., 2021a).

Another option to mitigate the effects of barriers in rivers is migration facilities, such as fish ladders at hydropower plants. These facilities function as an alternative corridor for organisms for up- and downstream connectivity restoration. To be used by the different species of interest, their design must meet the requirements of the most demanding migratory species concerning, e.g., swimming capabilities, preferred migration corridors, and space requirements (Seliger and Zeiringer, 2018). However, a migration facility does not restore the 'full' connectivity of a corridor (e.g. sediments are still trapped upstream of the barrier). Moreover, migration facilities also provide corridors for invasive species or pathogens, which has also to be assessed compared to the benefits for a species in need. See McKay et al. (2020a) for guidelines on criteria to identify priority areas for setting these facilities. Prioritising hydropower plants where such migration facilities should be built is mostly related to the species that should benefit from such a facility. For example, the ICPDR developed an '*Ecological Prioritisation Approach River and Habitat Continuity Restoration*' approach that combines structural as well as functional connectivity aspects where the functional aspects are addressed by different migratory guilds of fish (mainly medium- and long-distance migratory).

Overall, rivers, wetlands and riparian land have been identified as priority areas for restoration as corridors, increasing connectivity for multiple purposes as they contain both blue and green

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elements. Thus, they are seen as a backbone of green-blue infrastructures (e.g., de la Fuente et al., 2018). More pragmatic approaches have also been suggested by stakeholders to prioritise restoration efforts, namely selecting the areas where restoration efforts can be more easily implemented for technical and/or political reasons. This, however, may have the disadvantage of not targeting the most cost-effective areas.

In intensive agricultural areas, connectivity can be increased through the introduction of the so-called landscape features, small fragments of non-productive natural or semi-natural vegetation including hedges, ponds, ditches, non-productive trees, field margins, terrace walls, dry-stone or earth walls, or fallow land. These are expected to contribute to the target of the EU Biodiversity Strategy for 2030, of achieving 10% of cover by landscape features in the agricultural area of the EU, and will benefit a diversity of taxa including amphibians, reptiles and farmland birds. The maintenance or uptake of low-intensity traditional agricultural practices, which maintain a significant amount of natural or semi-natural habitats, can also be seen as a kind of restoration effort contributing to the creation of ecological corridors breaking the intensive agricultural landscape matrix.

6.6 Implementation, Monitoring & Evaluation

The actual **implementation** of the now designed connectivity network will likely be the hardest part of the process. This is where investing the time from the beginning to involve and have buy-in from community and professional stakeholders will especially start to pay off. Compared to traditional protected areas (PA), the corridors and stepping stones that may make a connectivity network may not be able to achieve any level of legal protection. Therefore, these networks can become a patchwork of PA designations, other effective area-based conservation measures or area agreements. Therefore, having a coordinated **governance structure** including members of municipal or regional councils (or equivalent governing bodies), local environmental organizations, regional planners, and other environmental decision-makers will assist greatly in slowly building up the protection and regulations of the network to meet project objectives and ensure connectivity into perpetuity (McGuinn et al. 2017, WWF 2020).

During and after the network is established it will be vital to **monitor and evaluate** the effectiveness of the connectivity conservation actions. Monitoring ecological corridors or stepping stones typically involves remote sensing, field sampling, and genetic analysis, combined with different forms of ecological modelling. Remote sensing data can be used to monitor changes in land cover and land use patterns in and around ecological corridors and stepping stones. For instance, it can be used to track the effects of human activities, such as deforestation or urbanisation, on the structural and functional integrity of corridors (e.g., Cisneros-Araujo et al., 2021).

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Field sampling methods such as transect surveys for plants and animal sign (e.g., pellets), camera trapping, and passive acoustic sensors can be used to in conjunction with monitor dynamics of different species. These data in conjunction with abundance, occupancy, and species distribution models allow researchers to more accurately estimate the seasonal or yearly dynamics of population and habitat use. GPS and radio tracking can facilitate targeted studies on wildlife movement, for example, to examine the effectiveness of constructed crossing structures (i.e., green bridges). These methodologies thus allow researchers to evaluate different ecological indicators to determine if corridors are meeting their initial project objectives and targets.

Evaluating the effectiveness of crossing structures of roads or railways is especially prudent given the high cost invested in their construction and the enormous potential benefit, particularly for mammal populations (Soanes et al., 2024). Evaluating the effectiveness of such **mitigation measures** must include the use of benchmarks, which can include the use of control sites and before data (Rytwinski et al., 2015), as well as comparing unmitigated and “no construction” sites (Soanes et al., 2013). The choice of appropriate benchmarks should also consider that control sites should have the same qualities as mitigation sites (e.g., regarding habitat quality or movement paths) to ensure comparability between them (Abbott et al., 2012). If the crossing structures are not being used effectively management actions can be implemented such as increased fencing to better funnel individuals across the structure, changes to the ecosystem planted on the structure, and mitigation of human activity on or near the site.

Genetic analysis involves the use of molecular techniques to study the genetic diversity and gene flow of species across the total landscape. By analysing DNA samples from individuals across different habitat patches, genetic analysis can provide insights into the connectivity and genetic exchange between populations. This approach helps identify potential barriers to gene flow and assess the long-term effectiveness of a connectivity network (e.g., Proctor et al., 2005). I can also assist in the generation of resistance surfaces for future connectivity model iterations.

Integrating the data from remote sensing, field sampling, genetic analysis, and ecological modelling, researchers and conservation practitioners can gain a better understanding of how connectivity and protected area network is operating and its impact on biodiversity conservation. This thus informs the adaptive management of the network allowing for new and likely improved connectivity models.

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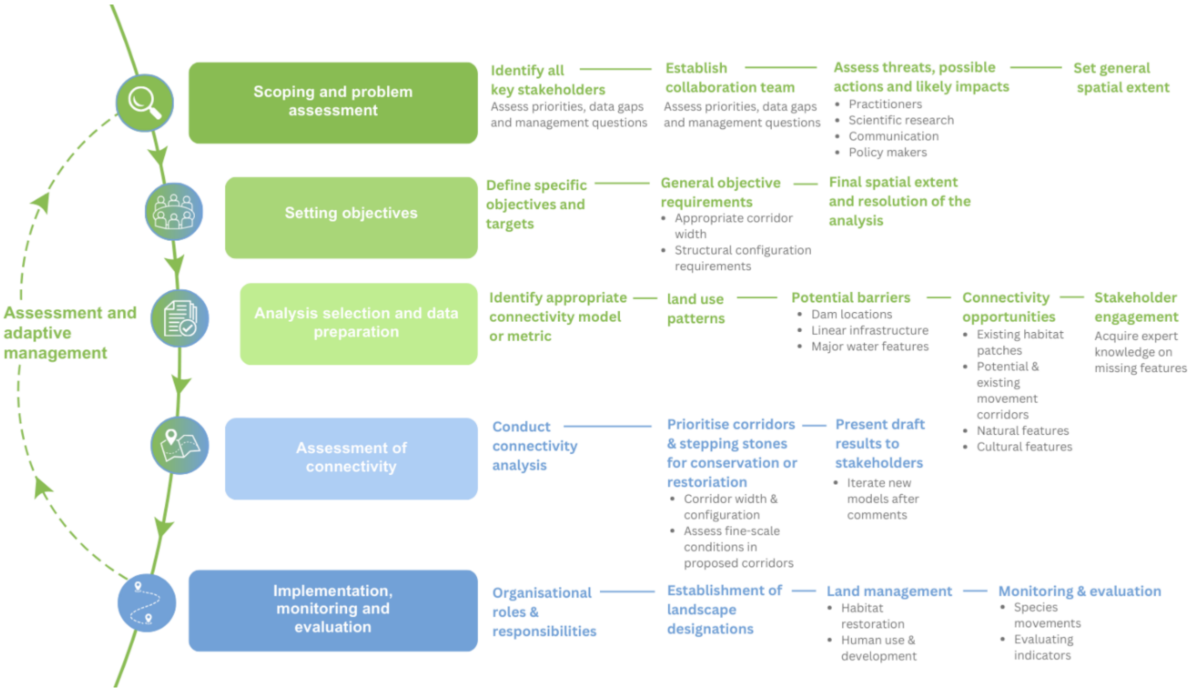

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Annex S1. Survey of connectivity projects

S1.1 Questions

Survey of ecological connectivity projects in Europe

The NaturaConnect project (https://naturaconnect.eu) is an EU-funded Research and Innovation action that develops knowledge, tools, and capacity- building to support the implementation of a coherent network of protected areas across Europe - the Trans-European nature network (TEN-N). The present survey aims to collect information on ecological connectivity projects in Europe undertaken at Regional to National and Pan-European levels. Projects may include public and private conservation action plans and strategies, connectivity conservation and restoration measures, research and innovation projects, etc. The inputs will be used to produce a public repository of connectivity projects that can support knowledge sharing.

Contact: The NaturaConnect Project (naturaconnect@iiasa.ac.at)

* Indicates required question

Section 1: Project information

1. Name of the project *

____

2. Acronym

____

3. Responsible institution(s) *

____

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4. Country or countries of application *

____

5. Name of contact person(s) *

Note: This information will not be public

____

6. E-mail *

Note: This information will not be public

____

7. Other participating institutions

____

8. Project website

____

9. Abstract

____

10. Start and end date (e.g. 2010-2014) *

____

11. Funding sources *

Check all that apply.

- [ ] Nature conservation funds from National and/or Regional Administrations
- [ ] National and/or regional Research & Innovation funds
- [ ] Development funds from National and/or Regional administrations

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☐ LIFE programme

☐ European research & innovation funds (E.g., Horizon, Biodiversa, etc.)

☐ European funds associated to other sustainability policies (e.g., climate, agriculture, Interreg, etc)

☐ Cohesion funds

☐ Biodiversity offsets

☐ Private funds

Other:

12. Name of funding programme(s)

______

Section 2: Project scope and users

13. Connectivity goals. Please select only those categories explicitly addressed in the project. *

Check all that apply.

☐ Protection of one species or a particular group of species

☐ Protection of multiple species (non-species-specific target)

☐ Connectivity between protected areas

☐ Connectivity between specific habitat types (forests, EU directives habitats, etc)

☐ Small landscape features (e.g. hedgerows and tree lines, riparian forest remnants, green urban spaces, etc)

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Other:

14. In case the project is focused on selected taxa, please indicate which.

______

15. Has the project been commissioned by a competent administration (yes/no)? If yes, please specify which. *

______

16. Regardless of who commissioned the project, who are the target users of the results?

Check all that apply.

- [ ] No specific user identified
- [ ] Regional and/or local administration(s)
- [ ] National administration
- [ ] European institutions
- [ ] Private organizations, foundations and/or NGOs
- [ ] Protected area managers

Other:

17. What is the spatial scope of the project? *

Check all that apply.

- [ ] Local (e.g., covering one or several municipalities, or a specific infrastructure)
- [ ] Sub-national (spatially comprehensive for one or several administrative regions)
- [ ] National
- [ ] Transboundary (connecting across 2 or more countries)

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- [ ] Other multiple countries
- [ ] Pan-European

Other:

18. Will the project be used for supporting any of the following policies? *

Check all that apply.

- [ ] Biodiversity conservation policy and strategies
- [ ] Green and Blue Infrastructure
- [ ] Spatial planning of protected areas
- [ ] Restoration plans and/or actions
- [ ] Climate policies
- [ ] Sustainable development
- [ ] Human health

Other:

19. Thematic scope: does the project aims to enhance any of the following? *

Check all that apply.

- [ ] Increase the permeability of linear infrastructures such as roads or railways
- [ ] Ecosystem restoration
- [ ] Ecological corridors (i.e., continuous corridors or stepping stones)

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- [ ] New protected areas and/or expansion of other existing protected areas
- [ ] Adaptation to climate change
- [ ] Urban green spaces

Other:

20. Biogeographical region(s) included

Check all that apply.

- [ ] Alpine
- [ ] Anatolian
- [ ] Arctic
- [ ] Atlantic
- [ ] Black sea
- [ ] Boreal
- [ ] Continental
- [ ] Macaronesia
- [ ] Mediterranean
- [ ] Pannonian
- [ ] Steppic

21. Ecosystem type(s) included *

Check all that apply.

- [ ] Forests

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- [ ] Shrublands
- [ ] Grasslands
- [ ] Wetlands
- [ ] Coastal areas
- [ ] Rivers
- [ ] Agricultural areas
- [ ] Urban and periurban

Other:

Section 3: Technical approaches used in the project

22. Approaches for assessing connectivity *

Check all that apply.

- [ ] Analyses using species movement data (e.g., from tracked individuals)
- [ ] Analyses using genetic data and/or models (e.g., genetic diversity, gene flow, etc.)
- [ ] Analyses using data and/or models for population size and demography
- [ ] Analyses using species distribution models
- [ ] Land cover and land-use analyses
- [ ] Analysis of infrastructures (e.g. roads, railway) and urban sprawl
- [ ] Expert-based

Other:

23. Does the project provide spatially explicit information on: *

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Check all that apply.

- [ ] Locations for ecological corridors
- [ ] Locations for stepping stones
- [ ] Locations to increase permeability of linear infrastructures (e.g., wildlife passes)
- [ ] Locations for habitat restoration
- [ ] Locations for proposed protected areas
- [ ] None

Other:

24. Does (or will) the project monitor the effectiveness of * connectivity conservation for biodiversity or ecosystem services (yes/no)? If yes, please specify which.

25. Does the project consider other benefits in addition to * biodiversity conservation?

Check all that apply.

- [ ] Climate regulation (e.g. carbon sequestration, cooling effect)
- [ ] Water quality
- [ ] Prevention of natural hazards (e.g., fires, floods)
- [ ] Pollination
- [ ] Recreation
- [ ] Soil quality
- [ ] None

Other:

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26. Does the project identify any potential negative impacts of connectivity? *

Check all that apply.

- [ ] Increased human-wildlife conflicts
- [ ] Increased risk of natural hazards (e.g., fires)
- [ ] Increased spread of invasive species
- [ ] Increased risk of spreading diseases
- [ ] Genetic homogenization
- [ ] None

Other:

27. Do you know of any other connectivity projects that we may be interested in? Please add the name of project and contact information.

______

S1.2 Structure

The survey was composed of 27 questions covering project information, scope, users and selected approaches. The survey featured 15 open-ended questions and 12 multiple-choice questions which also included an open-response field for additional options.

S1.3 Distribution and response rates

We began by compiling a comprehensive list of ecological connectivity projects by conducting internet searches, utilizing European project databases such as Network Nature, Biodiversa, and LIFE Public Database, and seeking suggestions from NaturaConnect's consortium members. Our initial list comprised a total of 105 projects. Subsequently, we distributed a survey via email to all contacts on our list, requesting additional suggestions for

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ecological connectivity projects and encouraging recipients to share the survey with colleagues involved in similar projects. To expand our reach, we also leveraged NaturaConnect's social media platforms to promote the survey. This outreach resulted in 57 additional projects being submitted through the survey by entities we had not initially contacted. The response rate, based solely on the projects we had reached out to, was 31.4%.

The survey was conducted using Google Forms (https://forms.gle/7D2kJqU83eHpGYWS9) from May 2023 to January 2024.

S1.4 Response processing

Some answers needed to be processed further to facilitate the subsequent analysis. Several multiple-choice questions provided respondents with an open field where they could add additional information that they felt was not covered by the available options. Three team members reviewed each of these answers and determined if they provided new information not covered by the available options or if it could be reclassified as one of the existing options.

In the case of “Question 25 - Does the project consider other benefits in addition to biodiversity conservation?”, we added some answers to a newly created category called “Other (e.g. Human safety and well-being)”. In “Question 26 - Does the project identify any potential negative impacts of connectivity?”, we added one answer to a new category called “Other (e.g., economic costs). Concerning “Question 14 - In case the project is focused on selected taxa, please indicate which” we reclassified the answers in group categories (e.g., large carnivores, ungulates etc). When we found answers that were out of the scope of the question, we added them to a new category called “Answer out of scope”.

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Annex S2. Connectivity workshop Miro boards examples

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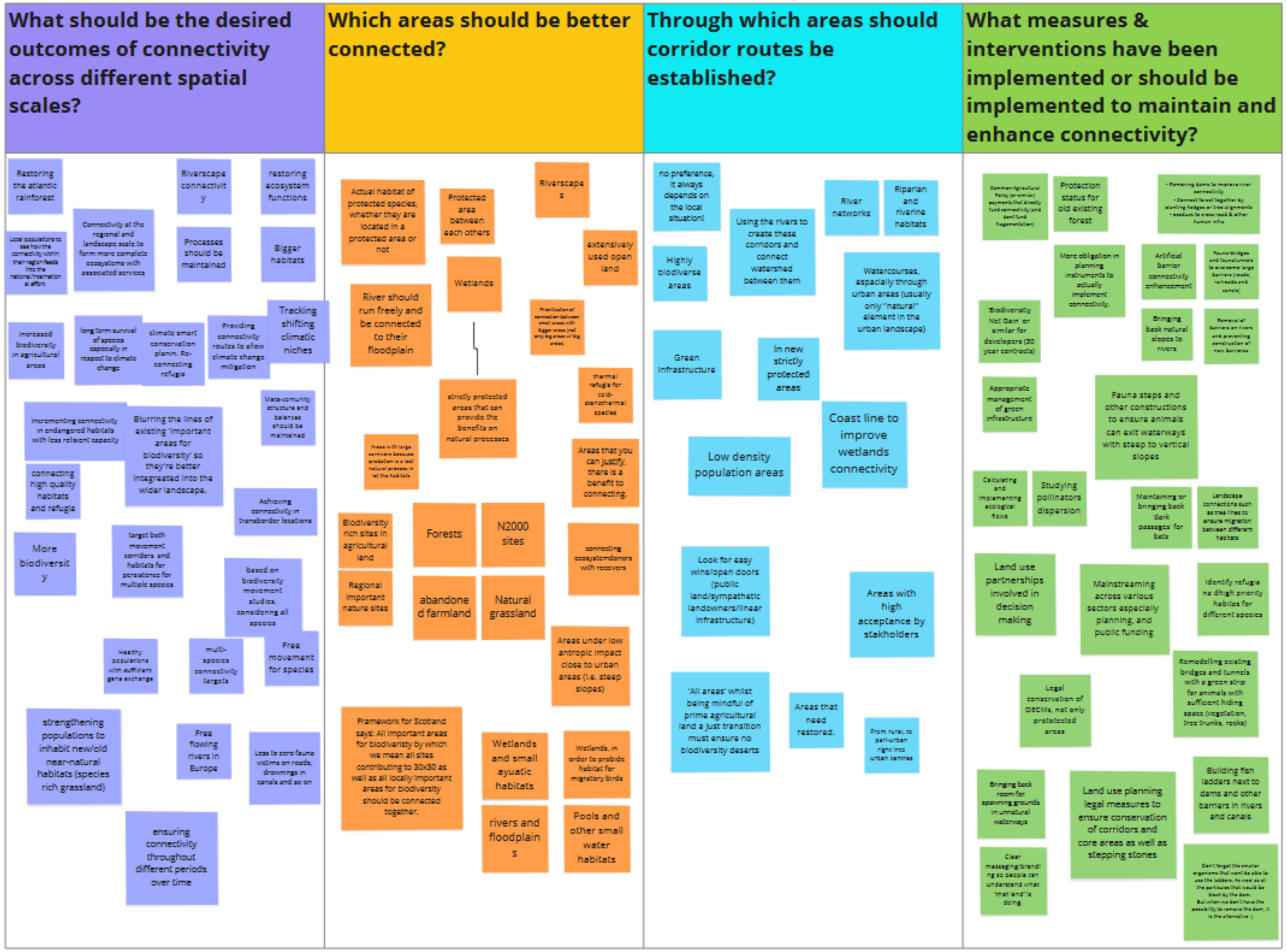

Figure S2.1: Miro board from the "Terrestrial and Freshwater Habitats" breakout group on day 1 of the workshop.

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Figure S2.2: Miro board from the "Ecosystem Processes & Services" breakout group on day 1 of the workshop.

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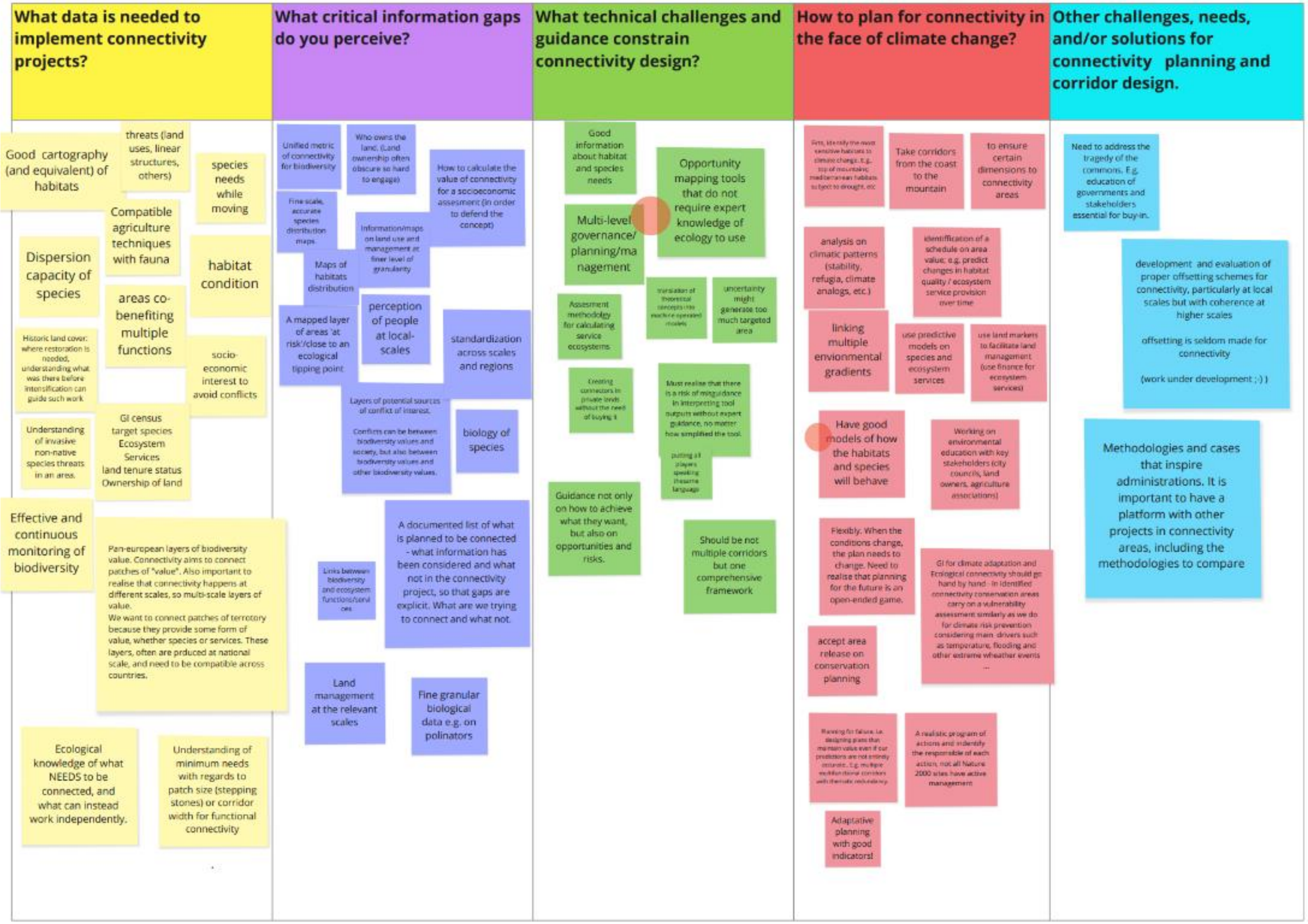

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Figure S2.3: Miro board from the "Planning & Management of Multifunctional Corridors" breakout group 1 on day 2 of the workshop.

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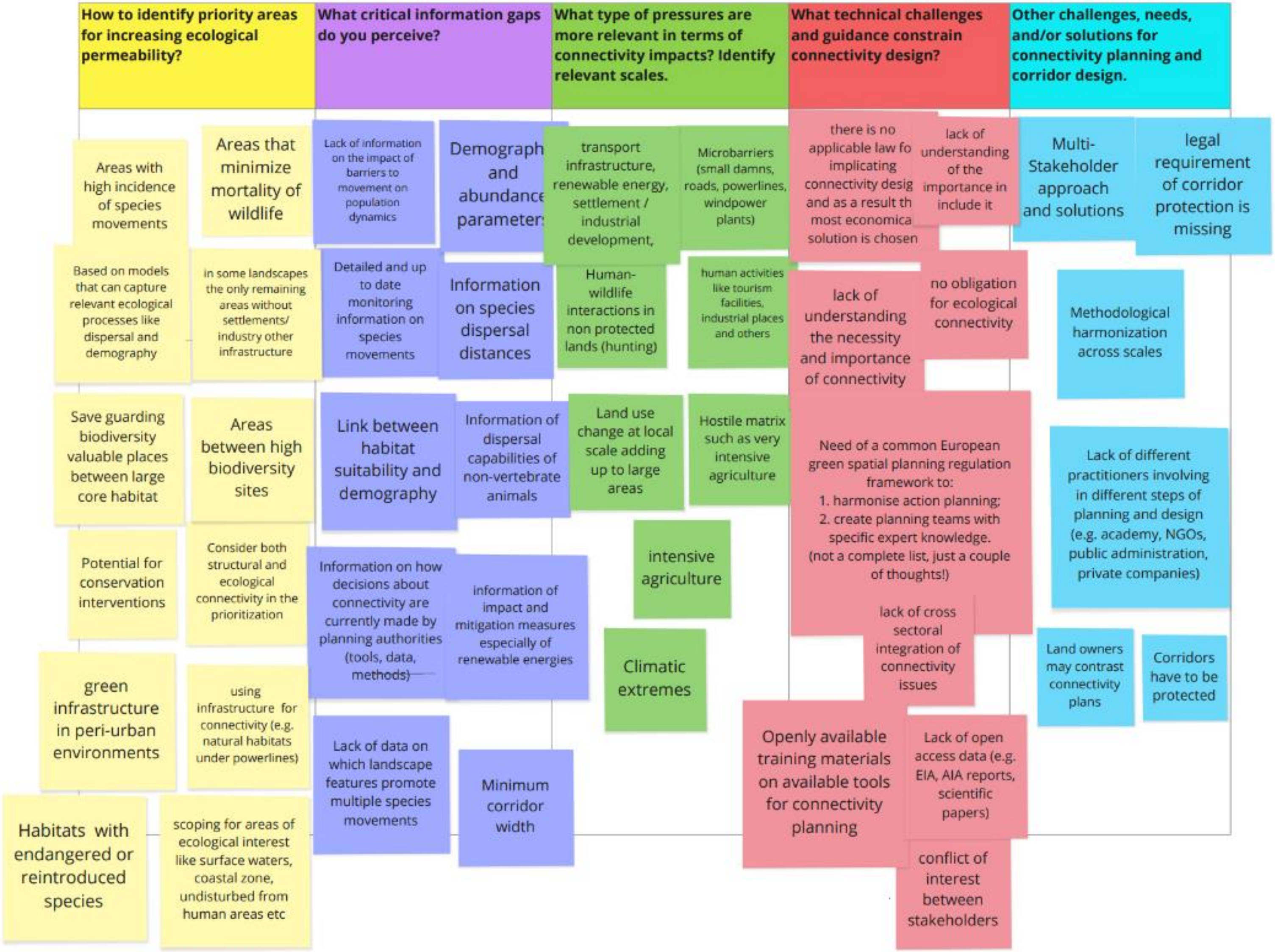

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Figure S2.4: Miro board from the "Human Infrastructure & Land Use Impacts" breakout group on day 2 of the workshop.

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Annex S3. Archetypes

S3.1. Archetypes definition

We considered all European tetrapods (amphibians, reptiles, breeding birds, mammals) naturally occurring in Europe. We followed the taxonomy proposed by GBIF (www.gbif.org). For each species, we gathered trait data directly from online repositories or by using the R package ''*traitdata*'' (Table S3.1) which includes most of the ecological trait datasets currently available. For each class of tetrapods, we considered all the relevant datasets to gather as much data as possible (raw data stored in https://zenodo.org/doi/10.5281/zenodo.10842629).

Given the ecological differences between the different classes of tetrapods, as well as the different availability of traits in existing databases, to identify the different archetypes we conducted separate analyses for functionally homogeneous groups, mostly selected at the level of orders or sub-orders. Among mammals, the order Chiroptera (bats) was considered a priori to be a cluster due to its specialisation for flight, while all other species were analysed together in a single group. For amphibians, we considered frogs (Anura) and salamanders (Caudata) as two separated groups, and for reptiles, we focused our analyses on three groups (turtles, snakes, lizards). No detailed subdivision was applied to birds.

We selected ecological traits related to dispersal capacity and movement dynamics like morphological (e.g., adult body mass, snout to vent length) and life-history traits (e.g., litter or clutch size, maximum longevity) that can be used as proxies for each species' spatial requirements. We also considered traits directly related to dispersal distance and home range size (Santini et al., 2013; Tamburello et al., 2015; Weeks et al., 2022; Alencar and Quental, 2023). As a proxy of species size, we used body mass for non-volant mammals, birds, turtles, and snakes, the snout to vent length for frogs, salamanders, and lizards, while for bats we considered the forearm length. For breeding birds, we considered the beak depth and width as proxy for their trophic ecology. Among reproductive traits, we considered the litter size for all analyzed groups except for bats. While, only for salamanders, we considered the reproductive modalities (viviparous, larval stages, direct development). We used female maturity as a proxy for generation length for all tetrapods except reptiles, and the number of incubation days for turtles and lizards. Finally, we considered the maximum longevity for all mammals, birds, turtles, and snakes. In addition, for amphibians we also used the type of locomotion, while only for lizards we included the type of substrate used by the species (arboreal, terrestrial, saxicolous).

Since dispersal data were not available for most species, we predicted dispersal distances following Weeks et al. (2022) for birds, and Santini et al. (2013) for mammals. Different studies have suggested using migration distances as a proxy for dispersal in birds. However, the link between migration distances and dispersal distances is not clear nor direct. In fact, although migratory species tend to disperse more, this may be related to their high flight efficiency rather than an effect of migratory movements (Claramunt, 2021). Additionally, migrant birds often have strong philopatric tendencies which could reduce or potentially nullify any effect of migratory movements on dispersal distance (Chu and Claramunt, 2023). We also imputed missing data on home range following Tamburello et al. (2015) for both birds and reptiles.

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In amphibians and reptiles, we could not define archetypes considering dispersal distances due to a lack of data. The few estimates available are highly heterogeneous in terms of summary measures provided (median, maximum, or minimum) and the approach used to measure the dispersal distances (GPS, radio tracking, or laboratory experiment). Additionally, while several articles claim to report "dispersal distances", in most cases these are not dispersal movements *sensu strictu*, including migration distances, pond-to-pond movements, daily movements, movements from hibernacula, or other movements not classified. Therefore, the representativeness of the measures provided is undermined by the large variance of this type of data. For instance, the yellow-bellied toad (*Bombina variegata*) showed a mean dispersal distance of 444 m (metres), but the longest dispersal distance is estimated at 3141 m (Cayuela et al., 2019). Similarly, the maximum dispersal distance reported for the common wall lizard (*Podarcis muralis*) is 1000 m (Popescu et al., 2013), albeit Williams et al. (2021), modelling the range expansion of this species, estimated a dispersal distance from 5 to 16 metres. In fact, given the lack of data, there are examples in the literature of modelled dispersal abilities by using a trait-based proxy (e.g., snout to vent length or body size in Alencar and Quental, 2023), however, the reliability of these derived data is undermined by the lack of comparative empirical data. For these reasons, we preferred to not consider unreliable or unrepresentative dispersal estimates in the definition of archetypes of amphibians and reptiles, focusing only on size, locomotion mode, reproductive traits, and home range size when available.

For each analysis group, we conducted a principal component analysis (PCA) in order to reduce the dimensionality of the dataset while preserving most of the initial variance existing in the dataset. Then, we performed a k-means cluster analysis considering the PCA axes that cumulatively explained at least 80% of the variance. K-means clustering is one of the simplest and popular unsupervised machine learning algorithms. The objective of K-means is to group similar data points together and discover underlying patterns. The number of clusters is chosen *a priori* according to the average silhouette method and on expert-based evaluation. With this analysis, we were able, therefore, to identify homogeneous clusters within each group of tetrapods (Tables S3.2-S3.9).

Table S3.1: Trait databases considered for the archetypes analysis.

Database	**Taxonomic coverage**	**Reference**
AmnioteDB	Amphibians, birds, mammals, reptiles	Myhrvold, N. P., Baldridge, E., Chan, B., Sivam, D., Freeman, D. L., & Ernest, S. M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles: Ecological Archives E096-269. Ecology, 96(11), 3109-3109. https://esapubs.org/archive/ecol/E096/269/
Amphibian traits database	Amphibians	Huang, N., Sun, X., Song, Y., Yuan, Z., & Zhou, W. (2023). Amphibian traits database: A global database on morphological traits of amphibians. Global Ecology and Biogeography, 32(5), 633-641.

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AmphiBIO	Amphibians	Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C., & Costa, G. C. (2017). AmphiBIO, a global database for amphibian ecological traits. Scientific data, 4(1), 1-7.
AnAge	Amphibians, birds, mammals, reptiles	De Magalhaes, J. P., & Costa, A. J. (2009). A database of vertebrate longevity records and their relation to other life-history traits. Journal of evolutionary biology, 22(8), 1770-1774. http://genomics.senescence.info/species/
AvianBodySize	Birds	Lislevand, T., Figuerola, J., & Székely, T. (2007). Avian body sizes in relation to fecundity, mating system, display behaviour, and resource sharing: Ecological archives E088-096. Ecology, 88(6), 1605-1605.
AVONET	Birds	Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J., Yang, J., Sayol, F., ... & Schleuning, M. (2022). AVONET: morphological, ecological and geographical data for all birds. Ecology Letters, 25(3), 581-597.
Bird_behav	Birds	Tobias, J. A., & Pigot, A. L. (2019). Integrating behaviour and ecology into global biodiversity conservation strategies. Philosophical Transactions of the Royal Society B, 374(1781), 20190012.
COMBINE	Mammals	Soria, C. D., Pacifici, M., Di Marco, M., Stephen, S. M., & Rondinini, C. (2021). COMBINE: a coalesced mammal database of intrinsic and extrinsic traits.
EAmphDB	Amphibians	Trochet, A., Moulherat, S., Calvez, O., Stevens, V. M., Clobert, J., & Schmeller, D. S. (2014). A database of life-history traits of European amphibians. Biodiversity Data Journal, (2).
EltonTraits	Mammals, birds	Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological Archives E095-178. Ecology, 95(7), 2027-2027.
Eubirds	Birds	Storchová, L., & Hořák, D. (2018). Life-history characteristics of European birds. Global Ecology and Biogeography, 27(4), 400-406.
EuroBaTrait	Bats	Froidevaux, J. S., Toshkova, N., Barbaro, L., Benítez-López, A., Kerbiriou, C., Le Viol, I., ... & Razgour, O. (2023). A species-level trait dataset of bats in Europe and beyond. Scientific data, 10(1), 253.
HomeRange	Mammals	Broekman, M. J. E., Hoeks, S., Freriks, R., Langendoen, M. M., Runge, K. M., Savenco, E., ... & Tucker, M. A. (2023). HomeRange: A global database of mammalian home ranges. Global Ecology and Biogeography, 32(2), 198-205. https://github.com/SHoeks/HomeRange

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LHT_ERep	Reptiles	Grimm, A., Ramírez, A. M. P., Moulherat, S., Reynaud, J., & Henle, K. (2014). Life-history trait database of European reptile species. Nature Conservation, 9, 45-67.
LizardTraits	Reptiles	Meiri, S. (2018). Traits of lizards of the world: Variation around a successful evolutionary design. Global ecology and biogeography, 27(10), 1168-1172.
MammalDiet	Mammals	Kissling, W. D., Dalby, L., Fløjgaard, C., Lenoir, J., Sandel, B., Sandom, C., ... & Svenning, J. C. (2014). Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. Ecology and Evolution, 4(14), 2913-2930.
panTHERIA	Mammals	Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... & Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecological Archives E090-184. Ecology, 90(9), 2648-2648. https://tinyurl.com/5czp2t33
TetraDENSITY	Amphibians, birds, mammals, reptiles	Santini, L., Isaac, N. J., & Ficetola, G. F. (2018). TetraDENSITY: A database of population density estimates in terrestrial vertebrates. Global Ecology and Biogeography, 27(7), 787-791.

Table S3.2: Median values of traits used to define the five European non-volant mammals archetypes.

	1	2	3	4	5
Body mass (g)	170875.0	35383.2	7518.3	234.5	23.4
Maximum longevity (d)	9909.8	8030	7300.0	4015.0	1761.1
Female maturity (d)	883.8	548	429.6	305.2	51.4
Litter size (n)	1.9	1.4	3.7	4.4	5.2
Dispersal (km)	45.8	6.5	11.6	0.8	0.1
Home Range (km^2)	289.1	2.1	8.0	0.1	<0.001

Table S3.3: Median values of traits used to define the three European bats archetypes.

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	1	**2**	**3**
Maximum longevity (y)	29	26	21
Female maturity (d)	456	502	730
Forearm Length (cm)	37.6	40.4	47.7
Home Range (km^2)	2.61	54.4	33
Dispersal (km)	0.68	50	1.46

Table S3.4: Median values of traits used to define the four European birds archetypes.

	1	**2**	**3**	**4**
Maximum longevity (y)	45.0	22.9	16.2	13.1
Female maturity (d)	1277.9	726.9	545.2	364.2
Beak Width (mm)	18.2	12.9	4.3	4.7
Beak Depth (mm)	27.9	14.3	5.7	6.1
Kipps Distance (mm)	205.7	122.6	83.2	28.7
Body mass (g)	3846.9	866.0	132.5	36.0
Age of first breeding (y)	3	2	2	1
Long distance migrant	0	0	1	0
Dispersal (km)	26.5	23.0	38.7	15.1
Home range (km^2)	147.7	12.8	0.9	0.1

Table S3.5: Median values of traits used to define the three European frogs archetypes.

	1	**2**	**3**

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Snout to vent length (mm)	69.1	44.7	41
Sexual maturity (y)	3	1.5	1
Number of eggs/clutch	4000	350	1400
Walker	0	1	0
Jumper	1	1	1
Climber	0	0	1
Swimmer	1	1	0

Table S3.6: Median values of traits used to define the three European salamanders archetypes.

	1	**2**	**3**
Snout to vent length (mm)	102.3	63.3	54.6
Sexual maturity (y)	3	2.9	3.5
Number of eggs/clutch	28	250	10
Walker	1	1	0
Climber	0	0	1
Swimmer	0	1	0
Direct development	0	0	1
Larval stages	0	1	0
Viviparous	1	0	0

Table S3.7: Median values of traits used to define the two European turtles archetypes.

	1	**2**

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Body mass (g)	1430	469.1
Incubation (d)	78	91.8
Clutch size (n)	5	9
Maximum longevity (y)	127	72.3
Home range (km^2)	0.2	0.04

Table S3.8: Median values of traits used to define the three European snakes archetypes.

	1	**2**	**3**
Body mass (g)	2209.5	196	104
Clutch size (n)	8	10	4
Maximum longevity (y)	5.8	19	5.9
Home range (km^2)	1.2	0.06	0.03

Table S3.9: Median values of traits used to define the three European lizards archetypes.

	1	**2**	**3**
Snout to vent length (cm)	14.5	6.3	6.05
Incubation period (d)	61.8	47	48
Clutch size (n)	8.9	3.5	3.7
Arboreal	0	0	0
Terrestrial	1	0	1
Saxicolous	0	1	0

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S3.2. Habitat preferences

Understanding habitat composition is crucial for connectivity and spatial conservation planning. Therefore, we used the habitat preferences of European tetrapods to relate archetypes to a specific environmental context. Following the IUCN habitat classification scheme (Version 3.1), we identified several natural and artificial habitat types in Europe: Forest, Savanna, Shrublands, Grasslands, Wetlands, Rocky areas, Desert, and Artificial. For "Artificial", given the importance of anthropogenic factors especially upon habitat fragmentation and connectivity, we further followed the second level of IUCN classification distinguishing different artificial habitat types: Pastureland, Arable Land, Plantations, Rural Garden, and Urban Areas. In our final classification, we reduced the possible number of habitat types merging the classes Grassland, Savanna, Pastureland, Desert, and Rocky Areas in "Open natural"; while Rural Garden was associated with "Plantations" habitat class (Fig. S3.1). We maintained the original classification for Wetlands, Arable land, Shrublands, Urban areas, and we defined Forest as "Close Natural".

For each group of tetrapods, we strived to find a generalised habitat type representing most of the species included. However, from our analyses, we found that most species had species-specific habitat requirements with idiosyncratic combinations of habitats that cannot be generalised without losing most of the variance (Fig. S3.2). Therefore, we were forced to reclassify European habitats in two very broad classes: Natural and Artificial. We included in "Natural" habitats the following classes: Close Natural, Shrublands, Wetlands, Open Natural, and Pastureland; while Arable land, Plantations, and Urban areas were included into "Artificial" habitats (Fig. S3.1).

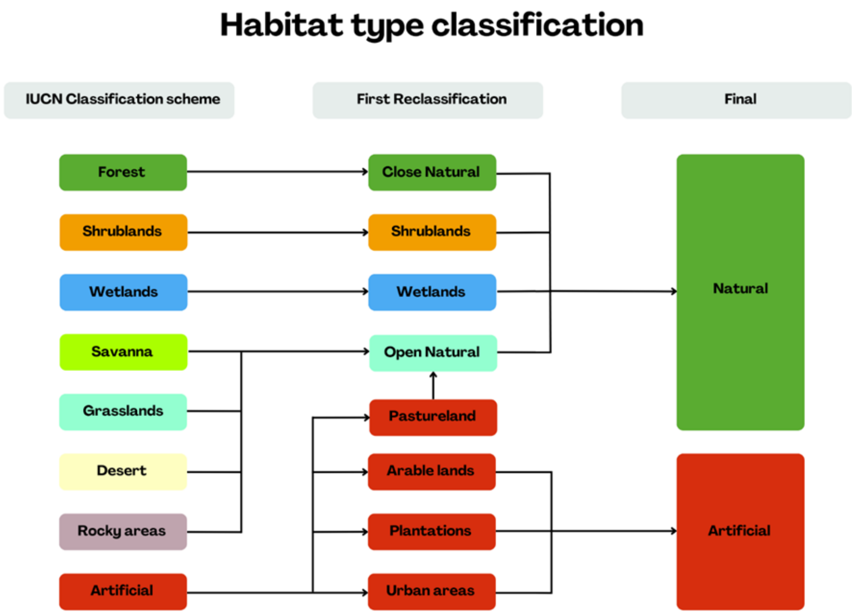

Figure S3.1: Aggregation of IUCN habitat classes (level 1) into natural and artificial classes.

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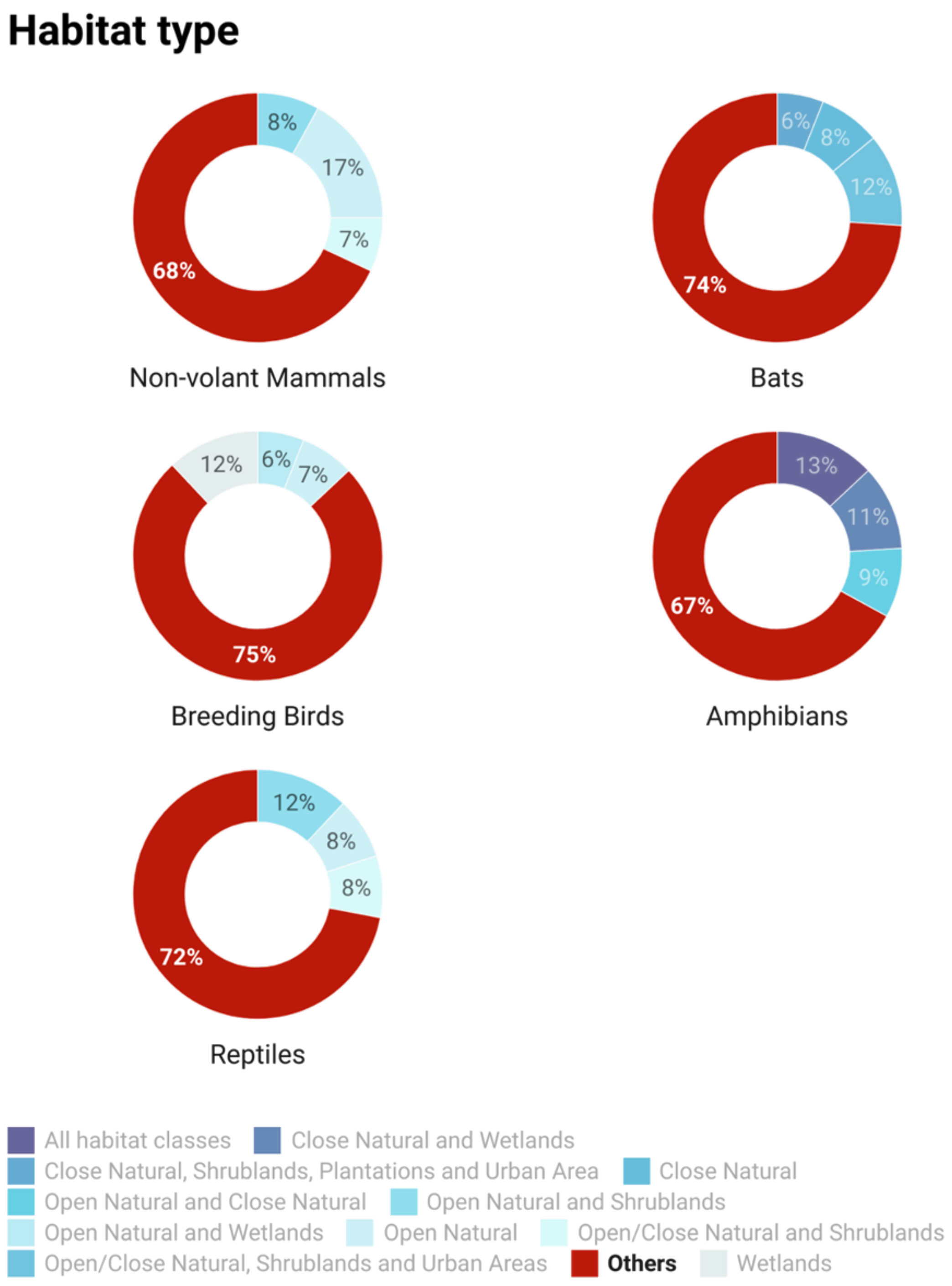

Figure S3.2: Habitat preferences of European tetrapods.

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Annex S4: Geospatial Data Sources for Europe

Sector	Data Source Name	Author	Authoring organization	Data location
Land use & Land cover	CORINE Land Cover	Copernicus	Copernicus-European Environment Agency	https://land.copernicus.eu/en/products/corine-land-cover
	High Resolution Layer Water and Wetness	Copernicus	Copernicus-European Environment Agency	https://land.copernicus.eu/en/products/high-resolution-layer-water-and-wetness
	Global Tree Cover 2010	Hansen, M.C. et al.	Global Forest Watch	https://glad.umd.edu/dataset/global-2010-tree-cover-30-m
	Forest management map for Europe	Oostdijk, Saskia et al.	Vrije Universiteit Amsterdam	https://dataverse.nl/dataset.xhtml?persistentId=doi:10.34894/HQIJN5
	Primary forest	Sabatini et al.	Nature	https://www.nature.com/articles/s41597-021-00988-7#Sec7
Roads & Linear Features	Open Street Map	Open Street Map	Open Street Map	https://www.openstreetmap.org
	EU Hydro Rivernet	Copernicus	Copernicus-European Environment Agency	https://land.copernicus.eu/en/products/eu-hydro/eu-hydro-river-network-database
Evalutation & Topography	European Digital Elevation Model (EU-DEM)	EEA	European Environment Agency	https://www.eea.europa.eu/en/datahub/datahubitem-view/d08852bc-7b5f-4835-a776-08362e2fbf4b?activeAccordion=735550
	Copernicus Global DEM	ESA	European Space Agency	https://spacedata.copernicus.eu/collections/copernicus-digital-elevation-model
Boundaries & Bioregions	Biogeographical regions 2016	EEA	European Environment Agency	https://www.eea.europa.eu/data-and-maps/figures/biogeographical-regions-in-europe-2
	EEA Administrative Boundaries based on GISCO NUTS and EBM	EEA	European Environment Agency	https://sdi.eea.europa.eu/catalogue/srv/eng/catalog.search#/metadata/94438969-2dd5-4ba3-b708-e4d29a8b7699

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Species Data	Global Biodiversity Information Facility (GBIF)	GBIF	GBIF	https://www.gbif.org/
Protected Areas	European network of protected sites Natura 2000	EEA	European Environment Agency	https://www.eea.europa.eu/en/datahub/datahubitem-view/6fc8ad2d-195d-40f4-bdec-576e7d1268e4
	Nationally designated areas (CDDA)	EEA	European Environment Agency	https://www.eea.europa.eu/en/datahub/datahubitem-view/f60cec02-6494-4d08-b12d-17a37012cb28

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More information about the project:

NaturaConnect has 22 partner institutions: International Institute for Applied System Analysis (project lead; Austria); German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (project co-lead; Germany); Associação Biopolis (Portugal); BirdLife Europe (Netherlands); Birdlife International (United Kingdom); Centre National De La Recherche Scientifique (France); Doñana Research Station - Agencia Estatal Consejo Superior De Investigaciones Cientificas (Spain); Europarc Federation (Germany); Finnish Environment Institute (Finland); Humboldt-University of Berlin (Germany); Institute for European Environmental Policy (Belgium); Netherlands Environmental Assessment Agency (Netherlands); Rewilding Europe (Netherlands); University of Evora (Portugal); University of Helsinki (Finland); University of Natural Resources and Life Sciences, Vienna (Austria); University of Rome La Sapienza (Italy); University of Warsaw (Poland); Vrie University of Amsterdam (Netherlands); WWF Central and Eastern Europe (Austria); WWF Romania and WWF Hungary.

NaturaConnect aims to design and develop a blueprint for a truly coherent **Trans-European Nature Network** (TEN-N) of conserved areas that protect at least 30% of land in the European Union, with at least one third of it under strict protection. Our project unites universities and research institutes, government bodies and non-governmental organizations, working together with key stakeholders to create targeted knowledge and tools, and build the capacity needed to support European Union Member States in realizing an ecologically representative, resilient and well-connected network of conserved areas across Europe.

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