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Spatial and temporal trends in the distribution of Western Palearctic target vertebrates in the context of Global Change: conservation and management at landscape scales

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Riassunto

La biodiversità globale è in declino, un fenomeno diffuso e generalizzato dovuto a cause molteplici e sinergiche. A livello globale, e in particolare in Europa, i principali fattori responsabili sono i cambiamenti climatici, il riscaldamento globale e le alterazioni nell'uso del suolo legate all'attività umana. A questi si aggiungono altri elementi concomitanti, come la diffusione di specie aliene, lo sfruttamento diretto delle risorse naturali e l'inquinamento.

Gran parte di queste pressioni sono strettamente connesse alle attività antropiche, il cui impatto è cresciuto significativamente dal 1970, spinto dall'aumento della popolazione umana e delle sue esigenze. Il benessere dell'uomo dipende dai sistemi ecologici e dai benefici che questi forniscono. Sebbene la natura stia attualmente sostenendo livelli senza precedenti di sfruttamento delle risorse, ciò è avvenuto a un costo molto elevato: il deterioramento degli ecosistemi, la perdita di integrità nelle comunità ecologiche locali e il declino nella ricchezza e nell'abbondanza delle specie selvatiche. Questi cambiamenti compromettono i benefici essenziali che la natura offre all'uomo e minacciano la qualità della vita delle generazioni future. La perdita di biodiversità non è soltanto una questione ecologica, ma rappresenta una minaccia diretta per l'umanità. Gli impatti di questa perdita sulla produttività primaria, ad esempio, sono comparabili a quelli causati da siccità, radiazioni ultraviolette, riscaldamento climatico, acidificazione e altre forme di inquinamento. Questo implica che il declino della biodiversità influenzerà la nostra vita in modo profondo, proprio come sta già accadendo per le altre specie con cui condividiamo il pianeta.

Quantificare con precisione l'entità di questo declino è complesso. La Lista Rossa dell'IUCN, che ha valutato circa 166.000 specie, stima che oltre 46.300 siano a rischio di estinzione, pari al 28% delle specie esaminate. Il rischio varia notevolmente tra i diversi gruppi tassonomici: il 41% degli anfibi, il 27% dei mammiferi e il 21% dei rettili risultano minacciati. Altre stime, basate su modelli predittivi e analisi della distribuzione, indicano una gamma di rischi che varia dallo 0 al 54%. Studi di metanalisi suggeriscono inoltre che il 7,9% delle specie potrebbe estinguersi esclusivamente a causa dei cambiamenti climatici. Oltre alle estinzioni globali, un fenomeno altrettanto preoccupante è rappresentato dalle estinzioni locali, in cui una popolazione di una specie scompare da una determinata area. Questo tipo di estinzione è già ampiamente diffuso e rappresenta uno degli effetti più gravi del cambiamento climatico. Le specie possono reagire a queste trasformazioni migrando, modificando il proprio areale o adattandosi a nuove condizioni, ma quando questi processi falliscono o le popolazioni sono vincolate, l'estinzione locale diventa inevitabile. Per mitigare questo rischio, è cruciale mantenere corridoi ecologici che favoriscano il movimento nell'ambito delle specie e supportino le dinamiche di metapopolazione. La connettività ecologica è ormai un tema centrale nella biologia della conservazione, come dimostrato dallo sviluppo di numerose metriche e algoritmi per quantificarla, sia dal punto di vista strutturale che funzionale. Questo è particolarmente rilevante in Europa, dove la frammentazione degli habitat è accelerata dai forti cambiamenti nell'uso del suolo e dall'elevata densità antropica.

Nel contesto di questa tesi, sono state affrontate tutte queste tematiche, con l'obiettivo di comprendere meglio le risposte di alcune specie ai cambiamenti globali in Europa, in

particolare per quanto riguarda la loro distribuzione spaziale e temporale, al fine di informare e supportare le misure di conservazione che possono essere utilizzate per migliorare lo stato della biodiversità in Europa.

Lo studio ha coinvolto diverse specie, con un focus particolare sui mammiferi. Questa scelta è motivata dalla loro maggiore vagilità, ma anche dai recenti successi legati agli sforzi di conservazione, protezione legale e programmi di reintroduzione. Tra i casi più rilevanti spicca il castoro eurasiatico (*Castor fiber*), la cui consistenza era stata ridotta in passato a soli 1.200 individui, distribuiti in otto popolazioni distinte. Grazie alla protezione legale e a estesi programmi di reintroduzione, il castoro ha riconquistato gran parte del suo areale storico e attualmente conta circa 1.500.000 di individui, rappresentando uno dei più significativi successi di recupero tra i vertebrati europei. Un altro esempio emblematico è la lince eurasiatica (*Lynx lynx*), che è riuscita a evitare l'estinzione nonostante la caccia abbia portato molte popolazioni alla scomparsa. Negli anni successivi, la specie è sopravvissuta esclusivamente in poche aree, come i Carpazi, i Balcani e la Scandinavia. A partire dagli anni Settanta, numerosi programmi di reintroduzione hanno permesso la ricostituzione di popolazioni in diversi paesi europei. Tuttavia, molte di queste restano isolate, caratterizzate da un numero esiguo di individui, una bassa variabilità genetica e alti livelli di inbreeding. Questi fattori rendono ancora oggi alcune popolazioni vulnerabili al rischio di estinzione. In Italia, entrambe le specie sono recentemente tornate, seppur attraverso processi molto differenti. Inoltre, il territorio italiano ha visto l'arrivo di un'altra specie, lo sciacallo dorato (*Canis aureus*), la cui espansione è stata favorita da una combinazione di fattori. Partendo da una distribuzione limitata all'Europa orientale, questa specie ha gradualmente colonizzato quasi tutto il continente, con segnalazioni di individui anche in Spagna e Finlandia.

Nella prima parte della tesi vengono descritti i metodi di indagine impiegati, includendo modelli di distribuzione delle specie (SDMs), analisi della connettività ecologica e modelli basati sugli individui (IBMs). Il primo capitolo presenta due casi di studio che evidenziano il potenziale degli SDMs nel fornire informazioni chiave sulle dinamiche spazio-temporali delle specie target. Questi risultati hanno implicazioni significative per la conservazione e per la comprensione delle possibili interazioni tra specie.

Il primo caso di studio riguarda il castoro eurasiatico (*Castor fiber*), una specie protetta inclusa nell'Allegato II della Direttiva Habitat (92/43 CEE). Attraverso gli SDMs, è stato possibile produrre predizioni sui cambiamenti di areale futuri considerando l'effetto combinato del cambiamento climatico in ambienti terrestri e acquatici. I modelli hanno incluso anche l'analisi di possibili variazioni nella portata fluviale in Europa. Inoltre, i risultati hanno fornito le prime proiezioni di idoneità ambientale a livello di fiume e bacino idrografico, dimostrando la loro utilità per la pianificazione di progetti di reintroduzione.

Il secondo caso di studio ha visto l'applicazione degli SDMs a due specie, la lince eurasiatica (*Lynx lynx*) e lo sciacallo dorato (*Canis aureus*), per analizzare le aree di potenziale simpatria. Le predizioni spaziali sono state binarizzate per identificare le zone di interazione, tenendo conto di osservazioni recenti di cleptoparassitismo tra le due specie in Slovenia. È stata inoltre considerata la presenza del lupo grigio (*Canis lupus*), per il quale è stato sviluppato un ulteriore SDM. I risultati indicano che, in futuro, si prevede un incremento della sovrapposizione tra gli areali delle specie, soprattutto a causa dell'espansione dello sciacallo dorato, la cui distribuzione è prevista in ulteriore crescita in tutta Europa.

La seconda parte della tesi è dedicata al concetto di connettività ecologica e presenta due casi di studio, focalizzati rispettivamente sul castoro eurasiatico, e sulla lince eurasiatica. Nel primo caso di studio, è stata analizzata la connettività strutturale e funzionale nelle penisole iberica e italiana, due regioni in cui il castoro sta espandendo il proprio areale, anche a seguito di reintroduzioni non autorizzate. I risultati hanno evidenziato diversi corridoi ecologici che potrebbero facilitare l'ulteriore espansione della specie in entrambe le aree di studio. Tuttavia, i modelli suggeriscono una bassa connettività tra i siti colonizzati naturalmente e quelli occupati in seguito a reintroduzioni illegali, confermando le limitazioni di una ricolonizzazione spontanea. L'analisi della connettività strutturale ha inoltre valutato l'impatto delle dighe, evidenziando come queste frammentino la rete fluviale. Le dighe con il maggior potenziale di frammentazione sono state identificate come prioritarie per interventi di conservazione.

Il secondo caso di studio ha riguardato la prima analisi su scala europea della connettività funzionale per la lince eurasiatica. I risultati mostrano una buona connettività ecologica nell'Europa settentrionale, dalla Scandinavia ai Paesi Baltici, mentre in altre aree, come l'Europa occidentale e centrale, la connettività risulta più limitata. Da un punto di vista conservazionistico, l'attenzione si è concentrata sulle popolazioni presenti in queste ultime regioni, per le quali sono stati individuati diversi corridoi ecologici. Tuttavia, questi corridoi risultano spesso scarsamente protetti. L'espansione della rete di aree protette potrebbe contribuire significativamente a garantire una maggiore tutela di tali corridoi, migliorando le possibilità di dispersione e la persistenza delle popolazioni in queste aree critiche.

La terza parte della tesi presenta due distinti casi di studio. Il primo caso di studio integra modelli di distribuzione delle specie (SDMs), analisi della connettività ecologica e modelli basati sugli individui (IBMs) all'interno di un unico framework progettato per supportare progetti di reintroduzione. Come esempio applicativo, è stata scelta la reintroduzione della lince eurasiatica negli Appennini. Il framework segue un approccio lineare: inizialmente viene valutata la compatibilità ecologica tra la potenziale popolazione sorgente e l'area target attraverso una comparazione delle nicchie ecologiche. Successivamente, vengono identificati i siti chiave integrando i dati di idoneità ambientale con quelli di connettività ecologica. Infine, sono stati simulati diversi scenari di reintroduzione tramite IBMs, ottenendo previsioni relative a parametri cruciali quali l'abbondanza della popolazione, i tempi di colonizzazione e la probabilità di presenza nelle aree idonee.

Il secondo caso di studio riguarda un'analisi della connettività ecologica a livello europeo, utilizzando un approccio multispecie specifico per i mammiferi. Il modello è stato costruito considerando l'impatto umano e includendo la diversa sensibilità delle specie a questo fattore. Sono stati inoltre integrati il costo energetico del movimento e la produttività primaria. L'analisi ha considerato quattro diverse distanze di dispersione, calcolando la connettività omnidirezionale tramite una finestra mobile. I risultati delle diverse specie sono stati mediati e validati utilizzando dati di telemetria raccolti per più specie in diverse regioni europee.

Le predizioni di connettività cumulativa indicano una maggiore connettività ecologica in aree con un impatto umano ridotto, come la Scandinavia e le principali catene montuose europee. Tuttavia, le mappe di connettività normalizzata evidenziano la presenza di corridoi anche in aree urbanizzate. I dati di telemetria hanno confermato che, nella maggior parte dei casi, le specie si spostano in aree con valori di connettività più elevati rispetto ai modelli nulli. Sebbene i valori di connettività siano generalmente più alti all'interno delle aree protette, queste ultime coprono solo una piccola porzione delle aree con valori di connettività normalizzata più elevata nella maggior parte dei paesi europei. Questi risultati possono supportare l'espansione della

rete di aree protette, come previsto dal Target 3 della Strategia Europea per la Biodiversità, che punta a proteggere il 30% della superficie terrestre, identificando aree prioritarie per la connettività ecologica.

I risultati complessivi della tesi confermano gli effetti del cambiamento globale sulle dinamiche spazio-temporali delle specie in Europa, documentando i potenziali cambiamenti di areale di alcune specie di rilevanza conservazionistica ed ecosistemica. Inoltre, evidenziano come gli SDMs e le tecniche di connettività ecologica possano supportare azioni di conservazione, sia per rispondere a necessità specifiche di singole specie, sia per affrontare questioni più ampie legate alla gestione e alla creazione di nuove aree protette, in linea con gli obiettivi della Strategia Europea per la Biodiversità 2030. I framework sviluppati rappresentano un utile strumento per pianificare strategie di conservazione e gestione a lungo termine della biodiversità, specialmente nel contesto degli attuali cambiamenti climatici.

Summary

Global biodiversity is in decline, a widespread and pervasive phenomenon driven by multiple, synergistic causes. On the global scale, and particularly in Europe, the primary drivers include climate change, global warming, and land-use alterations associated with human activities. These pressures are compounded by other factors such as the spread of invasive species, direct exploitation of natural resources, and pollution.

Most of these pressures are closely linked to human activities, whose impact has significantly increased since 1970 due to population growth and rising demands. Human well-being depends on ecological systems and the benefits they provide. Although nature is currently sustaining unprecedented levels of resource exploitation, this comes at a high cost: ecosystem degradation, loss of integrity in local ecological communities, and declines in the richness and abundance of wildlife. These changes undermine the essential benefits nature provides to humans and threaten the quality of life for future generations. Biodiversity loss is not merely an ecological issue but represents a direct threat to humanity. For instance, the impacts of biodiversity loss on primary productivity are comparable to those caused by droughts, ultraviolet radiation, climate warming, acidification, and other forms of pollution. This underscores that the decline of biodiversity will profoundly affect our lives, as it already does for other species with which we share the planet.

Precisely quantifying the extent of this decline is complex. According to the IUCN Red List, which has assessed around 166,000 species, over 46,300 are at risk of extinction, representing 28% of the evaluated species. The risk varies significantly across taxonomic groups: 41% of amphibians, 27% of mammals, and 21% of reptiles are threatened. Other estimates, based on predictive models and distribution analyses, indicate a range of risks from 0 to 54%. Meta-analyses further suggest that 7.9% of species could face extinction due solely to climate change. Beyond global extinctions, global change is driving an equally concerning phenomenon: local extinctions, where populations of a species disappear from specific areas. This phenomenon is already widespread and represents one of the most severe consequences of global change. Species can respond to these transformations by migrating, shifting their ranges, or adapting to new conditions. However, when these processes fail or populations are constrained, local extinction becomes inevitable. To mitigate this risk, it is crucial to maintain ecological corridors that facilitate species movement and support metapopulation dynamics. Ecological connectivity has become a central theme in conservation biology, as evidenced by the development of numerous metrics and algorithms to quantify it from both structural and functional perspectives. This is particularly relevant in Europe, where habitat fragmentation is exacerbated by rapid land-use changes and high human density.

In the context of this thesis, all these topics were addressed with the aim of better understanding how certain species respond to global changes in Europe, particularly concerning their spatial and temporal distribution. The ultimate goal is to inform and support conservation measures that can improve the state of biodiversity in Europe.

The thesis focused on various species, with a particular emphasis on mammals. This choice was motivated by their greater mobility and by recent successes tied to conservation efforts, legal protections, and reintroduction programs. Among the most notable cases is the Eurasian beaver (*Castor fiber*), whose population was once reduced to just 1,200 individuals distributed across eight distinct populations. Thanks to legal protection and extensive reintroduction

programs, the beaver has regained much of its historical range and now numbers approximately 1.5 million individuals, making it one of the most significant recovery successes among European vertebrates.

Another emblematic example is the Eurasian lynx (*Lynx lynx*), which narrowly avoided extinction despite widespread hunting that led to the disappearance of many populations. In subsequent years, the species survived in only a few areas, such as the Carpathians, the Balkans, and Scandinavia. Since the 1970s, numerous reintroduction programs have helped restore populations in several European countries. However, many of these populations remain isolated, characterized by small numbers of individuals, low genetic diversity, and high levels of inbreeding. These factors still leave some populations vulnerable to extinction.

In Italy, both species have recently returned through markedly different processes. Additionally, the Italian territory has witnessed the arrival of another species, the golden jackal (*Canis aureus*), whose expansion has been facilitated by a combination of factors. Initially limited to Eastern Europe, this species has gradually colonized much of the continent, with reports of individuals even reaching Spain and Finland.

The first part of the thesis describes the methods employed, including species distribution models (SDMs), ecological connectivity analyses, and individual-based models (IBMs). The first chapter presents two case studies that demonstrate the potential of SDMs to provide key insights into the spatial and temporal dynamics of target species. These findings have significant implications for conservation and for understanding potential interactions between species.

The first case study focuses on the Eurasian beaver (*Castor fiber*), a protected species listed in Annex II of the Habitats Directive (92/43/EEC). Using SDMs, predictions of future range shifts were generated, considering the combined effects of climate change on terrestrial and aquatic environments. The models also incorporated analyses of potential variations in river discharge across Europe. Additionally, the results provided the first projections of environmental suitability at the river and watershed scale, underscoring their utility for planning reintroduction projects.

The second case study applied SDMs to two species, the Eurasian lynx (*Lynx lynx*) and the golden jackal (*Canis aureus*), to analyze areas of potential sympatry. Spatial predictions were binarized to identify zones of interaction, considering recent observations of kleptoparasitism between the two species in Slovenia. The presence of the grey wolf (*Canis lupus*) was also considered, for which an additional SDM was developed. The results suggest that in the future, overlap between the species' ranges is expected to increase, primarily due to the expansion of the golden jackal, whose distribution is predicted to grow further across Europe.

The second part of the thesis is dedicated to the concept of ecological connectivity and presents two case studies, focusing on the Eurasian beaver and the Eurasian lynx, respectively. In the first case study, structural and functional connectivity were analyzed in the Iberian and Italian peninsulas, two regions where the beaver is expanding its range, partly due to unauthorized reintroductions. The results revealed several ecological corridors that could facilitate further expansion of the species in both study areas. However, the models suggested low connectivity between naturally colonized sites and those occupied after illegal reintroductions, confirming the limitations of spontaneous recolonization. The analysis of structural connectivity also

assessed the impact of dams, highlighting how they fragment the river network. Dams with the highest potential for fragmentation were identified as priorities for conservation interventions.

The second case study addressed the first European-scale analysis of functional connectivity for the Eurasian lynx. The results show good ecological connectivity in Northern Europe, from Scandinavia to the Baltic countries, while in other areas, such as Western and Central Europe, connectivity is more limited. From a conservation perspective, attention focused on the populations in these latter regions, for which several ecological corridors were identified. However, these corridors are often poorly protected. Expanding the network of protected areas could significantly contribute to ensuring better protection of these corridors, improving the chances of species dispersion and the persistence of populations in these critical areas.

The third part of the thesis presents two distinct case studies. The first integrates species distribution models (SDMs), ecological connectivity analysis, and individual-based models (IBMs) within a single framework designed to support reintroduction projects. As a practical example, the reintroduction of the Eurasian lynx in the Apennines was selected. The framework follows a linear approach: initially, ecological compatibility between the potential source population and the target area is assessed by comparing ecological niches. Subsequently, key sites are identified by integrating environmental suitability data with ecological connectivity data. Finally, different reintroduction scenarios are simulated through IBMs, generating predictions for crucial parameters such as population abundance, colonization times, and the probability of presence in suitable areas.

The second case study involved an analysis of ecological connectivity at the European level, using a multispecies approach specific to mammals. The model was built considering human impact and the varying sensitivity of species to this factor. It also integrated the energetic cost of movement and primary productivity. The analysis considered four different dispersal distances, calculating omnidirectional connectivity via a moving window. The results for different species were averaged and validated using telemetry data collected for multiple species across different European regions.

Cumulative connectivity predictions indicate higher ecological connectivity in areas with lower human impact, such as Scandinavia and the major mountain ranges of Europe. However, the maps of normalized connectivity also highlight the presence of corridors in urbanized areas. Telemetry data confirmed that, in most cases, species move through areas with higher connectivity values compared to null models. While connectivity values are generally higher within protected areas, these areas only cover a small portion of the regions with higher normalized connectivity values in most European countries. These results can support the expansion of the protected area network, as outlined in Target 3 of the European Biodiversity Strategy, which aims to protect 30% of terrestrial areas by identifying priority areas for ecological connectivity.

The overall results of the thesis confirm the effects of global change on the spatial and temporal dynamics of species in Europe, documenting potential range shifts of several species of conservation and ecosystemic importance. Furthermore, they highlight how SDMs and ecological connectivity techniques can support conservation actions, both to address the specific needs of individual species and to tackle broader issues related to the management and creation of new protected areas, in line with the objectives of the European Biodiversity Strategy 2030. The frameworks developed represent a valuable tool for planning long-term

biodiversity conservation and management strategies, particularly in the context of current climate change.

General Introduction

Climate and land-use changes driven species range shifts

The history of life on Earth is deeply tied to environmental changes across various spatial and temporal scales (Davis and Shaw, 2001). Species' ability to shift their ranges in response to tectonic, oceanographic, and climatic events is a key part of this (Davis and Shaw, 2001). However, the unprecedented pace of future climate change, combined with land use changes, threatens this balance between adaptation and migration, endangering many species (Davis and Shaw, 2001). Projected 21st-century climate changes, especially global warming, are comparable in magnitude to major global shifts in the past 65 million years (Diffenbaugh and Field, 2013; Kemp et al., 2015). Already, the speed and scale of climate change are driving a widespread biological response, with marine, freshwater, and terrestrial species shifting distributions to stay within suitable environments (Chen et al., 2011; Lenoir and Svenning, 2015).

Despite global agreements to reduce greenhouse gas emissions, climate change will likely continue for centuries due to the inertia of oceanic and atmospheric systems (Calvin et al., 2023). Since 1880, global temperatures have risen by an average of 1.1°C (Calvin et al., 2023), leading to notable species distribution shifts with significant consequences for human societies. Yet, future warming targets, like the 2°C goal from the Paris Agreement, may double this change, and current global commitments are expected to lead to 2.7° to 3.7°C warming—three to four times what has already occurred (Calvin et al., 2023).

Climate change impacts all levels of biodiversity, from individuals to ecosystems, often reducing fitness and resilience (Botkin et al., 2007). It alters community interactions and can lead to cascading effects across trophic levels (Gilman et al., 2010). For example, the extinction of one species can trigger further losses, as seen in pollinator-parasite systems (Koh et al., 2004). Phenological shifts, such as earlier springs, have been widely documented, though species responses vary (Parmesan and Yohe, 2003). Climate change may also disrupt ecological synchrony, increasing host outbreaks and affecting food webs (Hance et al., 2007). Life-history events in temperate regions, such as spring phenology, are shifting with rising temperatures. A global meta-analysis found that species advanced their phenology by an average of 2.3 days per decade, although responses vary (Parmesan and Yohe, 2003).

Numerous studies documented climate change’s "fingerprints," as species' behavioral and distributional shifts cause cascading effects through food webs (Parmesan and Yohe, 2003). Species interactions across trophic levels may be affected, and climate signals can induce regime shifts in ecosystems (Alheit, 2009). Species also might evolve tolerance to environmental changes, adding uncertainty to future impacts.

Temporal and spatial changes in species’ behavior and distribution are not isolated processes; they are connected through interactions with other species at the same or adjacent trophic levels, and beyond, through indirect effects of trophic cascades. Hence, changes at lower trophic levels may induce bottom-up effects through ecological networks and may induce feedback processes. Range shifts imply that species might be forced to interact with those from which they were formerly spatially separated. For example, top-down effects may also occur and strongly influence and modify community responses. Climate-induced range shifts are occurring along altitudinal and latitudinal gradients, typically toward higher elevations and latitudes. The presence of warm-edge contractions is critically important. A warm-edge

contraction occurs when populations from one or more localities at the lowest latitudes or elevations of a species' regional distribution disappear (i.e., are inferred to no longer occur at those localities), leading to an overall shift in the species range towards higher latitudes or elevations. These contractions indicate that species are failing to shift their niches sufficiently to tolerate these new conditions and that these populations are instead going extinct (referred to as "local extinction") (Wiens, 2016). However, responses vary; in some regions, habitat generalists shift faster than specialists (Le Roux and McGeoch, 2008). Field studies suggest three types of distributional change in response to climate: 'march' (parallel shifts of range edges), 'lean' (central range shifts), and 'crash' (widespread mortality) (Breshears et al., 2008).

At higher levels of biodiversity, climate change is expected to significantly alter vegetation communities, potentially threatening biome integrity. Effects on terrestrial plants include changes in physiology, species composition, and biomass production (Boone et al., 2018; Esquivel-Muelbert et al., 2019), which could shift vegetation and the global distribution of biomes. The Millennium Ecosystem Assessment predicts shifts in 5 to 20% of Earth's terrestrial ecosystems, particularly affecting cool conifer forests, tundra, scrubland, savannahs, and boreal forests (Grimm et al., 2013). Tropical biomes are expected to expand, while temperate biomes, especially tundra, will shift northward and decrease in size (Boonman et al., 2022).

Facing all these threats and changes, species responses can differ significantly.

Species responses to climate changes

As climate change shifts environmental conditions, many species may find themselves outside their climatic niche, meaning they are no longer suited to the climate of a given area. Since other components of species' niches remain unchanged, this discussion focuses on climatic niches, a part of the n-dimensional hypervolume as described by Hutchinson. To survive, species must produce adaptive responses, which can take various forms. A key question is whether species can adapt quickly enough to keep up with rapid climate shifts (Lavergne et al., 2010; Salamin et al., 2010).

Adaptive responses arise from two main mechanisms: microevolution, where species genetically adapt through mutations or selection of existing genotypes (Salamin et al., 2010), and plasticity, which provides short-term, within-lifetime adjustments (Charmantier et al., 2008). Plasticity involves variations in traits like morphology, physiology, or behavior within a species (Botkin et al., 2007; Chevin et al., 2010). Evidence suggests plasticity often plays a greater role than genetic adaptation (Hoffmann and Sgrò, 2018). However, rapid evolution, especially in invasive species, also occurs, enhancing their success (Alford et al., 2009).

In response to climate change, species can theoretically adapt along three axes: spatial, temporal, or self (Figure 1). The first two axes are well-documented responses to global warming (Parmesan, 2006). Species can track suitable conditions spatially, often through dispersal, but this also includes shifts to different habitats at local or micro-habitat levels. Latitudinal and altitudinal range shifts have been observed in over 1,000 species, particularly in birds, insects, and marine invertebrates with high dispersal capacities (Parmesan, 2006), leading to reduced range sizes in polar and mountain species (Forero-Medina et al., 2011).

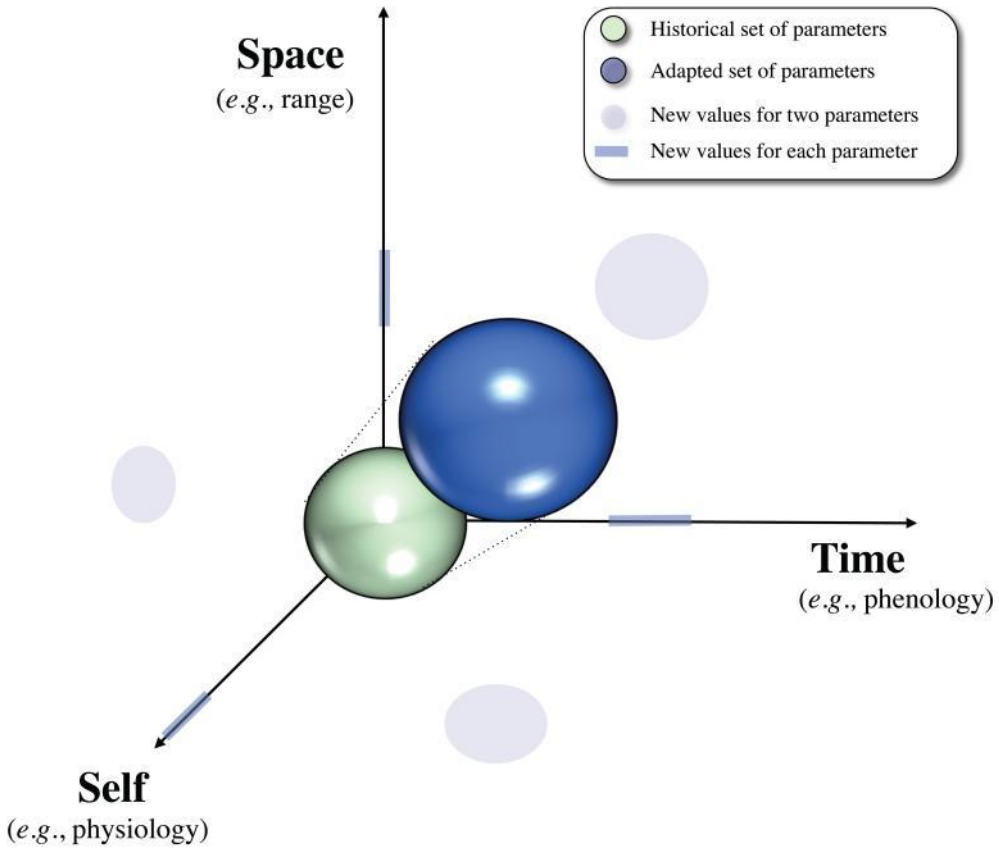


Figure 1. The three primary responses to climate change through phenotypic plasticity or evolutionary adaptation include: (1) moving in space, either by dispersing to areas with suitable habitat or shifting location on a microhabitat scale; (2) shifting life history traits in time, such as adjusting life cycle events—including phenology and diurnal rhythms—to align with new climatic conditions; and (3) modifying physiological life history traits to better cope with altered climatic conditions (Bellard et al., 2012).

While species may track their preferred climate, they might not be adapted to changes in other factors like photoperiod or new biotic interactions (Visser, 2008). To adjust to cyclic abiotic changes, such as temperature variations, species can shift their timing on a daily or seasonal scale. Phenology—seasonal timing of events like flowering and breeding—is a common response to climate warming. A meta-analysis shows species shifting their phenological events by an average of 5.1 days earlier per decade over the past 50 years (Root et al., 2003), with some plants shifting by over 10 days (Parmesan, 2006). While this maintains synchrony with abiotic factors, it can disrupt ecological interactions, risking extinction (Parmesan, 2006).

Lastly, species can adapt to new climatic conditions by adapting themselves, rather than shifting in space or time, to track their optimal conditions. This third axis, "self," involves in situ physiological or behavioral adaptations, allowing species to survive in their current range. For instance, species may adjust their physiology to tolerate warmer or drier conditions or change behaviors like activity patterns or diet. These adaptations, though less visible, are documented, especially in temperature-sensitive ectotherms (Tewksbury et al., 2008). However, plasticity has limits, and traits like body size or metabolism cannot change indefinitely (Chevin et al., 2010). When these limits are reached, strong selection is needed for

survival. Unlike spatial or temporal shifts, these self-changes impact ecosystems differently. Species that fail to adapt along any of these axes risk local or global extinction.

There is thus a multitude of possible responses for species to cope with climate change, and in fact relatively few taxa went extinct following climate change during the Quaternary period (Botkin et al., 2007). However, many populations are unlikely to keep pace with the speed and scale of current climate change. Additionally, unlike in the past, species now face extra threats that may act synergistically with climate change (Botkin et al., 2007).

Predicting extinction risk from climate change

Species are disappearing at rates that are 1000 times faster than those registered in the fossil record (De Vos et al., 2015), and accurate predictions of extinction risk are necessary to anticipate declines under past, current, and projected levels of human pressure.

Predictions of biodiversity loss due to climate change are crucial for alerting scientists and policymakers to future risks, linking biological changes to climate impacts, and guiding proactive strategies (Parmesan et al., 2011; Pereira et al., 2010). While current extinctions directly caused by climate change are rare, studies suggest climate change may surpass habitat destruction as the leading threat to biodiversity in coming decades (Leadley et al., 2010). However, the variability in approaches and projections makes it challenging to reach a consensus on future biodiversity under different climate scenarios (Pereira et al., 2010).

Though human land use is currently the primary driver of species extinction (Hoffmann et al., 2010), climate change is expected to rival or surpass this impact soon (Jetz et al., 2007; Urban, 2024). Modeling studies predict species loss due to climate change, with estimates ranging from 0% to 54% (Thomas et al., 2004; Urban, 2024, 2015; Warren et al., 2013). This uncertainty arises from differences in climate models, species' dispersal abilities, and their varied responses to climate change.

A meta-analysis of 131 multispecies studies assessing extinction risk from climate change found that, on average, 7.9% of species are predicted to go extinct due to climate change (Urban, 2015). The strongest predictor of extinction risk was the extent of future climate change. Global extinction risk is expected not only to increase but to accelerate as global temperatures rise (Urban, 2015). In fact, extinction risk is projected to rise from 2.8% currently to 5.2% under the 2°C warming scenario, which many experts now believe is unattainable. With a 3°C rise, the risk increases to 8.5%, and under a business-as-usual scenario with a 4.3°C rise (RCP 8.5), climate change could threaten 16% of species, or one in six globally (Urban, 2015).

Extinction risks also vary by region. North America and Europe show the lowest projected risks (5% and 6%, respectively), while South America (23%) and Australia and New Zealand (14%) face much higher risks (Urban, 2015). Furthermore, there is a bias in the geographic focus of studies, with 60% of extinction risk predictions concentrated on North America and Europe. This suggests an urgent need to redirect research efforts toward less-studied but more vulnerable regions (Urban, 2015). Certain groups of species are particularly at risk. Endemic species with restricted ranges, as well as amphibians and reptiles, are predicted to have higher extinction risks than more widespread species (Sinervo et al., 2010). Endemic species, in particular, face a 6% greater extinction risk compared to models that consider both endemic and non-endemic species (Urban, 2015).

Evidence of climate-related local extinctions

There is substantial evidence of climate-related local extinctions. Recent studies have demonstrated that local extinctions linked to climate change are already occurring (Ducatez and Shine, 2017; Wiens, 2016). A survey on climate-related range shifts found that 47% of the 976 species surveyed have already experienced local extinctions (Wiens, 2016). These extinctions were broadly consistent across climatic zones, taxonomic groups, and habitats, but were more common in tropical species (55%) than temperate species (39%), in animals (50%) compared to plants (39%), and in freshwater habitats (74%) compared to terrestrial (46%) and marine habitats (51%). These findings suggest that local extinctions due to climate change are already widespread, despite the relatively modest levels of climate change so far. As global warming intensifies over the next century, local extinctions are expected to increase dramatically—potentially by 2 to 5 times (Wiens, 2016).

Extinction risks due to climate change are not uniform across taxa. Research has shown that birds and amphibians are more susceptible to climate-driven extinction than reptiles or mammals (Ducatez and Shine, 2017). This suggests that some species are already unable to undergo the necessary niche shifts quickly enough to avoid local extinction. Even if the absolute amount of niche change needed for survival is theoretically achievable, the time required for such changes may exceed the rapid pace of anthropogenic climate change (Wiens, 2016).

The persistence of many species will likely depend on their ability to shift their geographic ranges, typically to higher latitudes or elevations, in order to remain within their climatic niche. Data show numerous instances of cool-edge expansions in species (367 of 904 species examined), where populations moved toward cooler areas, while some populations remained stable (371 species) or experienced contraction (166 species) (Wiens, 2016). However, this kind of range shift may be impeded by several factors. First, human infrastructure, such as roads, urbanization, and agricultural lands, can obstruct dispersal or leave no available habitat for species to migrate to (Brook et al., 2008). Second, species confined to islands, peninsulas, or mountaintops face physical barriers to dispersal, limiting their ability to move to suitable climates (Colwell et al., 2008). Finally, even when there are no barriers, species may still not disperse fast enough to keep pace with climate shifts (Schloss et al., 2012).

Factors affecting predictions

Despite the substantial evidence linking climate change to increased extinction risk, there are several sources of uncertainty in these predictions. Most assessments of climate change's impact on biodiversity rely on empirical niche models (or climate-envelope models), which define a species' "environmental space" based on the relationship between current climate variables and species distribution patterns (Guisan and Thuiller, 2005). These models are then applied to future climate scenarios generated by general circulation models (GCMs), predicting the shifts in species' geographic ranges under different climate conditions. While these models have issued stark warnings about biodiversity loss (Thomas et al., 2004; Urban, 2015), they primarily assess exposure to climate change, which is only one dimension of vulnerability.

Key model assumptions significantly affect predictions of extinction risk. One factor is extinction debt, where species are destined for extinction due to severe population decline but haven't yet vanished (Jackson and Sax, 2010). Studies vary in the thresholds for habitat loss leading to extinction, typically using 100%, 95%, or 80%. Lowering the threshold from 100%

to 80% increases predicted extinction risk from 5% to 15%, with further declines raising risks as temperatures rise. These thresholds depend on traits like generation time and population size, making understanding range reductions essential for accurate extinction predictions (Stanton et al., 2015).

Another assumption involves species' ability to disperse into new habitats as climates shift (Schloss et al., 2012). Dispersal assumptions range from none to universal dispersal, with reality likely somewhere in between. Universal dispersal estimates a 6% extinction risk, species-specific dispersal raises it to 10%, and no dispersal further increases it to 12%, with risks rising more sharply at higher temperatures.

Different modeling techniques also yield varying extinction predictions, from simpler species distribution models to more complex mechanistic models. While the modeling technique had only a marginal effect on extinction risk, the highest extinction risks were associated with species-area models (22%) and expert opinion (18%). In contrast, mechanistic models and species distribution models resulted in lower risk estimates (8% and 7%, respectively). Species-area models explicitly account for extinction debt but may overestimate risks due to sampling artifacts (He and Hubbell, 2011). The high risk linked to expert opinion might stem from broader biological insight, greater uncertainty, or a more pessimistic view when translating qualitative data into quantitative extinction risk estimates.

Predicting the full biodiversity impact of climate change requires a more holistic approach that accounts for all aspects of vulnerability: exposure, sensitivity, and adaptive capacity (Williams et al., 2008). Populations exposed to climate change may demonstrate a variety of coping mechanisms, with different outcomes for their resilience at local and global scales. The ability to adapt depends on intrinsic factors such as species biology and genetic diversity, as well as extrinsic factors such as the rate, magnitude, and type of climate change (Dawson et al., 2011). This complexity adds significant uncertainty to predictions of extinction risk, highlighting the need for more comprehensive models that include both species' biological traits and the changing environment.

Effects of land-use changes

Most biodiversity scenarios are based on narratives projecting socio-economic and policy-driven environmental changes (van Vuuren et al., 2012), but they often focus on a single threat, typically climate change, while neglecting other major factors like land use changes (Titeux et al., 2016).

Habitat destruction and degradation remain the most significant threats to biodiversity today (Leadley et al., 2014). More than 85% of threatened terrestrial mammal, bird, and amphibian species are affected by habitat loss due to human activities such as agriculture, infrastructure, and resource extraction, while less than 20% are impacted by climate change (Figure 2) (Pereira et al., 2012). Similarly, habitat alteration has been identified as the main threat across species groups, affecting 64%-86% of species (Ducatez and Shine, 2017).

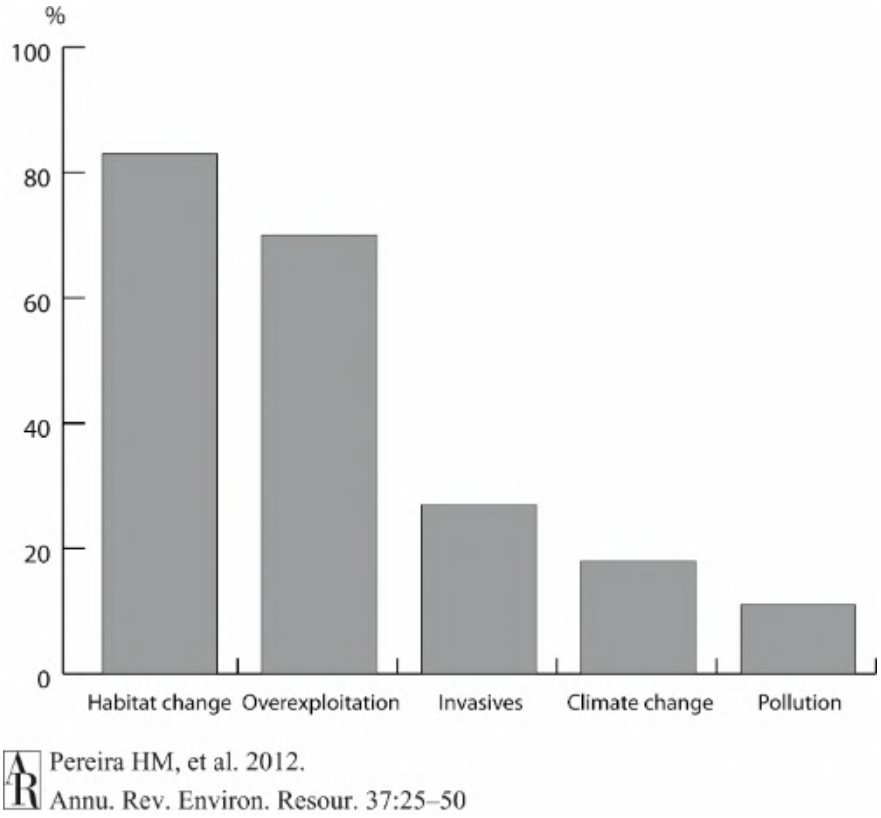


Figure 2. The proportion of threatened species affected by each driver is analyzed across 4,259 species, including mammals, birds, and amphibians classified as critically endangered, endangered, or vulnerable according to Red List categories. The main threats are categorized as follows: habitat change (encompassing residential and commercial development, agriculture and aquaculture, energy production and mining, transportation and service corridors, and natural system modifications), overexploitation, invasive species, climate change, and pollution (Pereira et al., 2012).

A study using global decadal land-use projections to 2070 assessed the impacts of land-use changes on around 19,400 species of amphibians, birds, and mammals. It predicted substantial declines in suitable habitats globally, with about 1,700 species at risk of becoming imperiled due to land-use changes alone (Powers and Jetz, 2019). Another study analyzed global biodiversity responses to land-use pressures, finding that species richness in the most affected habitats dropped by 76.5%, with total abundance and rarefaction-based richness also substantially reduced. By 2100, a continued loss of within-sample richness is projected globally, with losses concentrated in biodiverse yet economically disadvantaged regions (Newbold et al., 2015).

When mapping species richness in relation to land-use changes, regions with extensive human activity, such as Europe, have shown marked reductions in local diversity, with the most impacted areas experiencing a 31% drop in average local species richness, which may disrupt ecosystem functioning (Newbold et al., 2015). The concept of the human footprint (HFP), which reflects cumulative human pressure on the environment, has been used to link increasing HFP values to rising extinction risks for terrestrial mammals. Areas with low prior human pressure (HFP < 3) are the most significant predictors of extinction risk changes, indicating that the conversion of natural and semi-natural habitats in these areas is driving higher extinction risks (Di Marco et al., 2018). Preventing further conversion of habitats with higher

HFP values is crucial for species conservation, especially since threatened species are more likely to have faced greater human pressure historically (Di Marco et al., 2018).

These findings align with other studies highlighting deforestation in intact landscapes as the strongest driver of decline in forest species, exacerbating risks through mechanisms like hunting, disease spread, and invasive species introduction (Betts et al., 2017). Importantly, while high-risk species have faced greater pressure in moderately disturbed areas, low-risk species have seen pressure increases in areas with minimal previous disturbance (HFP < 2), suggesting that future habitat conversion will push currently low-risk species into higher-risk categories (Di Marco et al., 2018).

Consequences of climate and land-use changes on species distribution

The ongoing biodiversity crisis is driven by a combination of human-induced factors, including land-use change, climate change, pollution, overexploitation, and invasive species, all of which have contributed to global declines in species and ecosystem integrity (Pereira et al., 2012; Leadley et al., 2014).

A study modeled the individual and combined impacts of climate and land-use change on terrestrial vertebrates under four scenarios, showing that by 2070, climate change may surpass land-use change as the dominant threat to biodiversity (Newbold, 2018). Combined, these pressures could cause a 37.9% species loss in vertebrate communities under a 'business-as-usual' scenario, with tropical grasslands and savannahs particularly affected. While land-use change has historically been the top threat, climate change is expected to drive future extinctions. Under RCP 8.5, some communities may lose over half their species, with amphibians and reptiles predicted to suffer greater declines than birds and mammals (Newbold, 2018).

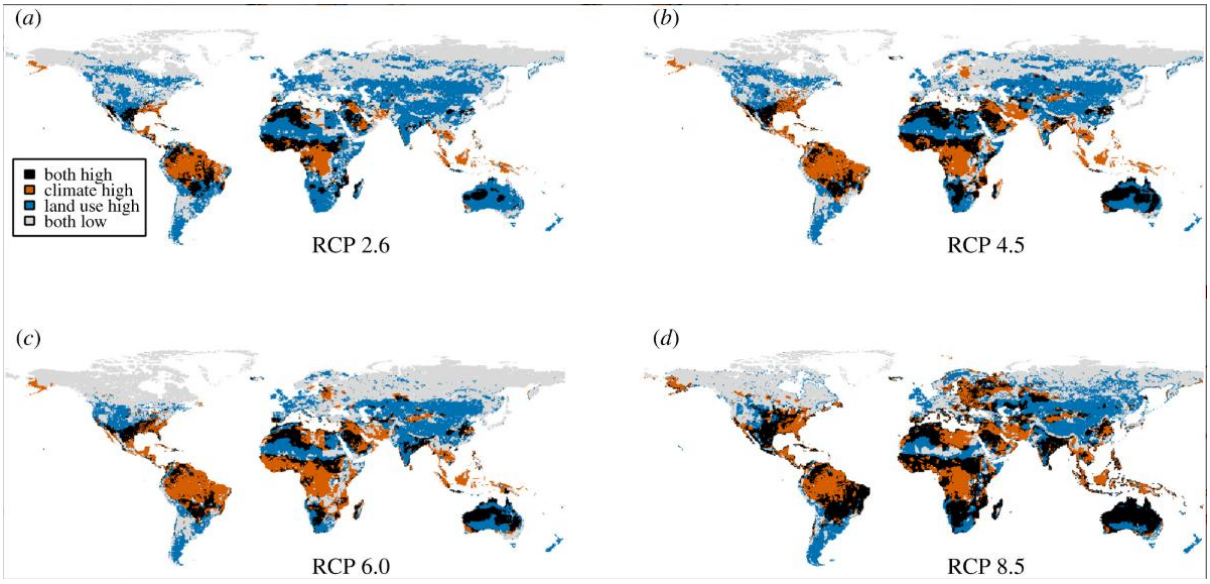


Figure 3. The spatial patterns of biodiversity loss by 2070 due to climate and land-use change are depicted as follows: areas experiencing more than 10% net species loss from climate change are shown in brown, those with more than 10% species loss from land-use change are in blue, and areas with overlapping losses exceeding 10% from both pressures are in black. Regions with less than 10% species loss from both pressures are shown in grey. Projections are provided for each socio-economic and greenhouse gas emission scenario: (a) RCP 2.6, (b) RCP 4.5, (c) RCP 6.0, and (d) RCP 8.5 (Newbold, 2018).

Spatial variation in biodiversity loss is also expected. Tropical forests, which have seen less land conversion, are predicted to experience significant species losses from climate change, while temperate regions, already impacted by land-use change, may see smaller shifts (Figure 3) (Newbold, 2018). Tropical grasslands and savannahs are forecasted to face severe species declines from both climate and land-use changes. Additionally, the intensification of these pressures could reduce functional diversity within animal communities, threatening essential ecosystem services (Flynn et al., 2009).

SDMs as a tool to predict climate and land-use changes extinctions

As shown, ongoing climate and land-use change is predicted to cause significant loss of biodiversity, meaning loss of species, genes and ecosystems. This could lead to multiple negative consequences for human society as important ecosystem functions are also being lost. Understanding and predicting species extinctions for scenarios of future climate change is thus of main interest for science and people.

Most estimates of future extinction risk rely on correlative species distribution models (SDMs) (a.k.a. habitat suitability model, ecological niche model and environmental envelope model, among others; Elith and Leathwick, 2009) (Figure 4) (Urban, 2015; Warren et al., 2018), despite inferring extinction risks from SDMs is controversial (Araújo and Peterson, 2012; Dormann, 2007). These relate the observed distribution of the focal species to observed environmental characteristics within statistical or machine-learning frameworks and then make forecasts where the species will find suitable environmental conditions in the future.

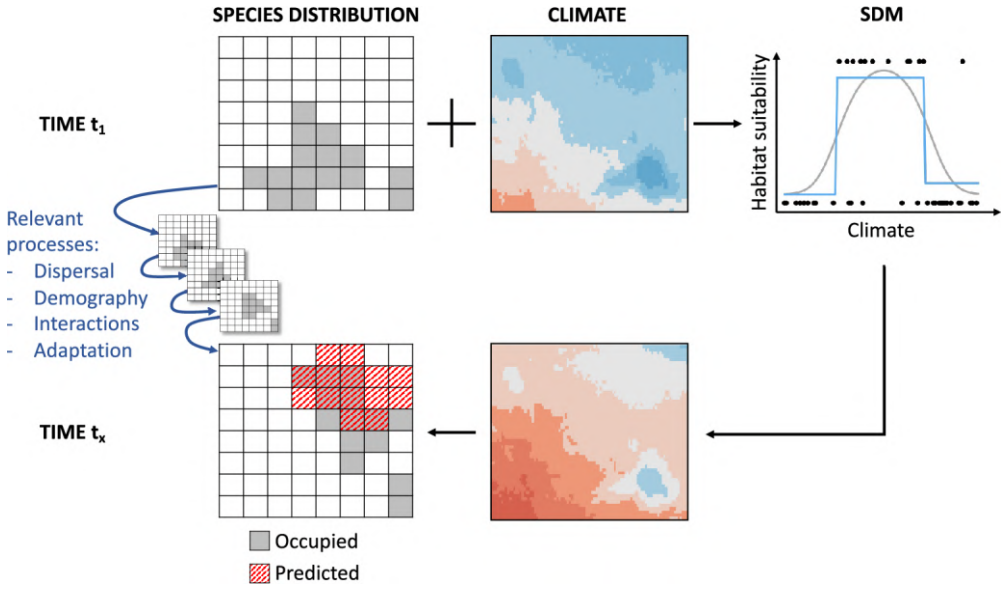


Figure 4. A conceptual overview of correlative species distribution models (SDMs) for predicting climate change impacts is as follows: SDMs are calibrated using observed occurrence data and climatic (or broader environmental) data at time step t_1 (upper row), employing statistical or machine-learning approaches (e.g., the grey curve and blue step function in the top-right plot). The fitted species–environment relationship is then applied to predict habitat suitability and potential distribution at a future time step t_x, based on projected climate (or environmental) layers (lower row). However, the potential future distribution inferred from SDMs may differ from the true distribution at t_x, as the latter also depends on biological processes such as dispersal, demography, species interactions, and genetic or behavioral adaptations, leading to transient dynamics (depicted in the middle row) (Zurell et al., 2023).

Currently, SDMs are the most widely used tools for assessing climate change's impacts on biodiversity (Araújo et al., 2019) and for evaluating current and future ranges of species (e.g., Thomas et al., 2004). Many SDM studies have attempted forecasts under climate scenarios, for example, assessing climate change vulnerability of species in terms of potential range loss (Martín-Vélez and Abellán, 2022), differences in seasonal range loss for species with different IUCN Red List status (Zurell et al., 2018) or contrasting effects of dispersal or local adaptation on climate-related extinction risk (Román-Palacios and Wiens, 2020; Thuiller et al., 2006). Also, SDM-derived extinction risk estimates regularly inform political processes (Calvin et al., 2023).

Although controversial, the use of SDMs in global change studies continues to grow, with 76% of climate-related extinction risk studies relying on SDMs (Urban, 2015). As more suitable methods are lacking, SDMs remain the most practical tool for estimating climate-driven extinction risk (Araújo et al., 2019). Most SDMs use climatic variables to predict future scenarios, though validation of predictive accuracy remains challenging due to limited independent data (Yates et al., 2018). By applying a threshold approach (Liu et al., 2013), the model output of habitat suitability can be transformed into predicted presence (and predicted absence), which can be interpreted as potential distribution of the species given the environmental conditions.

Recent advances in SDM algorithms and biodiversity data availability (Valavi et al., 2022) have contributed to the widespread adoption of SDMs. A study found that between 1900 and 2021, more than 40,000 SDM-related studies were published, with the first SDM mentioned in 1969 and a steady increase since 1990, and with climate change mentioned in ~20% of them (Zurell et al., 2023). Of 300 randomly selected studies, 203 used SDMs, 161 applied them to climate scenarios, 134 examined range changes, and 74 inferred extinction risk (Zurell et al., 2023).

However, how extinction risk can be assessed through SDMs?

Extinction risk estimates derived from SDMs often assume that as suitable habitat declines, extinction risk rises, based on the species–area relationship (SAR; Macarthur and Wilson, 1967) (Figure 5). They reflect theoretical understanding from island biogeography that smaller areas can harbor less individuals and smaller populations face a higher risk of extinction (MacArthur and Wilson, 1967), which is based on well-documented correlations between species richness and geographical area size (Matthews et al., 2021). However, the exact relationship between range reduction, population decline, and extinction risk is unclear for most species (Mace et al., 2008). Commonly, SDM-derived range declines are translated into extinction probabilities using the IUCN Red List guidelines (IUCN, 2024), though this approach lacks robust empirical backing (Mace et al., 2008).

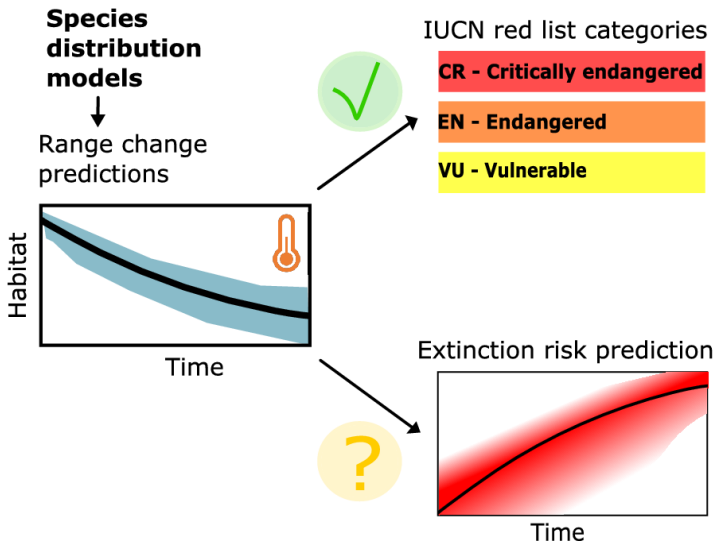


Figure 5. Current extinction risk, as predicted by species distribution models (SDMs), is linked to an increased extinction risk driven by a reduction in suitable habitat, consistent with the species–area relationship (Zurell et al., 2023).

Originally, IUCN threat categories assessed extinction likelihood using quantitative analyses such as population viability analyses (Mace and Lande, 1991). However, simpler estimates, like species range declines, are also used to classify species as "critically endangered" or "endangered" under IUCN subcriteria A3 and A4, which focus on predicted future range reductions (IUCN, 2024; Mace et al., 2008). For example, a species predicted to lose ≥80% of its range may be classified as critically endangered.

This method can predict changes in species richness in response to projected habitat area changes under climate change (Pimm et al., 1995). However, this approach has faced criticism due to its dependency on specific species and environmental characteristics (Matias et al., 2014), the lag time often seen between habitat loss and extinction (Triantis et al., 2010), and its inability to accurately reflect the distribution of the last individuals while distinguishing actual losses from sampling issues (He and Hubbell, 2011). Furthermore, SARs do not provide species-specific predictions but rather assess relevant areas of habitat loss to estimate species richness, making them more suitable for addressing habitat loss due to land use rather than extinction linked to climate change. Thus, they do not adequately inform conservation efforts focused on individual species extinction risk.

In summary, while SDMs represent the most viable species-specific prediction tool for assessing extinction threats under climate change, their application should be approached with caution (Zurell et al., 2023). Translating projected declines in range size from SDMs into quantitative extinction risk estimates—especially through the IUCN criterion E—is challenging. The foundational relationship between extinction and range decline is poorly understood and likely varies across taxa and environments. Nonetheless, in the absence of more robust methodologies, judicious application of IUCN criteria to SDM projections can help categorize species-level extinction risks from future climate change under certain assumptions. The subsequent sections will delve into the conceptual and methodological challenges of SDMs pertinent to this process.

Conceptual challenges behind SDMs

The use of species distribution models to predict future extinctions relies on the assumption that these models provide reliable forecasts. However, there are several reasons why this assumption may not hold true. SDMs are based on critical assumptions, particularly that species are currently in equilibrium with their environment, will achieve equilibrium in future conditions, and that all environmental constraints are sufficiently understood and represented in the model (Elith and Leathwick, 2009; Zurell et al., 2020). These assumptions are unlikely to be consistently met in many cases. Additionally, SDMs presume that species will conserve their ecological niches over time, assuming no adaptive evolution in response to environmental changes like thermal tolerance—an assumption that is questionable given the strong selective pressures species may face (Dawson et al., 2011).

There is mounting evidence that many species are lagging behind their climatically suitable habitats, meaning they have not yet colonized areas that are now suitable for them, a phenomenon referred to as "colonisation credit" (Svenning et al., 2008). This lag demonstrates a departure from the equilibrium assumption underpinning SDMs. Moreover, global change drivers such as habitat destruction and fragmentation can further hinder species' abilities to track shifting climates, leading to a higher extinction risk than SDM predictions suggest (Travis, 2003). Dispersal ability is a key factor in climate tracking, but reliable empirical data on species' dispersal capabilities are often lacking (Fandos et al., 2023).

SDMs frequently operate under two extreme assumptions regarding species' dispersal: full dispersal or no dispersal (Thuiller et al., 2019). Full dispersal assumes species can entirely track shifting climates in space, while no dispersal assumes species cannot shift their ranges and therefore lose currently suitable habitats. The conclusions drawn about range size declines can vary dramatically depending on which of these assumptions is applied, and these differences are further influenced by the geographic scope of the study area.

In reality, species' ability to track climate and shift ranges is influenced by demographic processes, adaptive evolution, and species interactions (Buckley and Kingsolver, 2012; Schleuning et al., 2020). Furthermore, species with long life spans may temporarily survive under unfavorable conditions, delaying local extinctions and creating "extinction debts" (Kuussaari et al., 2009). While the full versus no dispersal scenarios can capture some aspects of the uncertainty, it remains unclear where any particular species might fall along this continuum. Therefore, caution is required when interpreting SDM projections in the context of extinction risk.

Ecological processes that shape species distributions operate at different spatial scales: broad-scale patterns may be governed by climatic factors, while fine-scale distributions are often determined by factors like local resources (Guisan and Thuiller, 2005) or microclimatic conditions (Suggitt et al., 2011). Consequently, the ability of species to track climate and shift ranges may be constrained by fine-scale resources, which are often not captured in SDMs (Dormann, 2007; Skov and Svenning, 2004). Ignoring these fine-scale environmental and biotic factors can introduce bias into SDM predictions, potentially leading to under- or over-estimation of suitable habitat.

Another major challenge for SDMs projecting into the future is the availability and reliability of environmental scenarios. While climate models are continuously updated, producing advanced scenarios for the IPCC (Knutti et al., 2013), future scenarios for land use—a major

determinant of species distribution—are much more uncertain due to the unpredictability of political and economic developments (Cabral et al., 2024).

Relying solely on the explanatory power of variables can be misleading, as random spatial factors might predict species distributions as well as commonly used environmental predictors (Fourcade et al., 2018). Since SDMs are essentially phenomenological models, it is critical not to confuse correlation with causation (Dormann et al., 2012). Misinterpreting correlational relationships in SDMs can lead to errors in both current and future predictions.

When using species distribution models to estimate extinction risks and inform policy or management decisions, ensuring that the models are fit for purpose is essential. This can be hampered by both conceptual and methodological challenges. Although SDMs are often considered a straightforward tool, few studies meet the rigorous standards needed for reliable extinction risk assessment, as outlined by the IUCN (2024). Several recent studies offer guidance on improving the credibility of SDMs for biodiversity assessment and decision-making (Araújo et al., 2019). Nogués-Bravo (2009), in discussing the use of SDMs to predict past species distributions, outlined potential pitfalls that apply equally to forecasting, warning that poor methods can result in "a cascade of errors and naïve ecological and evolutionary inferences." These methodological challenges are summarized in four key areas: (1) model specification, (2) selection of environmental predictors, (3) model validation, and (4) uncertainty from novel climates (Barry and Elith, 2006; IUCN, 2024; Nogués-Bravo, 2009).

(i) Model Specification: Several studies demonstrate that algorithm choice significantly affects predictions of species ranges, both current and future (Valavi et al., 2022). SDM algorithms vary in complexity, from simpler envelope models to advanced machine-learning methods (Guisan et al., 2017). Machine learning often achieves higher prediction accuracy by closely fitting the data (Elith et al., 2006; Valavi et al., 2022), but risks overfitting, which can reduce transferability to new times and locations. For future range predictions, simpler models may sometimes perform better (Merow et al., 2014). The IUCN advises using at least three SDM algorithms of moderate complexity to account for uncertainty in species–environment relationships (IUCN, 2024).

(ii) Selection of Environmental Predictors: The number of predictor variables in future-oriented SDMs should be kept minimal (Brun et al., 2020). Including too many variables can increase uncertainty, particularly when the environmental data sources themselves are uncertain or inconsistent. Given the growing use of SDMs in global change research, ensuring model transferability across contexts is crucial (Yates et al., 2018).

(iii) Model Validation: Validation of SDMs is typically done by partitioning the data into training and testing sets (Araújo et al., 2005), but the latest advancements recommend using spatial or environmental block cross-validation. This method holds out data clustered spatially or environmentally, forcing extrapolation during validation and better reflecting the uncertainty of future predictions (Valavi et al., 2019). However, more guidance is needed to design these blocks properly to ensure robust validation of predictions. Additionally, global changes could cause non-stationarity in the processes governing species–environment relationships, further complicating validation (Rollinson et al., 2021).

(iv) Uncertainty from Novel Climates: Predicting into the future requires accounting for uncertainty when extrapolating into novel environmental conditions. Different algorithms handle this extrapolation differently, and it is essential to assess the extent of environmental novelty explicitly (Elith et al., 2010).

Together, these methodological considerations (Figure 6) underscore the complexity of using SDMs for policy-relevant extinction risk projections. While these models offer valuable insights, care must be taken to ensure they are rigorously constructed, validated, and interpreted within the limits of their assumptions.

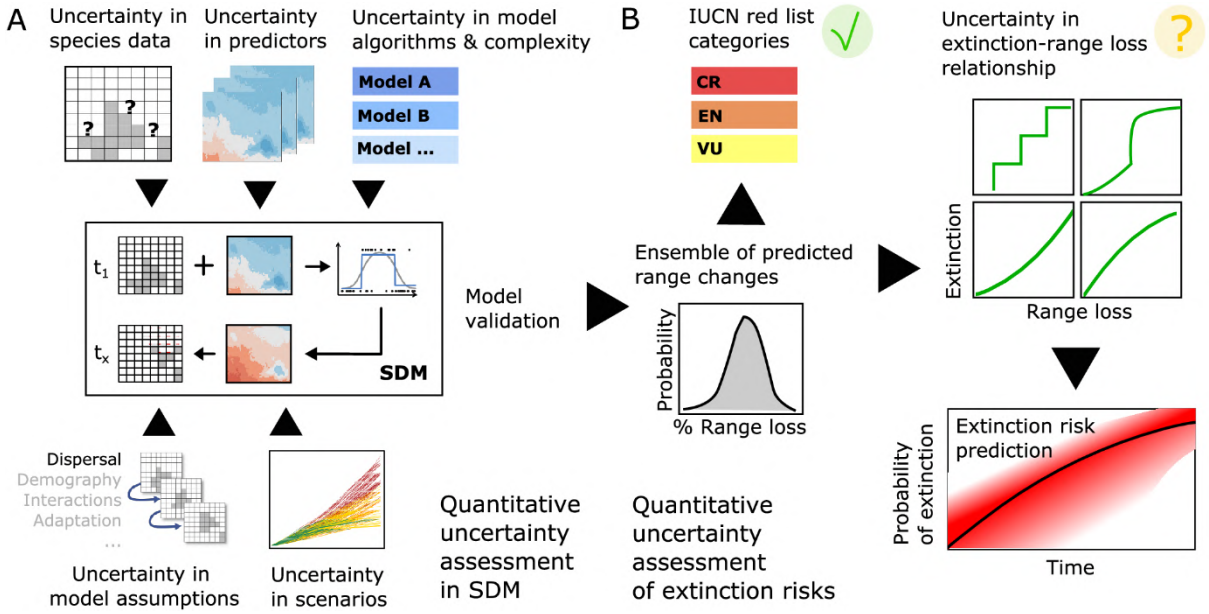


Figure 6. Workflow and challenges in predicting range loss and extinction risk using correlative species distribution models (SDMs) include the following: (A) The development of SDMs involves addressing several methodological and conceptual challenges, with the resulting uncertainties needing clear communication; While SDM-predicted range loss can be directly applied to classify species into IUCN Red List categories (CR: critically endangered; EN: endangered; VU: vulnerable) according to IUCN Red List guidelines, the IUCN advises against using SDM predictions to derive quantitative extinction risk estimates. To achieve reliable predictions, further research is needed to refine extinction–range loss relationships and improve uncertainty propagation (Zurell et al., 2023).

While the conceptual and methodological challenges of using SDMs for predicting extinction risk highlight several limitations, these models remain the most applicable tool for estimating species' future distributions under climate change.

The role of habitat fragmentation in the context of range shifts

Habitat fragmentation, driven by land-use and climate changes, results in the division of larger habitats into smaller, isolated fragments surrounded by human-transformed landscapes. The associated reduction in habitat area, increased isolation, and greater exposure to human activities at fragment edges lead to long-term structural and functional changes within the remaining habitat patches (Figure 7) (Haddad et al., 2015).

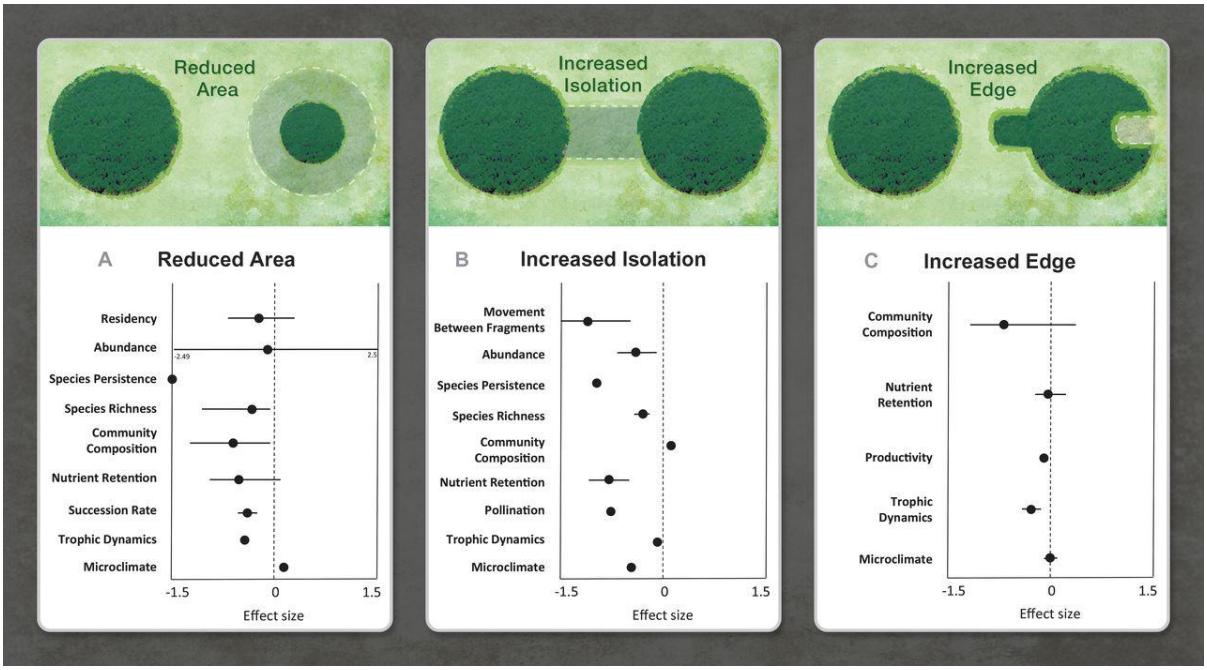


Figure 7. Fragmentation effects propagate across entire ecosystems (Haddad et al., 2015): (A–C) For each fragmentation treatment—reduced area (A); increased isolation (B); and increased edge (C)—major findings are summarized for ecological processes at various levels of ecological organization. Each dot represents the mean effect size, calculated as the log response ratio [ln(mean in more fragmented treatment/mean in non- or less-fragmented treatment)] for a given ecological process.

However, the exact role of habitat fragmentation has been the subject of debate. Early theories, such as those based on island biogeography (Macarthur and Wilson, 1967), provided a framework for understanding extinction dynamics in fragmented landscapes, which conceptualized natural habitats as "islands" surrounded by a "sea" of human-dominated landscapes. Despite this, the specific impact of fragment size and isolation, as opposed to the broader effects of habitat loss, remains a topic of contention (Fahrig et al., 2019).

Part of the controversy stems from the limitations of observational studies, which are often correlative in nature and tend to focus on single aspects of fragmentation (e.g., edge effects, isolation, or fragment size) (Collinge and Forman, 2009). However, experimental studies alongside correlative data reveal that habitat fragmentation exerts multiple, interconnected effects over long time periods, which further complicates the picture.

A comprehensive synthesis of fragmentation experiments across various biomes, continents, and timescales has shown that habitat fragmentation can reduce biodiversity by 13 to 75% and disrupt key ecosystem functions by reducing biomass and altering nutrient cycles (Haddad et al., 2015). These effects are most pronounced in smaller and more isolated fragments and intensify over time. This reinforces the concept of "extinction debt," where species' extinctions occur gradually after fragmentation, sometimes taking decades to fully manifest. Haddad et al. (2015) found that species richness in plants, arthropods, and birds in fragmented mature forests and replicated landscapes decreased by 20 to 75% after fragmentation. Some losses occurred almost immediately, while others continued to increase over the experiment's duration, demonstrating that fragmentation’s impacts can be long-lasting. On average, biodiversity loss exceeded 20% after just one year, 50% after a decade, and continues to rise in experiments

spanning more than two decades. Moreover, extinction debt is paid off more slowly in larger fragments, as theory predicts (Orrock and Watling, 2010).

In addition to extinction debt, two other key effects emerge. First, there is an "immigration lag," where small or isolated fragments take longer to accumulate species during community assembly (Jackson and Sax, 2010). Second, ecosystem function debt arises, manifesting as delayed declines in ecosystem processes like nutrient cycling and plant-consumer biomass. In small and isolated fragments, functional loss averaged 30% after one year and increased to 80% after a decade, compared to larger, more connected fragments (Haddad et al., 2015). These delayed effects underscore the complexity of fragmentation's impact, affecting both biodiversity and ecosystem functions on extended timescales.

Habitat fragmentation significantly alters functional connectivity, which refers to how an organism's behavior interacts with landscape structures to either facilitate or hinder movement among resource patches (Baguette et al., 2013). These changes in functional connectivity influence species distributions by modifying movement patterns, habitat use, and dispersal, which subsequently impacts population and community dynamics (Legrand et al., 2016). Furthermore, changes in dispersal ability due to phenotypic shifts can directly affect functional connectivity, and vice versa.

Fragmentation not only reduces suitable habitat, which directly lowers the carrying capacity of an area, but also increases population vulnerability. Smaller populations face heightened risks from genetic drift, demographic stochasticity, and environmental fluctuations. Empirical studies consistently show that local population extinction probability increases with isolation and decreases with population size (Pimm et al., 1993). Additionally, fragmentation increases distances between suitable habitat patches, reducing the likelihood of immigrant settlement, leading to functional isolation of local populations. This isolation diminishes the "rescue effect" (Brown and Kodric-Brown, 1977), where incoming individuals bolster declining populations, and lowers the recolonization rate of vacant habitats (Hanski, 1999), ultimately contributing to broader-scale extinctions.

A key approach to mitigating such extinctions is to promote connectivity among populations—reducing functional isolation—can support larger metapopulations, where individual movement among habitat patches enables persistence (Hanski, 1999). Metapopulation dynamics not only facilitate demographic rescue and recolonization but also enhance genetic mixing, reducing the risk of inbreeding and genetic erosion, which helps populations resist extinction.

The metapopulation concept offers a robust framework for species conservation in fragmented landscapes. One practical conservation strategy, derived from this theory, is enhancing landscape connectivity through the creation of corridors or stepping-stones. These facilitate movement between habitat patches, integrating them into functional ecological networks (Baguette and Van Dyck, 2007; Sawyer et al., 2011). Dispersal is the crucial process that allows these networks to function. Within landscape ecology and conservation biology, this process is generally conceptualized as landscape connectivity, which is essential for maintaining biodiversity and ecosystem functions in fragmented environments.

Functional connectivity is closely related to landscape connectivity, which refers to the degree to which landscape features either impede or facilitate the movement of organisms (Taylor et

al., 1993). This concept is fundamental in landscape ecology, movement biology, and conservation (Crooks and Sanjayan, 2006). Landscape connectivity influences individuals, populations, and communities through mechanisms such as demographic rescue, inbreeding avoidance, colonization of unoccupied habitats, altered species interactions, and the spread of disease (Hanski, 1999). It is particularly relevant for conservation strategies aimed at mitigating the negative impacts of human-induced environmental changes on biodiversity (Acevedo et al., 2015). A review examining the effects of connectivity on biodiversity found predominantly positive outcomes, including increases in occurrence, abundance, gene flow, or diversity. In fact, studies reporting positive effects outnumbered those reporting negative effects by more than five to one (Fletcher et al., 2016). Genetic studies overwhelmingly reported positive effects of connectivity, although research on species interactions showed more variability, with the highest proportion of negative effects (Fletcher et al., 2016).

Improving and maintaining landscape connectivity has the potential to alleviate the negative effects of climate and land-use changes. However, experimental evidence on fragmentation consistently demonstrates that habitat fragmentation has strong, degrading impacts on biodiversity and ecological processes. These effects are pervasive, affecting a significant portion of the Earth's terrestrial surface. Reduced fragment size, increased isolation, and greater edge exposure initiate cascading changes in ecosystems. Fragmentation can lead to persistent and often unpredictable consequences, including unexpected increases in the abundance of certain species, and many system responses only become apparent over long time scales (Haddad et al., 2015).

As human populations continue to expand, natural areas will face ongoing reductions and fragmentation, unless agricultural productivity and efficiency see significant gains (Foley et al., 2011). Currently, 1.53 billion hectares of the Earth's land surface are devoted to cropland, and this area could expand by 18% by mid-century (Tilman, 1999). Furthermore, urban areas are expected to triple in size, covering 0.18 billion hectares by 2030 (Seto et al., 2012). The capacity of surviving forests and other natural habitats to sustain biodiversity and ecosystem services will depend on the total remaining habitat area, its quality, the degree of connectivity between fragments, and the additional pressures from human activities such as climate change and invasive species.

Chapter 1

1.1 Principles and basis of Species Distribution Models

Species distribution models are among the most used tools in the fields of ecology, biogeography, and conservation. Common terms used synonymously for SDMs, or closely related models, include ecological niche models (ENMs), species range models, environmental or climate envelopes, habitat suitability and habitat distribution models, occupancy models, resource selection functions, abundance and N-mixture models. Often, these names emphasize different aspects of the entities being modelled: the niche, the distribution or the habitat preferences of species, or the data type used (Elith and Leathwick, 2009; Guisan et al., 2017; Peterson and Soberón, 2012). Species distribution modelling commonly requires two categories of data: (1) species data and (2) environmental data (Figure 8).

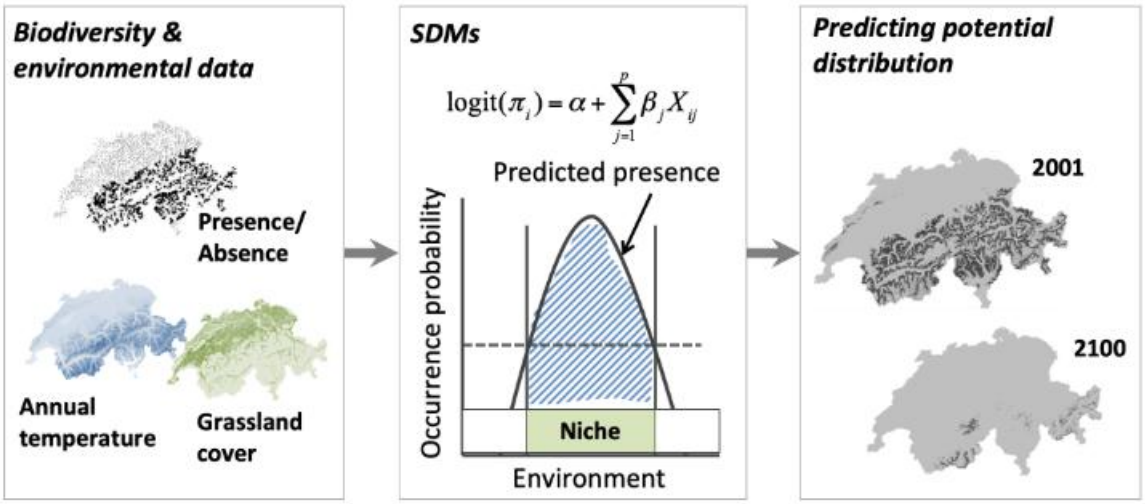


Figure 8. Schematic summary of SDMs: from main inputs to algorithms and spatial predictions (Damaris Zurell Github, https://damariszurell.github.io/SDM-Intro/).

Species data can be nominal (presence/absence records), ordinal (ranked abundances), or ratio (abundance and richness). Environmental data refers to both biotic and abiotic conditions. The most common types of environmental data in species distribution modelling are climatic and topographical variables since these two sets of variables represent, respectively, the large-scale conditions and small-scale conditions. There are various techniques for building SDMs. The choice of modelling technique is affected by the availability of data and in turn affects modelling outcomes. The accuracy of SDMs can be measured with respect to two characteristics: discrimination capacity and reliability; generally, discrimination capacity has been seen as a more crucial metric of model performance. Accuracy is an important challenge faced by SDMs. Several factors affect the accuracy of SDMs such as environmental data, species data, the ecology of the species, available computational resources, the model being utilized, and spatial resolution (Farashi and Alizadeh-Noughani, 2023).

The main five steps for building SDMs are: (1) conceptualization, (2) data preparation, (3) model fitting, (4) model evaluation, and (5) spatial predictions (Figure 9).

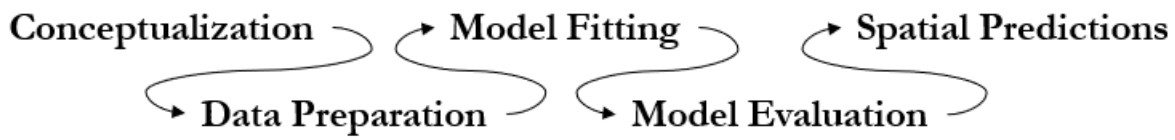


Figure 9. Main steps for building SDMs.

Interest in SDMs has grown significantly in the last 40 years. By the time, several important gaps have been filled, and significant steps forward have led to the development of several algorithms, and different types of SDMs, applied to address various issues in ecology, biogeography, evolution and, more recently, in conservation biology and climate change research (Guisan and Thuiller, 2005). The number of studies employing SDMs has increased tremendously over recent decades (Araújo et al., 2019; Sequeira et al., 2018), with > 1000 publications related to SDMs being released every year (Peterson and Soberón, 2012). Today, SDMs present the most widely used modelling tool for forecasting global change impacts on biodiversity (Ehrlén and Morris, 2015; Guisan et al., 2013). This increase in SDM studies is likely related to the increasing availability of digital data (Jetz et al., 2012) and easy-to-use software packages (e.g., Naimi and Araújo, 2016; Phillips et al., 2006; Thuiller et al., 2009) accompanied by detailed guides, manuals and textbooks (Guisan et al., 2017; Merow et al., 2013).

1.2 Conceptualization and overview

The conceptualization phase starts with the formulation of the aims of the study and the research questions; then, model and study setup based on any previous knowledge on the species and study system (Zurell et al., 2020). All the conceptual considerations should be summarized in the Overview section, which captures the skeleton of the analyses, providing enough information for readers to understand the model setup and workflow (Guisan and Zimmermann, 2000). In this phase, it is important to specify the focal organism(s), the type of biodiversity data, the type of environmental predictor variables, the spatiotemporal scale of the analyses, the underlying hypotheses about the biodiversity–environment relationship, the critical model assumptions, the chosen SDM algorithms and desired model complexity, and, lastly, the software used (Zurell et al., 2020). Overview thus provides a brief but informative summary of the basic modelling decisions and the modelling pipeline.

Following Araújo et al. (2019) it is suggested to clearly distinguish between three potential purposes of modelling: 1) explanation, 2) mapping and 3) transfer. If several or all of these purposes apply, it is recommended to regard these as nested (explanation < mapping < transfer). Nesting accounts for the fact that transfer should not be attempted without first having a thorough understanding of the model (inference) (Araújo et al., 2019). ‘Explanation’ (also termed inference) regards detailed analyses of species–environment relationships and aims to provide or test specific hypotheses about the main factors driving the species distributions. ‘Mapping’ or ‘Predicting’ (also termed interpolation) means that the estimated species–environment relationships are used to map (or interpolate) the species distributions in the same geographic area and time period in which the model was calibrated. ‘Transfer’ (also termed forecast or projection; but these terms are less precise) means that the estimated species–environment relationships are transferred to a different geographic region or time period – future or past (Zurell et al., 2020).

The data-related subsections of Overview should specify the focal taxon/taxa, the location of the study, the type of biodiversity data, the type of predictors and the spatial and temporal scales of analysis (Zurell et al., 2020). Then, it is suggested to specify the type of biodiversity observation (e.g. standardized monitoring, field survey, range map, citizen science, GPS tracking) and the data/response type used (e.g. presence-only, presence–absence, counts). In addition, the type of predictor variables should be indicated (e.g. climatic, topographic, habitat-related) (Zurell et al., 2020). Finally, information should be provided regarding the spatial and temporal resolution and extent of the study system. In all cases multiple answers are possible, to allow for studies across multiple regions, taxa and data types (Zurell et al., 2020).

Hypotheses about the expected biodiversity–environment relationship should clearly be presented, justifying what abiotic and biotic factors are taken into account to model the focal taxon, and the rationale behind these choices (Zurell et al., 2020). Occasionally, studies may not seem to build on a priori hypotheses but may be rather exploratory, particularly when modelling many species in an automated way. For instance, one could use climatic layers in an exploratory way because climate was known to be an important driver of species distributions at a continental scale.

Underlying model assumptions are often overlooked or unreported in SDM studies (Zurell et al., 2020). For example, when transferring SDMs under scenarios of global change, critical assumptions are that 1) all relevant environmental drivers are included in the model, 2) the species' observed distribution is in pseudo-equilibrium with the environment, 3) the entire realized niche is encompassed by data, 4) the correlation structure between predictors does not change between source and target landscape and 5) if extrapolation is involved, that the model extrapolates in a biologically sensible manner (Dormann et al., 2013; Elith, 2017; Feng et al., 2019).

Important technical aspects include the SDM algorithms being used, along with a verbal description of model complexity. The choice and number of SDM algorithms contained in any study may vary depending on modelling objectives and personal experience. For example, when SDMs are used for transfer under scenarios of global change, some scientists advocate using ensembles of SDM algorithms to account for algorithmic uncertainty (Araújo et al., 2019; Thuiller et al., 2019). In contrast, if explanation or mapping is the goal, many users select only one algorithm; for example, MaxEnt (Elith et al., 2011; Merow et al., 2013; Phillips et al., 2006) has been particularly prominent in recent years. However, the modelling decisions need to be clearly described and justified, and model complexity needs to be aligned with the model objective. Models can be more or less complex depending on the algorithm, but complexity also depends on several parameter settings that determine the flexibility of the response surface (Merow et al., 2014). Lastly, the Overview section should contain a brief description of the overall model workflow (or point to a flowchart in main text or appendix) and information on the software packages and version, and software environment used for modelling. Importantly, the availability of codes and data needs to be specified.

1.3 Data preparation

The Data section provides details about the species and environmental data, and about data processing. There are two mandatory subsections that should always be described: biodiversity data, and environmental data (Zurell et al., 2020). Two other subsections are optional: data

partitioning (for model assessment/evaluation), particularly important for mapping and transfer, and transfer data (Zurell et al., 2020).

The biodiversity data section should provide the taxon name(s). Although species are the most often used focal taxonomic unit, biodiversity models could also focus on populations, demographic traits, operationally defined taxa, functional types or traits, ecological communities, community traits or species richness, among others. Next, the data source needs to be described. If the data does not stem from one's own field surveys, then proper reference to the data source needs to be given. If the data stem from online data repositories such as GBIF (<http://data.gbif.org>), then information on accession date and/or of the source should be provided (Zurell et al., 2020). Sampling design and any details regarding temporal replications or nestedness of the data should also be described. If the data stems from online data repositories such as GBIF and OBIS, information should be supplied regarding the type of observations used, as these databases may include mixed data from museum specimens, opportunistic observations and monitoring data. It is crucial that authors report the sample size for the focal taxa, as well as prevalence in the case of presence–absence data (Zurell et al., 2020).

Absence, pseudo-absence and background data are an important topic for most SDM applications, and thus crucial to report. It is crucial to report how these absence data were obtained and how accurate they are. Many SDM studies are based on presence-only data. Most algorithms then require background data (also called 'pseudo-absences') against which the observed presences are compared (Renner et al., 2015). For example, when presence records are spatially biased, one could sample the background data such that they reflect the same spatial bias (Kramer-Schadt et al., 2013; Phillips et al., 2009). Or if GPS tracking data are used, then the background data derived for each logged GPS location could be drawn dependent on empirically observed distributions of movement distances and directions (Thurfjell et al., 2014). Thus, it is important to specify the geographic region from which background data are drawn, any biases induced in the background data, the number of background data points, and whether different strategies for background data derivation are used for different algorithms (Barbet-Massin et al., 2012).

Also, any steps taken to clean and scale the data, both spatially and temporally, should be detailed. Common data cleaning steps include the removal of outliers, duplicates, records pre-dating a specified year, and records with insufficient accuracy or associated information. A crucial step concerns the assessment of spatial autocorrelation (SAC) between presence data. Testing for spatial patterns both in the raw data and model residuals should be part of any SDM study, as spatial sampling bias could lead to environmental bias, resulting in an over-representation of some environmental conditions, altering SDM' performances and outcomes (Dormann et al., 2007). Methods include the use of Moran's I or Geary's c to measure the amount of SAC. In all cases a measure of similarity (Moran's I, Geary's c) or variance (variogram) of data points (i and j) is plotted as a function of the distance between them (dij) (Dormann et al., 2007). Moran's I-based correlograms typically show a decrease from some level of SAC to a value of 0 (or below; expected value in the absence of SAC: $E(I)=-1/(n-1)$, where n=sample size), indicating no SAC at some distance between locations (Dormann et al., 2007). Then, this distance could be used to filter and remove presence records (such as the R package 'SpThin' (Aiello-Lammens et al., 2015). However, this is just one among all the available methods to filter occurrences. However, when filtering the occurrences is important

to reduce the effects of biased sampling without reducing the signal of the species' niche (Anderson, 2012). The thinning of the occurrences can be obtained with a spatial (geographic space) or environmental procedure. Moreover, spatial thinning can be obtained with a stratified random sampling or with a nearest neighbor distance (as mentioned above) (Aiello-Lammens et al., 2015). Moreover, an important and common error is related to differences between the spatial resolution of environmental predictors and biodiversity data (Sillero and Barbosa, 2021).

Most ENM studies use gridded environmental data, such as raster maps, as predictor variables.

Setting an adequate spatial extent to calibrate the models is crucial for accurately capturing species–environment relationships and predicting potential species distributions (Chevalier et al., 2021; Thuiller, 2004). However, as conservation decisions and precise sampling campaigns are mostly taken at national, regional, or local levels, SDM studies are in turn rarely conducted at large spatial extents. This could lead to a spatially truncated representation of the range of the species (Chevalier et al., 2022). Spatial truncation may lead to environmental niche truncation when the calibration extent covers just a portion of species' geographical and environmental range (Pearson et al., 2004; Thuiller, 2004). Niche truncation implies an incomplete representation of species' ecological niche that underestimates the environmental conditions in which the species could exist. SDMs affected by niche truncation usually result in model transferability issues when projecting them to other periods or areas (Scherrer et al., 2021). Furthermore, geographically-restricted calibration extents are prone to greater dissimilarity between calibrated and projected environmental conditions (i.e., environmental extrapolation), which reduce SDMs transferability and accuracy (Qiao et al., 2019).

In such cases, the pixel size of environmental variables should correspond to the spatial resolution of the species records (Araújo et al., 2019; Feng et al., 2019).

This also applies to point occurrence records that may actually represent centroids of larger grid cells, such as many records available in online databases such as GBIF. Even when the spatial error is not explicitly reported, a visual inspection of the species occurrence map often reveals that many points are evenly spaced (e.g. currently on GBIF, many European mammals, amphibians and reptiles show regularly spaced points 10 km apart in both longitude and latitude). This indicates that those points result from surveys within grid cells of a fixed size, and their spatial error or resolution is the regular distance between those points (Sillero and Barbosa, 2019). The error in the species coordinates should be equal or inferior to the spatial resolution of the environmental variables. Otherwise, each occurrence record will count as if the species was observed exactly at the central pixel of the corresponding grid cell, while the environmental values at that pixel may be far from those at the place where the species was actually observed within the cell (e.g. a central valley in a mountainous region or vice-versa). Therefore, if species coordinates correspond to a grid of 10×10 km^2, then the environmental variables should be rescaled or aggregated (e.g. by calculating the mean, median, mode, minimum, or maximum) at this resolution (Sillero and Barbosa, 2019). Also, it is not necessarily useful to filter species records with a distance threshold (e.g. 10 km) corresponding to the spatial resolution of the variables (e.g. 10 km^2). Filtering records at such a level will not resolve the clustering degree of the species data. Clustering level must be analyzed at the spatial resolution of the environmental variables (in this case, 10 km^2) and not at a higher resolution (e.g. 1 km^2) (Sillero and Barbosa, 2019). To account for these potential issues, most SDMs'

packages have the opportunity to filter the occurrences removing all but one occurrence per cell.

In most SDM studies, one will assess model performance using data independent from those used for model fitting. If truly independent data from different sources are not available, it is common practice to partition data into training and testing sets. Any such data partitioning should be clearly specified (Zurell et al., 2020). It is recommended to clearly distinguish 1) training data that are being used for model fitting, 2) validation data that are withheld from model fitting and are used for estimating prediction errors for model selection, model averaging and ensemble building and 3) independent test data that are used to assess the generalization error of the final model. Here, the strategy for partitioning the data should be detailed. For example, validation data could be obtained by splitting the data randomly, or into spatially or environmentally stratified blocks for cross-validation (Roberts et al., 2017).

Although the overall types of environmental predictor variables (e.g. climatic, topographic) should be mentioned in the Overview section, the Environmental data subsection should clearly specify the individual environmental variables used. All relevant information should also be given about the data sources, the original spatial and temporal resolution and extent (Zurell et al., 2020). Furthermore, all data processing steps need to be described in detail, for example spatial and temporal scaling, thematic scaling (e.g. collapsing of categories), transformations and normalizations. Spatial and temporal coverage, resolution, and/or coordinate reference systems are likely to differ amongst predictor variables obtained from multiple data sources. Thus, any data harmonization steps need to be clearly described in the Data section (Zurell et al., 2020). In recent years there was an upsurge in the availability of digitally available geoinformation relevant for biodiversity modelling, spanning climatologies (e.g., Fick and Hijmans, 2017), land cover data (e.g., Copernicus Repository), and human impact data (Venter et al., 2016), among others. As these databases are under constant development, it is crucial to provide information on accession date and versioning. Environmental data are often subject to some form of dimension reduction, e.g. in the case of multi-collinearity (Dormann et al., 2013), meaning that not all available environmental predictors will enter the model fitting step.

If the main modelling objective is to transfer the model to different geographic regions and/or different time periods (Yates et al., 2018), then authors need to report information on the data used in the model transfer, i.e. the environmental data to which the model is projected (Zurell et al., 2020). If the transfer data stem from scenario modelling, for example future or past climate scenarios and land cover scenarios it should be explicitly specified and justified which underlying models (e.g. global circulation model, regional circulation model, global vegetation model) and scenarios (e.g. representative concentration pathway, shared socioeconomic pathways) have been used (Zurell et al., 2020). When transferring models, it is important to assess environmental novelty because the transfer data may include conditions do not present in the calibration data (i.e. in non-analogue situations) and, thus, the calibrated model may be forced to extrapolate (Sequeira et al., 2018). Thus, is important to specify exactly how novelty was defined and quantified; for example, novel environments along single environmental gradients (Elith et al., 2010) or novel combinations of environments (Zurell et al., 2012). In addition to environmental novelty, modeling algorithms may also be sensitive to differences in collinearity structures of training and projection environments (Dormann et al., 2013), thus assessments of collinearity shifts can help evaluate the accuracy of model projections (Feng et al., 2019).

1.4 Model fitting

The Model section reports all the information necessary to repeat the model building. Six subsections have been identified: three are mandatory (multicollinearity, model settings/model complexity, analysis of non-independence of data), two are context-dependent (variable pre-selection, model selection/model averaging/ensembles) and one is relevant for mapping and transfers only (threshold selection) (Zurell et al., 2020).

Different strategies exist to deal with multicollinearity, some of which will reduce the number of environmental variables to a set of reasonably correlated predictors (Dormann et al., 2013). In that sense, dealing with multicollinearity could also be seen as a data processing step. However, some strategies also involve the response variable and some preliminary model fitting, or deal with multicollinearity as part of the model building process (e.g. regularization). The strategy and rationale for selecting the final set of predictors should be clearly described. Building models with highly correlated variables can have several undesired effects (Júnior and Nóbrega, 2018): the null hypothesis can be wrongly rejected; coefficients can significantly change and even reverse their sign; insignificant variables can be selected. Moreover, the model can suffer from over-fitting, being adjusted excessively to the data (possibly reflecting noise); and it may be not possible to disentangle correctly the response curves for each variable, as each variable will interact with others, hampering to obtain the actual response curves. Collinearity affects models trained on data from one region or time and projected to another with a different or unknown structure of collinearity (Dormann et al., 2013). However, truly independent response curves can only be obtained when using orthogonal variables, such as the results of a principal components analysis (PCA). Since is very difficult to have completely uncorrelated variables, a compromise is to select among the most correlated variables for the analysis. Traditionally, the correlation threshold is around 0.7 or higher (Dormann et al., 2013), because going below is very difficult as the number of variables might become too low. Other approaches for dealing with collinearity are latent variable methods, shrinkage and regularization (Dormann et al., 2013). When models are projected to other scenarios in space or time, PCA cannot be computed directly for those new scenarios, as the collinearity structure between variables can change with space and time. Individual PCAs may not be equivalent with different dimensions of predictors when transforming the variables over independent orthogonal spaces. Thus, a PCA for the baseline climate must be computed, using its coefficients to compute the components from the other scenarios. As is required in PCAs, all variables must be standardized and centered by using the parameters from the baseline climate. The most important variable for the model will be the first component, as it accounts for the highest variability of the set of variables. It will be necessary to analyze the contribution of each variable inside each principal component. In the remaining methods, it is necessary to evaluate the correlations between variables and exclude redundant ones (e.g., Leroy et al., 2014). Also, the Variable Inflation Factor (VIF) can aid in the selection of variables to be included in the models: the R package usdm provides useful tools for this issue (Naimi, 2015).

Detailing the choice of algorithms, specific model settings and model complexity is key to ensure methods reproducibility.

Building SDMs typically includes fitting a statistical relationship between species occurrence data and environmental data. Many techniques and implementations exist to fit these mathematical functions, but this rapidly developing field still lacks consensus regarding which algorithms are the best for which purposes (Araújo et al., 2019). Regression-based models

extend envelope and similarity approaches by modeling variation in species occurrence or abundance within the occupied environmental space and selecting predictors according to their observed importance. GLMs were commonly used in early analyses of presence-absence and count data, often with simple additive combinations of linear terms. As the common occurrence of nonlinear species' responses to environment was recognized, more studies included quadratic, cubic, or other parametric transforms. Generalized additive models (GAMs) are similar to GLMs but use data-defined, scatter plot smoothers to describe nonlinear responses (Elith and Leathwick, 2009). They have provided useful additional flexibility for fitting ecologically realistic relationships in SDMs. Regression methods are widely used by ecologists. More generally, many SDM methods are regression-like, assuming that a species' occurrence or abundance can be modeled using additive combinations of predictors, and sometimes also including manually selected terms representing interactions between predictors (Elith and Leatwick, 2009).

As SDM applications focused more on prediction, researchers looked to methods developed especially for prediction, including those in the machine learning and data mining communities. Examples include ANNs (Olden et al., 2008), multivariate adaptive regression splines (MARS) (Moisen and Frescino, 2002), classification and regression trees and ensembles of trees (random forests (RF) (Prasad et al., 2006); boosted regression trees (BRT) (Elith et al., 2008)), support vector machines (SVM) (Drake et al., 2006), and maximum entropy models (MaxEnt) (Phillips et al., 2006). Some of these provide well-controlled variable selection and coefficient estimation, and several are capable of automatically detecting and fitting interactions between predictors. As a consequence, their predictive performance may exceed that of more conventional techniques (Elith et al., 2006). While the complex and sometimes "black-box" nature of these techniques has perhaps limited their use, particularly for studies focusing on ecological insight, tools for visualizing and summarizing these models in ways relevant to ecologists are increasingly available.

Currently, most packages implement several algorithms, and in some cases the chance to make ensemble of different algorithms (e.g., Velazco et al., 2022; Vignali et al., 2020). The great availability of model algorithms poses challenges about their choice. In addition, SDM predictions can vary depending on the fitted model (Hallgren et al., 2019), which could result in substantial change in decisions made based on their prediction (Muscatello et al., 2021). Consequently, there is ongoing interest in assessing the predictive performance of different modeling methods to understand whether some tend to perform generally better than others.

Basically, is possible to classify the algorithms in three different groups: regression-based models, tree-based models, and other models.

Regression-based models, such as GLMs and GAMs are commonly used in species distribution modeling. GLMs use parametric functions such as linear or higher-degree polynomials to model the relationship between the response and predictors. GAMs use nonparametric smooth functions to allow nonlinearity in the fitted functions. There are several options for fitting GLMs, with modern regularization methods often performing well (Reineking and Schröder, 2006). Lasso and ridge regression (L1 and L2 regularization, respectively) penalize the coefficients and shrink them toward zero (Friedman et al., 2010). This shrinkage reduces the variance of the regression model (i.e., its stability over different data samples), hence the fitted model may generalize better. Unlike ridge regression, lasso can reduce the coefficient of

variables to exactly zero, de facto excluding those variables and resulting in sparser models (Hastie et al., 2009). A recent comparison showed penalized regression to perform as well as MaxEnt (Gastón and García-Viñas, 2011). Since MaxEnt is often regarded as having strong predictive performance, this suggests these regularization approaches may be useful for predicting species distributions. MARS is a flexible nonparametric regression similar to GAMs but using piecewise linear basis functions instead of smooth functions (Elith and Leathwick, 2007). MaxEnt is a popular modeling method for predicting species distributions, specifically developed for modeling presence-only species data (Phillips et al., 2006), and its related to regression methods (even if also similar with tree-based models). MaxEnt has the flexibility to fit more or less complex models depending on the number of species records and user-defined settings. Complexity is controlled by use of transformed features of the predictor covariates (including linear, quadratic, product, hinge, and threshold) and by choice of regularization settings (Elith et al., 2011). MaxNet is a new, alternative implementation of MaxEnt (Phillips et al., 2017), motivated by new understandings of the link between MaxEnt and Poisson point process models (Renner and Warton, 2013). It uses infinitely-weighted logistic regression (Hastie and Fithian, 2013) to fit the MaxEnt model and it is developed as an R package with no need for external software. Both MaxEnt and MaxNet use L1 regularization (Elith et al., 2011), similar to Lasso.

Tree-based models, such as classification and regression trees are nonlinear (and nonparametric) models that recursively partition ("split") the predictor space into sections with similar values of the response variable (Elith, 2019). This is a conceptually simple method that has several advantages such as reliably selecting influential covariates and allowing automatic fitting of interactions between covariates (Strobl et al., 2009). Single trees are high-variance methods, changing with each training data set. They are also poorly suited to estimating smooth functions. This limits their predictive performance, but they are commonly used as the base learner in ensembles of trees, often highly effective for prediction (Hastie et al., 2009). Tree-based models are often categorized as machine-learning models. With the BRT hundreds to thousands of regression trees are selected into an ensemble in a forward stagewise fashion. At each step of model fitting, the algorithm focuses on the weakest parts of the model built so far (the observations that so far are not predicted accurately) by fitting each new tree to the residuals of the previously fitted trees (Elith et al., 2008). The XGBoost algorithm (Chen and Guestrin, 2016) is a new and slightly different form of gradient boosting with several features intended to improve its scalability and control over-fitting (Prasad, 2018). The application of XGBoost in species distribution modeling is rare. This might be due to the fact that XGBoost is relatively new and that, as it is highly flexible, it includes many hyperparameters that need careful tuning (Muñoz-Mas et al., 2019). RF has become popular for SDMs. This modeling method approaches ensemble creation differently to BRT, not using a stagewise approach but instead using bagging (bootstrap aggregation) to combine many trees. Bagging involves taking many bootstrap samples from the training data, fitting a tree to each sample and making an average prediction over all fitted trees (Strobl et al., 2009). Unique to this method, RF uses only a random subset of the predictor variables (parameter mtry) on each split while growing each tree. This creates decorrelated trees and reduces the variance of the final model, with consequent gains for predictive performance (Hastie et al., 2009). An advantage of RF compared to similar methods such as BRT and XGBoost, is that it is not very sensitive to tuning the model parameters (Freeman et al., 2016; Strobl et al., 2009). These characteristics have made RF a relatively common SDM approach (Mi et al., 2017).

Among the other models there is SVM, a nonparametric machine-learning technique for regression and classification problems that has been used for modeling species distributions (Ashraf et al., 2017; Drake et al., 2006). SVMs work by defining linear hyperplanes that best separate different classes in the data. Similar to linear regression models, SVM can use nonlinear forms of the predictor variables for increased flexibility.

Model averaging, or ensemble, is a popular technique for reducing the uncertainty of model predictions (Dormann et al., 2018). For SDMs, it has become popular to average across predictions from different methods, based on the idea that prediction uncertainty due to the choice of method is decreased (Araújo and New, 2007). The package BIOMOD is specifically written for modeling species distributions (Thuiller et al., 2009), building ensembles across several modeling methods. It includes 10 algorithms, some of them used in our study (including GAM, GLM, BRT, RF, and MaxEnt), and combines the prediction of these models (e.g., by weighted averaging of the predictions). The BIOMOD model has become a popular modeling approach with widespread use but narrower dedicated exploration of its predictive performance (Hao et al., 2019). Now, several R packages have implemented several single algorithms with the possibility of creating an ensemble, with different average strategies. It is possible also to build several models, and then 'manually' create an ensemble.

Most algorithms have several parameters that need to be defined. Since this step could require a huge processing time, most algorithms can be hyper-parameterized with a tuning procedure, where several parameters are defined and the models are run while their performance is measured, with the aim to select the model's parametrization leading to the best performance. Several R packages (such as 'SDMtune', 'flexsdm', and 'biomod2') have specific functions for tuning the models, but the hyperparametrization can be also computed manually.

Another technique is the weighting approach, where the background points (or the pseudoabsences) are down-weighted to have a total (summed) weight equal to the total weight of the presences, and there are several specific techniques to assign the weights.

After obtaining the final model, and projecting it into space, it is possible to select a threshold to obtain binarized predictions. In the case of a binary response variable, most SDM approaches produce continuous outputs such as habitat suitability indices or probabilities of occurrence. Whilst there are good arguments for retaining predictions on a continuous scale (Lawson et al., 2014), some users prefer to threshold them for certain applications. To do so, they need to define an adequate threshold to transform the data. Several different thresholds have been proposed depending on whether the presence–absence or presence-only data are being used for modelling (Liu et al., 2013).

1.5 Model Evaluation

After model building, typically a series of analysis steps are aimed at assessing whether the modelled biodiversity–environment relationships are fit for purpose. Irrespective of the model aim, assessing predictive performance on (semi-)independent data informs about generalizability and overfitting (Hastie et al., 2009). Constructing partial plots (= effect plots, response curves, marginal responses, Elith et al., 2005) provides an intuitive way to evaluate the ecological plausibility of the fitted model. Plausibility could also be checked by inspecting the spatial (and/or temporal) predictions. Both plausibility checks are a form of expert judgement.

Performance statistics are important for assessing the validity of a model for a specific goal and for comparing models, and different statistics are under constant development and testing. For most response variables, e.g. for abundance and presence–absence data alike, distance measures between hold-out data and prediction are potentially suitable (Sequeira et al., 2018). These include the root–mean–square–error (RMSE), log-likelihood, various variations of R^2. For presence–absence data, it is distinguishable threshold-independent measures such as the AUC (area under receiver-operating characteristic curve ROC, Swets, 1988), explained deviance and log-likelihood, and threshold-dependent indices (Guisan et al., 2017). The latter are typically based on the confusion matrix (e.g. correct classification rate, sensitivity and specificity, precision, Fielding and Bell, 1997), are sensitive to the prevalence and cannot be interpreted without it. When reporting thresholded indices, such as the true-skill statistic (Allouche et al. 2006). Lastly, for presence-only methods alternative performance measures have been introduced that avoid using a confusion matrix, such as the Boyce index (Boyce et al., 2002; Hirzel et al., 2006).

The ecological plausibility of the model and model predictions can be checked by inspecting the response shape of the fitted biodiversity–environment relationship and by inspecting the mapped predictions. Response shapes are one of the most important outputs of SDMs as they summarize the estimated species–environment relationship and can thus be directly subjected to plausibility checks against available biological knowledge. For example, when the input data were selected to approximate drivers known to be ecologically important, we can determine whether the model represents plausible relationships between the drivers and the species' occurrence. Checking the plausibility of the functional relationships in a model is also particularly important when the model is used to transfer the species–environment relationship to new time periods and regions (Thuiller et al. 2004). Generally, response shapes can be visualized using more traditional partial dependence plots, evaluation strips (Elith et al., 2005) or inflated response curves, which also help to identify extrapolation (Zurell et al., 2012). Furthermore, such plots indicate the range of predictor values present in the calibration data, beyond which predictions would rely on modelling assumptions (Qiao et al., 2019) and become less reliable.

1.6 Spatial Predictions

Often SDMs are used to make spatial (or temporal) predictions to new sites including mapping (interpolating) and/or transferring (extrapolating). These predictions can be on a continuous scale (e.g., 0-1), or presence-absence map, based on the selected threshold. Also, for some SDM algorithms there may exist alternative interpretations of outputs, e.g. MaxEnt and point process models where predictions could be interpreted as relative occurrence rates or relative densities, depending on assumptions about the data (samples of species versus samples of individuals, respectively). Second, any post-processing steps undertaken after predicting are detailed here. This could include clipping the predictions to a specific region or land cover map, e.g. clipping predicted butterfly occurrences to where the host plant is predicted to occur.

Chapter 2

2.1 Connectivity Modeling

Landscape connectivity, commonly defined to be the extent to which a landscape facilitates organism movement, is an emergent and dynamic phenomenon based on the cumulative movement pathways of individuals across time and space. Conceptually, it provides a tractable and powerful methodology for analyzing and mapping organism movement patterns, and its widespread utility has been established across an enormous body of ecological work (Rudnick et al., 2012). As such, the theory, modelling and prediction of landscape connectivity has grown to become a central focus of applied ecology and conservation science (Cushman et al., 2013a). Consequently, several techniques have been developed to compute different measures of functional connectivity.

Simplified approaches to connectivity models such as identifying the most efficient movement route (i.e., least cost path (LCP)) (Adriaensen et al., 2003) between focal patches, or the range and relative likelihood of potential pathways in response to a modeled landscape (i.e., Circuitscape) (McRae et al., 2008). These approaches facilitate the modeling of movement processes and can be used alone or in combination to consider many types of conservation and management questions. Furthermore, recently new techniques have been developed, such as the Stochastic Movement Simulator (SMS) (Palmer et al., 2011). The most used techniques are LCP and Circuitscape. Circuitscape, based on electrical circuit theory, runs current across resistance surfaces where each pixel is a node and the resistance values between pixels are the resistors. The Circuitscape algorithm results in an estimated current density for each pixel on the landscape, with higher values of current representing higher probabilities that a random walker will pass through a pixel. LCP algorithms calculate the cumulative cost from source points across a resistance surface. Cost distance surfaces from two source points can be paired, and troughs can be identified where the cumulative cost and distance between the two points are minimized. Most often, a single, least-cost corridor is derived from these surfaces, although the surfaces can also be bounded at some upper connectivity value to derive multiple paths. The advantage of Circuitscape is that it does not assume an individual has complete knowledge of the landscape through which it is travelling (Zeller et al., 2018).

2.2 The resistance surface concept

Most of the techniques are based on the creation of a resistance (or cost) surface. This layer represents the willingness of an organism to cross a particular environment, the physiological cost of moving through a particular environment, the reduction in survival for the organism moving through a particular environment, or an integration of all these factors (Zeller et al., 2012). The use of resistance surfaces allowed the transition from connectivity models based on homogeneous landscapes to those capable of incorporating the effect of different landscape characteristics on the species dispersal and gene flow (Spear et al., 2010; Zeller et al., 2012).

Resistance estimation is most commonly accomplished by parameterizing environmental variables across a 'resistance' or 'cost' to movement continuum, where a low resistance denotes ease of movement and a high resistance denotes restricted movement, or is used to represent an absolute barrier to movement.

There are different methods to quantify resistance to movement, and in general there is no general consensus. Indeed, in most cases resistance surfaces are computed based on expert-opinion, genetic data, and habitat models (e.g., based on presence-only data) (Zeller et al., 2018, 2012). Even if resistance estimation from dispersal data may be the most appropriate technique, these data are extremely difficult to obtain and when it is available, sample sizes are typically low (Fagan and Calabrese, 2006). However, several studies have shown that while some connectivity patterns are influenced by the method in which the resistance surface is created, others, such as circuit-based algorithms, show no difference (Zeller et al., 2018). Furthermore, when Circuitscape and LCP algorithms have been compared, the first tended to outperform the latter in capturing dispersal movements (Jackson et al., 2016; McClure et al., 2016).

In recent years, the use of SDMs (and thus of habitat suitability layers) to obtain a resistance layer is increased. When using a habitat suitability layer as the basis for the creation of a resistance surface, several studies demonstrated that a linear transformation is not the most appropriate (Keeley et al., 2016; Zeller et al., 2018). Particularly, a negative exponential transformation to resistance from habitat suitability is more appropriate than a negative linear transformation (Keeley et al., 2016; Zeller et al., 2018).

$$\mathrm{R} = 1{,}000 - 999 \times \frac{1 - \exp(-\mathrm{c} \times \mathrm{h})}{1 - \exp(-\mathrm{c})}$$

2.3 Resistance-based connectivity modelling: least-cost path (LCP)

Landscape resistance is point-specific: each pixel reflects the estimated difficulty of moving through that specific location in the landscape. It inherently does not account for the emergent routes through the landscape, which is the central focus of landscape connectivity. Resistance-based connectivity models thus typically work by applying a movement algorithm to a resistance surface to obtain predictions of landscape connectivity (Cushman et al., 2013a). The first resistance-based models of landscape connectivity calculated the 'least-cost path' between two points on the resistance surface, as an approximation to the most favorable movement paths in a landscape (Adriaensen et al., 2003). LCP models were first developed in the geographic transport context and consist of identifying the path with the lowest cost distance among all possible paths linking predefined sources and destinations (Etherington, 2016). Most LCP methods convert the resistance surface into a weighted lattice graph, structure where raster cells are represented by their centroids (nodes) connected by weighted edges, which are in turn

determined as functions of both Euclidean distance and cost or resistance units (Etherington, 2016). Then an algorithm (the graph theory shortest-path the most commonly used (Dijkstra, 1959)) is applied to find the combination of edges with the lowest accumulated cost-distance linking a pair of source/destination sites. In the end, the calculated LCP distance will be the sum of the edge weights along the LCP (i.e., its accumulated cost (Etherington, 2016)). In other words, they computed the route which minimizes the accumulated cost of movement between two points. This was later extended by Cushman et al., (2009) to produce a network of least-cost paths between all combinations of any number of source points. However, there are severe limitations to these least-cost path approaches in practice. Centrally, there is little reason to assume that an animal knows (or even thinks in terms of) the route of the least-cost path. Moreover, the destination point may not be known to the animal prior to or during movement—and even if this were so, obtaining the knowledge of their precise destination can be very difficult in practice, especially with dispersing animal (Unnithan Kumar et al., 2022b). Finally, the LCP path has a 1-pixel width, which is dependent on the resistance surface resolution, and proposing these narrow paths as corridors may not be suitable for many species.

To work around these problems, some authors have modified and implemented additional steps inside the classic LCP path routine. A factorial application, for instance, computes the LCP paths for all pairwise combinations among the sources/destinations, thereby providing a broader perspective of species population connectivity (Rudnick et al., 2012). Considering multiple additional suboptimal routes or smoothing the LCP paths using a probability density function have been used to deal with the unrealistic assumption of a single optimal path with a 1-pixel width (Landguth et al., 2012; Pinto and Keitt, 2009). For example, Cushman et al., (2013b) implemented factorial least-cost corridor analysis which couples' computation of all pair-wise paths in a system of nodes with resistant kernel buffering to provide a spatially synoptic and biologically realistic model of connectivity across a continuously distributed population in a heterogeneous landscape.

Further algorithms for predicting connectivity have since been developed, with the great majority still using the framework of landscape resistance. Presently, two major connectivity models in use are 'resistant kernels' and 'Circuitscape' (Compton et al., 2007; McRae et al., 2008). Resistant kernel is a cost-distance approach based on Dijkstra's algorithm, which estimates connectivity as a function of landscape resistance and dispersal thresholds; it produces a map of connectivity by summing together the expected dispersal density in the pixels around each source point. Circuitscape uses electrical circuit theory, in which the resistance surface is treated as a circuit and animals are modelled as electrons 'flowing through this circuit', with mortality and connectivity quantified by the mathematical relationships of circuit theory. This algorithm produces a map in which the current flowing through each pixel of the resistance surface is assumed to reflect the degree of connectivity (McRae et al., 2008). In both cases, animals are modelled as automatons moving according to simple rules from graph theory or random walk theory.

Basically, the choice among the different possible techniques depends essentially on the purpose of the study (Kool et al., 2013). For example, some studies aim to evaluate the importance of discrete landscape elements for connectivity (e.g., habitat patches), while others focus on identifying potential movement routes. In the first case, connectivity indices, such as the popular habitat availability indices, are commonly used (e.g., Diniz et al., 2018); in the

second one, approaches based on movement path modeling can be applied (e.g., Osipova et al., 2019).

2.4 Resistance-based connectivity modelling: circuit-theory techniques

The application of a circuit theory-based model to understand evolutionary and ecological processes was only possible thanks to the previously established theoretical relationship between electric circuits and random walk on analogous graphs (Dickson et al., 2019; McRae et al., 2008). A random walk is a modeled movement of an organism where one step is taken independently of the previous one, making the displacement process absolutely stochastic in a landscape. Electrical nodes in a circuit are used to represent landscape matrix cells and habitat fragments, and the resistors that connect them indicate functional connections such as dispersal (McRae et al., 2008). The resistance value offered to the current in the resistors represents the difficulty imposed by a landscape element (e.g., land cover) or a set of them to animal movement.

Circuitscape, which is the reference models among the circuit-theory techniques, requires a raster representation of the landscape, where cells with finite resistance will be transformed into electrical nodes while cells with infinite resistance are dropped and used to represent complete barriers to movement (McRae et al., 2008). Cells belonging to habitat patches that are sources and destinations of individuals' movement have zero resistance and are converted into single nodes (McRae et al., 2008). Resistors are placed between each node and its four or eight neighboring nodes, with resistance values generally defined as the means of the cells' resistance being connected (McRae et al., 2008). After the landscape has been converted into a large electrical circuit, to analyze the current flow between two habitat patches, one node is usually connected to a current source (source patch) and the other is connected to ground (destination patch). The Ohm's and Kirchhoff's laws are applied through the nodal analysis method to determine voltages at each node, and then the currents passing through individual resistors or nodes are calculated (McRae et al., 2008). As circuit theory is linked to animal movement via random walk, the current value flowing through a resistor is equal to the expected net number of times that individuals moving randomly starting at a source location or patch will cross that branch before reach a destination patch (McRae et al., 2008). From the mapping of current density along the landscape, it is possible to visualize and identify movement patterns and, consequently, the most important routes for connectivity throughout the study area (e.g., McClure et al., 2016). The higher the current value in a landscape cell, the greater the net passage probability for individuals moving randomly from a source to a destination (McRae et al., 2008). The current values also allow the identification of pinch points, generally narrow areas that have a high current value because they condense many potential paths (McRae et al., 2008; Pelletier et al., 2014).

Moreover, Circuitscape can be run in four different methods: 'pairwise', 'one-to-all', 'all-to-one', and 'advanced'. In the 'pairwise' mode, the current is computed between each pair of nodes so that each node is both the source and the destination, differently with what happen in the 'one-to-all' and the 'all-to-one'. In contrast, in the 'advanced' mode, the user needs to specify the sources and the destinations, and the current will be computed only one time between them. A common issue within Circuitscape is the crucial importance of the nodes for the connectivity predictions. In fact, sometimes these nodes can be rarely identified, and moreover, the position of the nodes can influence even heavily the results. Thus, an omni-directional implementation of Circuitscape has been proposed several times (Koen et al., 2014;

McRae et al., 2016; Pelletier et al., 2014). In some approaches, the nodes are positioned within a buffer, but out of the study area, and in every direction, so that their position did not alter the final results, where the nodes within the buffer are clipped out (Koen et al., 2014). More recently, a new model has been implemented, called Omniscape, which is a circuit-theory technique similar to Circuitscape and greatly flexible (Landau et al., 2021). Omniscape applies Circuitscape in the 'advanced' mode iteratively within a moving-window framework where the user needs to specify the search radius, by computing connectivity between the cells (the user specify if all cells are potentially a source, or if only the cells with certain values can be used as sources). Moreover, Omniscape allows the integration of nodes, modelling connectivity between these nodes, but always considering the specified search radius, which should reflect the movement ability of the target species (Landau et al., 2021).

2.4 Individual-based models and approaches to connectivity

The connectivity models described so far use resistance surfaces to parameterize the energetic 'cost' of moving through the landscape, but this is only one of many factors influencing movement. For example, resistance-based connectivity models do not account for the autocorrelated nature of animal movement (Cushman, 2010)—as acknowledged with Circuitscape in McRae et al., (2008)—despite the present state of an animal's movement being strongly influenced by their immediate past direction of travel (Dray et al., 2010).

By the time, research in connectivity modelling has sought to craft detailed individual-based models which also attend to variations in landscape composition. Despite some approaches in the recent past (e.g., DeAngelis and Mooij, 2005), interesting steps forward have been made in the last years, with the implementation of Pathwalker (Unnithan Kumar et al., 2022a), HexSim (Schumaker and Brookes, 2018) and RangeShifter (Bocedi et al., 2021), the latter also available in R ('RangeShiftR', Malchow et al., 2021). Pathwalker simulates organism movement and predicts connectivity on a resistance surface as a function of several parameters other than energetic cost, including mortality risk, autocorrelation, and bias towards chosen locations, all at multiple spatial scales (Unnithan Kumar et al., 2022a). HexSim allows for the use of multiple resistance-like surfaces which approximate landscape features such as food and nesting resources, in addition to a measure of the energetic cost of movement from a traditional resistance surface (Schumaker and Brookes, 2018). RangeShiftR is a modular framework that is able to compute several outputs, from population viability analyses to connectivity. The latter is computed with three different methods: resistant kernels, stochastic movement simulator, and correlated random walk (Malchow et al., 2021). In particular, RangeShiftR take into account three different phases for the dispersal process: emigration, transfer, and settlement. Thus, it includes several species-specific parameters, making the dispersal process more realistic.

For example, the stochastic movement simulator, first introduced by Palmer et al., (2011), models animal movements between habitat patches across a heterogeneous matrix. The model integrates features of LCP, with stochastic movement processes, but relaxing some assumptions. In fact, it does not assume omniscience, nor does it assume that an individual has a planned destination when it leaves a habitat patch. The algorithm incorporates resistance values for matrix elements and parameters that relate to both perceptual range and to the degree of correlation in movement (Palmer et al., 2011).

Although these models still make use of resistance surfaces to provide the spatial input data, all three afford greater complexity to animal movement behavior than models like Circuitscape and resistant kernels and can straightforwardly be adapted to include additional parameters. For example, by simultaneously varying spatial input data with mortality risk, spatial scaling and directionality bias (Unnithan Kumar et al., 2022b).

Chapter 3

3.1 The Habitat Functionality Concept

Anthropogenic impacts on species' ranges are commonly evaluated using ecological models, such as species distribution models (Guisan and Zimmermann, 2000) and resource selection models (Manly et al., 2002). These models typically explore the factors influencing species and population distributions by assessing habitat suitability in environmental space, which reflects the conditions necessary for species' persistence (Guisan et al., 2017). While species distributions are shaped by both biotic and abiotic conditions, they also depend on the species' ability to access suitable habitats, as articulated in the biotic–abiotic–movement (BAM) framework (Figure 10) (Soberon and Peterson, 2005).

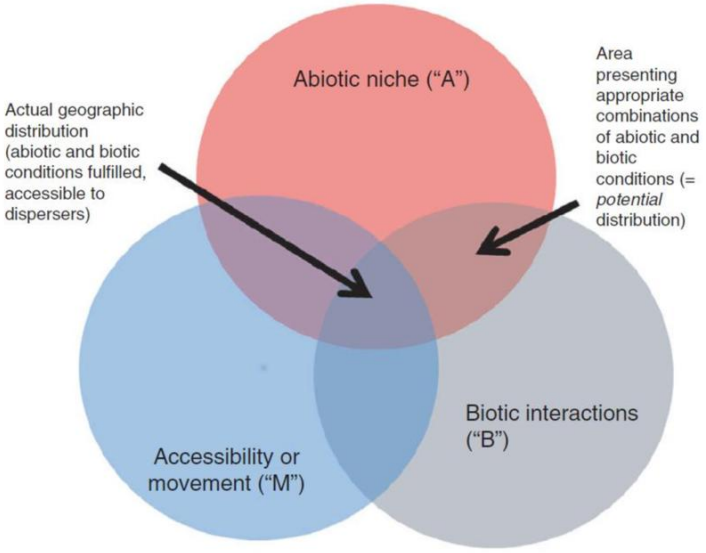


Figure 10. The BAM diagram, introduced by Peterson and Soberón (2012), is a conceptual framework used in ecology and biogeography to represent the factors influencing species' geographic distributions. It is based on three key components: Biotic factors (B): Interactions with other species, such as competition, predation, mutualism, and parasitism, which influence where a species can persist. Abiotic factors (A): Environmental and climatic conditions (e.g., temperature, precipitation, soil type) that define the fundamental niche of a species. Movement/Access (M): The spatial accessibility of areas to a species, determined by its dispersal abilities, historical biogeography, and barriers to movement (e.g., mountains, oceans, or human-made structures). The overlap of these three components defines the actual geographic distribution of a species.

Despite the importance of movement in determining species distributions, approximately 80% of studies fail to incorporate it (Holloway and Miller, 2017; Seaborn et al., 2020). This omission contributes to discrepancies between habitat suitability model predictions and actual observed distributions, where species may be absent from otherwise suitable habitats due to dispersal limitations (Matthiopoulos, 2022). A key challenge to integrating movement into niche models is that while habitat suitability is assessed in environmental space (E-space), accessibility must be evaluated in both geographic space (G-space, i.e., longitude, latitude, and altitude) and topological space (T-space, i.e., species-specific ecological connectivity between landscape units; (Jordán and Scheuring, 2004)).

Although habitat suitability maps are often projected onto G-space, spatial relationships—such as distance and connectivity between suitable habitat patches—are frequently overlooked

(Matthiopoulos et al., 2020). As a result, high-resolution maps can identify small, isolated habitat patches that, while suitable in E-space, are functionally unsuitable because they cannot sustain individuals or populations. In other words, despite biotic and abiotic conditions being favorable, a habitat may be inaccessible or disconnected from other suitable habitats in G- or T-space.

To address these limitations, recent research introduced the concept of 'habitat functionality' (Van Moorter et al., 2023), defining functional habitats as areas that are both environmentally suitable and connected to other suitable habitats.

Chapter 4

4.1 Individual-based models

As already described, to infer a species' niche from data and make predictions in space and time, correlative species distribution models (SDMs) are commonly used tools (Elith and Leathwick, 2009; Guisan and Zimmermann, 2000). However, these methods often incorporate little ecological theory (Guisan and Thuiller, 2005) and usually require making assumptions that are routinely violated in natural observed systems (Elith et al., 2010; Jarnevich et al., 2015). For example, SDMs assume that species are at equilibrium with their environment and ignore any transient dynamics (Zurell et al., 2016). An alternative that avoids some of these drawbacks is the development and application of mechanistic models, which aim to simulate relevant eco-evolutionary processes such as dispersal, demography and evolution (Urban et al., 2016).

The ambition for a more prominent representation of process-based models in ecological research led to the development of the standalone software RangeShifter 2.0 (Bocedi et al., 2021), a flexible individual-based model (IBM) that simulates spatial eco-evolutionary dynamics for a given species. It models population dynamics, dispersal and evolution as interacting processes, organized within a modular structure in which each process has a number of modelling options. This makes RangeShifter 2.0 a highly adaptable platform with a wide range of applications, including conducting population viability or connectivity analyses (Aben et al., 2016) and assessing the dynamics of genetic variation across complex landscapes. The software was then implemented as a package in R.

The package has a modular structure, with a first module for loading input maps and data, such as habitat maps, resistance layer, and species distribution. Then, specific parameters related to the demography, dispersal and genetics of the target species need to be specified together with some initialization rules, and simulation settings. Finally, several outputs are obtained, from population viability analyses to colonization statistics and dispersal heatmaps (Malchow et al., 2021).

Chapter 5

Case Study I: The Eurasian beaver range expansion reveals uneven future trends and possible conservation issues: an European assessment

Introduction

A global decline in biodiversity is underway: an average demographic decline of 68% was found in monitored populations of vertebrates between 1970 and 2016 (Living Planet Index 2022), including more than 1,300 mammal species (over the about 6,000 assessed) considered as currently threatened (IUCN 2021).

Among the biogeographic regions, the Palearctic shows the smallest decrease, with an average decline of the monitored populations of 24%, owing to several conservation measures which avoided severe declines (Pereira et al. 2010; Living Planet Index 2022). Indeed, in the last 20 years, this area hosted several species' comeback, thanks to focused management actions and international regulations: reintroduction programs succeeded, such as for the European bison (Bison bonasus), the red deer (Cervus elaphus), the alpine ibex (Capra ibex) (Sæther et al. 2002; Pucek et al. 2004; Apollonio et al. 2010) and for some European carnivores (Chapron et al. 2014). When properly planned, reintroductions have thus proven to give positive results (Frey and Walter 1989; Johnson and Cushman 2007; Linnell et al. 2009), especially when applied to keystone or umbrella species (Linnell et al. 2009; Ripple and Beschta 2012). Among these, an example of the successful reintroduction of a keystone species is the Eurasian beaver (*Castor fiber*) (Gaywood 2018). Reintroductions of this species have taken place in 25 European countries, most of which have been successful (Nolet & Rosell, 1998; Halley & Rosell, 2002). However, in some cases reintroductions have failed due to low numbers of individuals released, or mortality caused by the stress of moving individuals (Myrberget 1967; Nolet & Rosell, 1998; Dewas et al., 2012). Previous analysis revealed that of 87 past reintroductions, 53% were successful (Macdonald et al. 1995).

The Eurasian beaver, an herbivore with a semi-aquatic lifestyle, is the second largest rodent in the world and is recognized as an ecosystem engineer due to its ability to modify rivers and streams through the creation of dams (Wright et al. 2002; Rosell et al. 2005). It is also defined as a keystone species (Mills et al. 1993), considering its role in maintaining the stability and functionality of ecological communities it lives in, as well as its unmatched influences on the ecosystems (Mills et al. 1993; Rosell et al. 2005).

This species was widely distributed in Palearctic, but populations started declining during the Middle Ages, up to the 19th century, mainly due to hunting for fur, meat and castoreum (a secretion produced for scent marking and historically used by humans for medical purposes) (Halley and Rosell 2002; Halley et al. 2021). Some estimates account for only 1200 individuals surviving, divided into eight isolated populations in the Palearctic, of which five of them in its Westernmost part (Nolet and Rosell 1998; Halley et al. 2021). In recent times, legal protection and reintroductions (started since 1922), together with natural recolonization, allowing the species to recover (Halley and Rosell 2002; Halley et al. 2021).

These reintroductions played an important role in restoring populations of the Eurasian beaver within its old range, but they did not involve all the European countries: in fact, Italy, Portugal, Bulgaria, Liechtenstein, Slovenia, Luxemburg, and Moldova were not part of these programs (Halley et al. 2021). Still, beavers naturally recolonized some of them (Fasel 2018; Herr et al. 2018), except for Portugal (Halley et al. 2021). About Italy, although Halley et al. (2021) report a dubitative recolonization, some very recent findings of beavers' signs prove the occurrence of this species in two different Italian locations: in the north-east of the country (near the town of Tarvisio, bordering Slovenia) (Pontarini et al. 2018; Loy et al. 2019), and in Central Italy (Tuscany and Umbria regions) (Pucci et al. 2021; Viviano et al. 2022), even with a possible reproduction event (Mori et al. 2021; Pucci et al. 2021). Thus, we are now maybe witnessing a natural recolonization in north-eastern Italy, which could continue spontaneously, or which could be assisted by direct or indirect human mediation (i.e., reintroduction and/or area protection). The presence of the species in central Italy can instead be traced to an illegal reintroduction (Mori et al. 2021; Pucci et al. 2021). On the contrary, Portugal has no similar chances to date but could be involved (as done for other European countries) in reintroduction programs, especially after the very recent findings of beavers' signs at the Spain-Portugal border (Calderón et al. 2022).

Moreover, one must simultaneously consider the biodiversity crisis that species are facing (and will face in the next future) considering the ongoing global change, which threatens the Eurasian beaver itself as well as the ecosystems it contributes to shape. One of the main solutions to handle these issues is to support Eurasian beaver conservation through a suitability distribution model, which could both support reintroductions and predict current and future suitable territories for this species. In fact, the IUCN "Guidelines for Reintroductions and Other Conservation Translocations" stress the importance of verifying the availability of suitable habitats as a key part of planning reintroductions (IUCN/SSC 2013). Also, the knowledge of areas' suitability in time was shown to strongly aid protection measures, for instance finding gaps or fallacies in protected areas' (PAs) networks (Iannella et al. 2018; Cerasoli et al. 2019).

In this research, we aim at supporting both possible reintroduction measures and protection/management of areas, through a zonal-focused modeling approach. Starting from a climate-based Ecological Niche Modelling, we build finer Species Distribution Models sensu Soberon and Peterson (2005) through the weighted overlay framework presented by Iannella et al. (2021), assessing the suitability for each European river. We integrate into the weighted process the environmental predictors which are reported to be ecologically important for the Eurasian beaver. In fact, we encompass not only climate change scenarios but also rivers' flow changes inferred for the future (Blöschl et al. 2019), as these are one of the main predictors of the beavers' occurrence (Alakoski et al. 2020). Also, we consider habitats used and rivers' human disturbance level, to support landscape-scale management, projecting suitability from a river scale to basins, thus accounting for a higher territorial level. Finally, we couple the weighted models' predictions and the post-modelling analyses performed with a country-scale protected areas network analysis. Indeed, we assess PAs' coverage focusing both on Italy and Portugal, to identify and support the management of reintroductions or natural recolonizations.

Material and Methods

Target species and study area

The target species is the Eurasian beaver, a semi-aquatic rodent currently distributed in Central, Eastern and Northern Europe, with a recent increase of its population (Halley et al. 2021). Though, from the eight refugial populations where the species managed to survive from its initial decline to between the 19th and 20th centuries (Nolet and Rosell 1998), strong bottleneck deriving from genetic drift is observed (Halley et al. 2021). Notwithstanding natural recolonization and reintroduction programs, Italy, Portugal and southern Balkans remain uncolonized, with an exception for Italy. In fact, signs of the presence of the beaver have recently been found in two distinct areas in Italy as mentioned above: in the north-east of the country (near the town of Tarvisio, bordering Slovenia, and in Val Pusteria, Trentino Alto-Adige region), the species' occurrence is due to natural recolonization (Pontarini et al. 2018), while the central Italian records (Tuscany and Umbria regions) are attributable to illegal reintroductions (Pucci et al. 2021; Mori et al. 2022; Viviano et al. 2022).

We gathered occurrence localities for the Eurasian beaver from the online dataset GBIF (GBIF 2022); we applied a temporal (year > 1970) and spatial precision (coordinate uncertainty < 100 m) filter to discard old and low spatial-quality data. Then, we processed the resulting occurrences through the 'Spatially Rarefy Occurrence Data for SDMs' tool (set at = 10 km) of the SDMtoolbox 0.9.1 (Brown et al. 2017) for ArcGIS Pro 2.9.3 (ESRI Inc. 2022) to make the spatial resolution of both predictors and occurrences comparable (Sillero and Barbosa 2020).

We selected two different study areas' scales for the purposes of the present work. The first one is the European continent, considering the beaver's increase of populations occurred there and the threats that global change poses on these. To support the management of natural recolonization and/or reintroduction projects, we then focus on two sub-areas, targeting the biogeographic regions referring to Italy and Portugal, and not including Balkans considering that a detailed paper is already available (Smeraldo et al. 2017).

Environmental predictors

For the purposes of the species distribution modelling, we took into consideration several environmental variables. To encompass the climatic aspect, we downloaded nineteen bioclimatic variables from WorldClim (version 2.1, 2.5 arc-min) (Fick and Hijmans 2017) for both present and future (2050 and 2070) conditions. For each future scenario, we selected the Shared Socioeconomic Pathways (SSPs) 2.45, 3.70, and 5.85 to involve all but one (the 1.26, the most optimistic) different possible trajectories (Riahi et al. 2017).

We collected topography data from ETOPO1 (~ 1 km resolution, available at https://www.ngdc.noaa.gov/mgg/global/) and processed them through the 'Surface Parameters' tool in ArcGIS Pro. Specifically, considering that the speed of running waters is an important parameter for the Eurasian beaver to settle (Hartman and Törnlöv 2006; Dittbrenner et al. 2018), the Profile curvature was preferred to the Slope alone. This predictor is applied when one wants to differentiate the acceleration or deceleration of flow at a specific surface (ESRI Inc. 2022). This analysis is then useful to identify areas where slow- (or fast-) flowing water-adapted species may occur. We thus calculated the Profile curvature raster for the whole study area.

We obtained rivers' spatial data and their corresponding connectivity and annual mean flow from Grill et al. (2019). Then, for the "human impact" information, we performed a raster calculation ('Weighted sum' tool in ArcGIS Pro) by averaging three different parameters: the

degree of regulation of the rivers, the road density, and the degree of urbanization of the territory, obtaining this information from the HydroATLAS dataset (Lehner and Grill 2013; Linke et al. 2019). Also, we used sub-basin data from the HydroBASIN dataset (Linke et al. 2019), and starting from the data reported in (Blöschl et al. 2019) regarding the projected changes in flow rate in European rivers in the future, we created a map for future changes of rivers-related spatial information.

About the habitat predictors, we downloaded the 100 m-precision map of global terrestrial habitats from the Copernicus repository (https://land.copernicus.eu/global/products/lc), containing 47 different terrestrial habitat types, as defined by the IUCN habitat classification scheme (Jung et al. 2020).

Ecological niche modelling

The nineteen Worldclim bioclimatic variables were checked for multicollinearity through the Variance Inflation Factor (using the 'vifstep' algorithm of the 'usdm' R package (Naimi 2015), threshold = 10). To reduce the variability possibly caused by the use of individual General Circulation Models (GCMs) in future projections (Stralberg et al. 2015), we selected and managed three different GCMs, namely the BCC-CSM2-MR (Wu et al. 2019), the IPSL-CM6A-LR (Boucher et al. 2020) and the MIROC6 (Tatebe et al. 2019).

We used the 'biomod2' package (Thuiller et al. 2016) to build the ENMs. This package allows to create ensemble models, which are the result of the combination of individual algorithms' outcomes, corresponding to different modeling techniques. We first generated five sets of 2,000 pseudo-absences each using the Surface Range Envelope algorithm (quantile = 0.05) (Barbet-Massin et al. 2012). We parametrized the single models through the 'BIOMOD_ModelingOptions' as follows: GLM: type = "quadratic", interaction.level = 3; GBM: n.trees = 10,000, interaction.depth = 3, cv.folds = 10; GAM: type="s_smoother", interaction.level = 3; RF: n.trees = 10,000, bag.fraction = 0.75, shrinkage = 0.001. Then, the 'BIOMOD_Modeling' function was used to calibrate the single models, and the 'BIOMOD_EnsembleModeling' algorithm was subsequently run to obtain the Ensemble models, using as input only single models with high performance (AUC > 0.8 and TSS > 0.7) (Cerasoli et al. 2019; De Simone et al. 2020; Di Gregorio et al. 2021). We chose the 'wmean' algorithm to merge single models, as it averages models into the Ensemble one based on a weighted mean function, in which weights are the discrimination scores (Thuiller et al. 2016). Finally, we obtained the projections to future scenarios by using the 'BIOMOD_EnsembleForecasting' function.

To buffer the uncertainties deriving from future projections calibrated on each GCM and concurrently merge them into one year/SSP single model, we first checked for model extrapolation (i.e., the dissimilarity from the calibration conditions) by assessing the Multivariate Environmental Surface Similarity (MESS) (Elith et al. 2010), computed through the function 'mess' of the 'dismo' package (Hijmans and Elith 2016). Then, the MESS maps were included in the Multivariate Environmental Dissimilarity Index (MEDI) algorithm (Iannella et al. 2017), a form of weighted raster average which down-weights extrapolation based on projections and MESS, reducing the uncertainties in future projections.

Data preparation and weighted overlay process

To merge all the information into the weighted maps and the corresponding weighted workflow (Fig. 1a), we transformed in a 1-to-10 scale all the previously mentioned predictors to make them comparable each other through the 'Reclassify' tool in ArcGIS Pro.

The connectivity value available from the Grill et al. (2019) dataset, which divides rivers based on free flowing status into three categories, was reclassified to new values (i.e., 1, 5, and 10) for each study area's river. Moreover, we took into account the ecological needs and hydrographic preferences of the Eurasian beaver (Hartman and Törnlöv 2006; Dittbrenner et al. 2018) and reclassified the rivers' data accordingly, on the basis of their reported average annual flow (Grill et al. 2019). Also, the "human impact" information deriving from the processing of Road Density, Urban Extent and Degree of Regulation parameters of the RIVERAtlas dataset, was converted to the new scale, where the lowest human impact has the highest value.

To reclassify the profile curvature and habitat needs to the common scale, we calculated the frequencies of occurrence in each value of these two predictors by extracting this information in GIS ('Extract multi values to points' tool), following the procedure of Iannella et al. (2021).

The climate-related Ensemble Models' output maps were reclassified as well, converted from their 0-to-1,000 output to the 1-to-10 scale.

Finally, we used the 'Weighted Overlay' tool in ArcGIS Pro to merge the predictors (free flowing status, annual average flow, human impact, profile curvature, terrestrial habitat type, and bioclimatic-based ensemble models) into a single map. This tool merges a given set of rasters, sharing a common evaluation scale, through a weighted averaging in which each input raster is also assigned a specific percentage set by the operator. This workflow has been shown to increase the models' discrimination power if compared to the Ecological Niche Models alone (Iannella et al. 2021), deepening the species' distribution model to a more realistic one.

About the future scenarios, we kept all variables as fixed except two, namely the climate-based Ensemble models and the annual average flow. For this latter, we performed a raster algebra to increase or decrease the values based on the indications of published predicted future flow change rates in the study area (Blöschl et al. 2019).

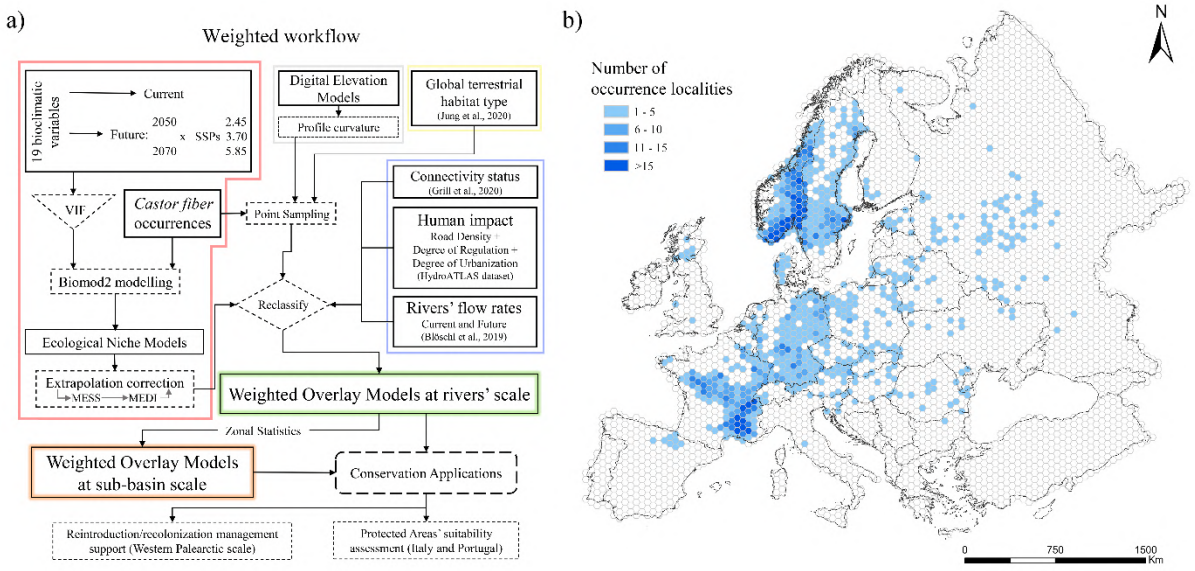


Fig. 1. (a) General workflow used for the whole analyses performed, and (b) current known *Castor fiber* distribution in Europe.

Landscape modelling and conservation applications

We applied the Zonal Statistics tool (which allows to perform stats on a geometry based on the values or attributes of another one) to the weighted models obtained and to the HydroBASINS dataset, which reports the boundaries of the European sub-basins (at Sub-Basin level = 10) (Lehner and Grill 2013). We thus linked the values of the rivers' averaged weighted suitability to the hydrographic basins, leading to an explicit spatial information at a landscape scale.

As one of the purposes of the present work is to support possible reintroductions of the Eurasian beaver, we focused on Italy and Portugal, countries where the species was present in historical times but where stable populations have still not re-established after its eradication. We thus took into consideration the PAs occurring in these countries and measured the environmental suitability within them. Subsequently, to summarize the vast amount of information, we divided Italy and Portugal based on their biogeographic sectors: Italy has therefore been divided into the Alps, the Po plain, the Northern, Central and Southern Apennines, and the Apulian province, excluding the two main islands. Similarly, we separated Portugal into four areas, namely the Luso-Extremadurense, the Carpetano-Iberico-Leonesa, the Cantabro-Atlantica and the Gaditano-Onubo-Algarviense sectors, based on the information from Costa et al. (1998).

We finally assessed the environmental suitability within the PAs for each biogeographic sector, thus obtaining these values at all the landscape scales: from the single river to the sub-basin level, for the whole Western Palearctic area. Aside from the numeric results, the maps we obtained permit to deepen the suitability of even a single river, which may be helpful if one wants to properly assess conservation and/or reintroduction measures within a certain territory (e.g., a protected area).

Results

After the filtering process, we gathered 2,848 occurrence localities for the whole European continent (Fig. 1b); also, taking into account the VIF results, we used for the modelling process nine bioclimatic variables, namely BIO2 (mean diurnal range), BIO6 (minimum temperature of the coldest month), BIO8 (mean temperature of the wettest quarter), BIO9 (mean temperature of the driest quarter), BIO11 (mean temperature of the coldest quarter), BIO15 (precipitation seasonality), BIO17 (precipitation of the driest quarter), BIO18 (precipitation of the warmest quarter) and BIO19 (precipitation of the coldest quarter). About the Eurasian beaver's habitat preferences (obtained through the extraction in GIS) used in the weighted process, we found the highest frequencies in the "Arable land", "Boreal forests", "Temperate forests", and "Boreal shrubland" categories (Appendix S1a). Also, when considering the Profile raster, we found the highest frequency in flat (or nearly-flat) areas, with a decreasing frequency as the slope increases (Appendix S1b).

The weighted map we obtained for the current conditions (Fig. 2) depict a suitability that is mostly in line with the species' current occurrence (Fig. 1b), with a plethora of small- and medium-sized rivers being more suitable to the larger ones (Fig. 2 and its example zoomed insets).

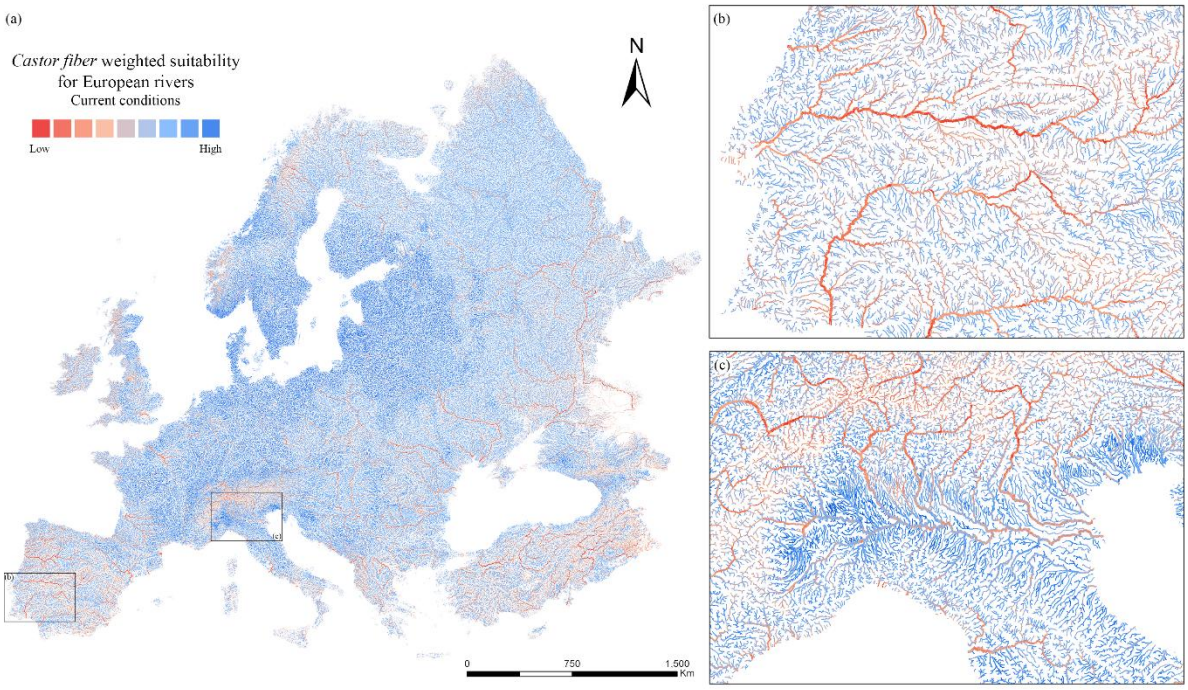


Fig. 2. (a) Weighted suitability model performed over climatic, topographic, and habitat related predictors for European rivers, with example focuses in (b) Iberian Peninsula and (c) Northern Italy.

Indeed, some territories not currently hosting the species are predicted as suitable, such as for a large part of Belarus, Estonia, Latvia, Lithuania, and western Russia (even though this latter shows slightly lower values), Finland, Great Britain, Croatia, and Italy (Fig. 2). On the contrary, the Iberian Peninsula, the Alps, some major eastern Balkans territories, and Turkey report a general low-suitable rivers' trend. This is also observed at a "surface" spatial scale: when projecting suitability to sub-basins, they spread the rivers' suitability values to a territorial scale, mostly highlighting the areas where low suitability occurs (Fig. 3a). Differences between the very high and very low patches become more marked, highlighting a wide eastern European area (from eastern Poland to southern Finland), but limited to the westernmost part of Russia (Fig. 3a). Similarly, a continuous suitable area is found in the southern Scandinavian peninsula (mostly occurring in Sweden), and not extending further north of the 10th parallel (Fig. 3a). Some medium-extent suitable areas appear in central Europe; even if interspersed with continuous major rivers' basins, they show high suitability values (Fig. 3a). About southern Europe, scattered and small-sized highly-suitable areas occur in the Balkans and, to a lesser extent, in northern and central Italy; the Iberian Peninsula reports some more scattered and smaller patches, with lower suitability values (Fig. 3a).

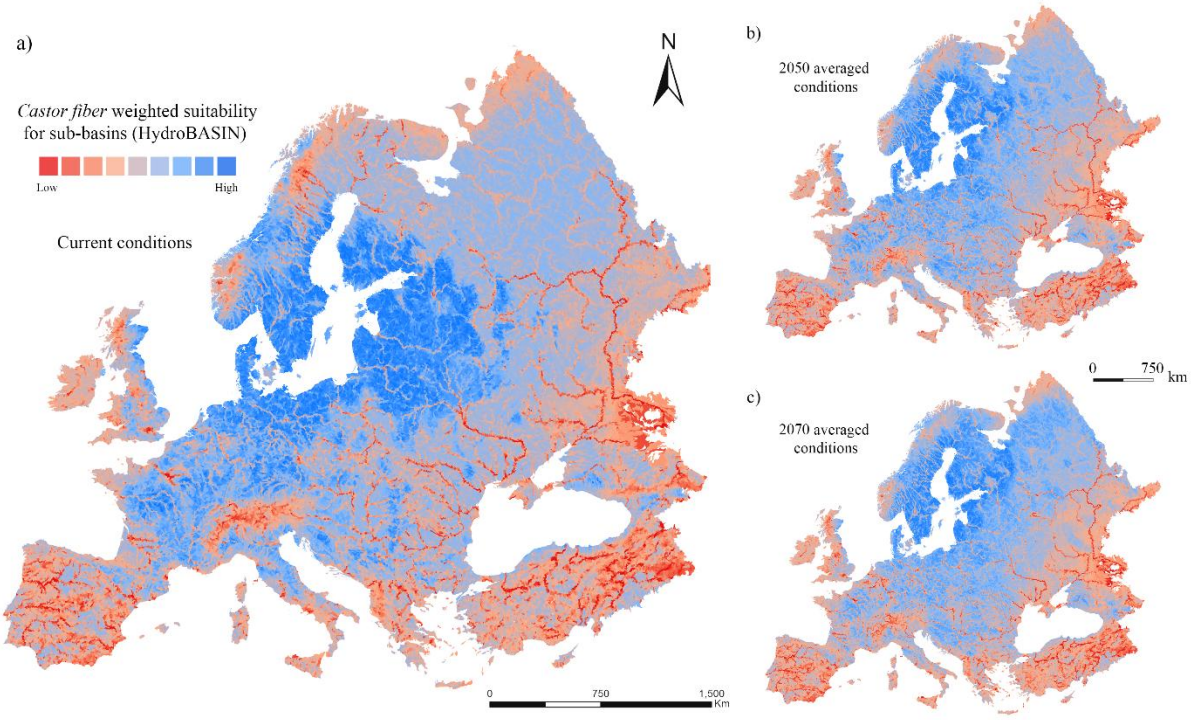


Fig. 3. (a) Weighted suitability river models for current and (b) averaged future 2050 and (c) 2070 conditions projected on the European sub-basins (HydroBASINS dataset).

In the future, a general deterioration of suitability in many wide areas is predicted, with 2070 being worse than 2050 (Fig. 3b,c). The central and northern Europe, which currently host highly suitable areas, are predicted to lower towards medium values (Fig. 3b,c). Specifically, the areas falling into Poland, Belarus, and Ukraine are predicted to shifting towards medium or low suitability, while Finland e Scandinavian peninsula remain suitable, with high suitability bypassing the 10th parallel. Also, some northern Russian territories will become more suitable with respect to the current conditions, even though this suitability increase would be negligible (Fig. 3b,c).

When applying this information to the Portuguese and Italian PAs' network, a complex framework emerges (Fig. 4). In Portugal, most of the PAs are predicted to currently cover medium-low suitable territories, with some very low ones in the inland (Carpetano-Iberico-Leonesa and Luso-Extramadurense, respectively PO2 and PO4) except for the southern part of the Luso-Extramadurense (the Beja region, Fig. 4a). On the contrary, some medium and medium-high patches occur in the coastal biogeographic sectors (PO3, the Gaditano-Onubo-Algarviense), as found, for instance, in the Leiria area (Fig. 4a). About Italy, we obtained a very diverse asset, even within a single biogeographic sector. For instance, the PAs hosting a high suitability occur at the westernmost and easternmost extremes of the Alps (IT1), while its central part results instead in very low values (Fig. 4a). The Padano-Venetian plain (IT2) is rather poor of PAs, but some of them report high or medium suitability; the Northern and Central Apennines (IT3 and IT4) score high suitability, especially in PAs occurring in the Apennine chain and in the southern coastal part of IT3 (the Maremma and Metalliferous Hills territories) (Fig. 4a). About the Apulian and Southern Apennines sectors (IT5 and IT6), we find a general medium-low and low patches, except for the karstic semi-mountainous territory of the Murge plateau, at the center of the IT5 (Fig. 4a).

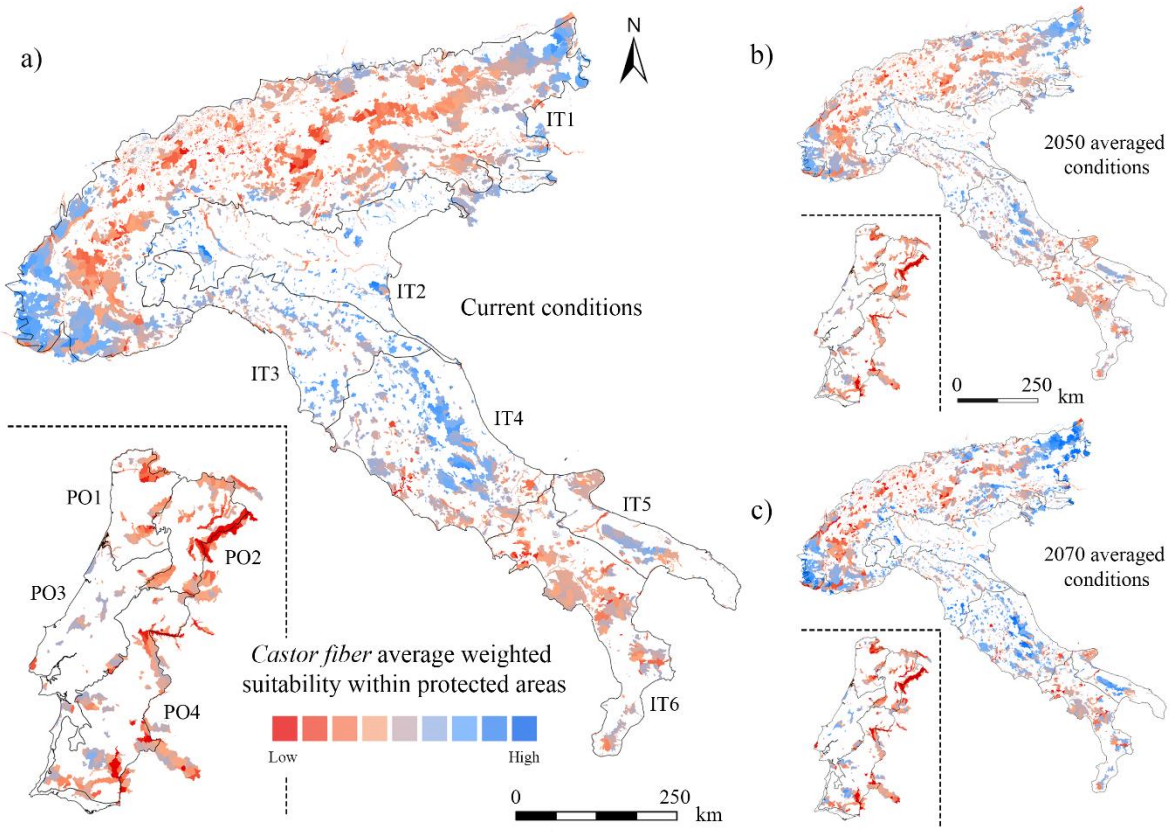


Fig. 4. (a) Weighted suitability river models for current and (b) averaged future 2050 and (c) 2070 conditions projected on both Nationally-Designated Protected Areas and Natura 2000 sites falling within Italian and Portuguese biogeographic sectors.

When projecting these results to future, some changes throughout the 2050 and 2070 scenarios may be noted in Italy, while minor ones resulted for Portugal (Fig. 4b,c). In fact, some suitable patches in the westernmost and easternmost extremes of the Alps, in the Maremma and Metalliferous Hills (IT3), in the Central Apennines, and in the Murge Plateau (IT5) are predicted to progressively increase from 2050 to 2070 (Fig. 4b,c). We also found a similar future, but with a lower magnitude, for the medium-suitability patches occurring in Leiria and Beja areas (PO3 and PO4, respectively). To give an overview at a landscape-scale of these specific trends, we report the averaged future changes (Fig. 5). As mentioned before, we predicted minor suitability changes within Portuguese PAs, with an overall trend of slight increases or decreases in suitability for all the four biogeographic sectors (Fig. 5a). Differently, we observed more pronounced variations for Italian PAs, with considerable losses for Padano-Venetian plain, Northern and Central Apennines sectors and slight gains for the other ones (Fig. 5b). Although the predicted negative changes or stability, it must be noted that the starting values are not less than a medium-high suitability.

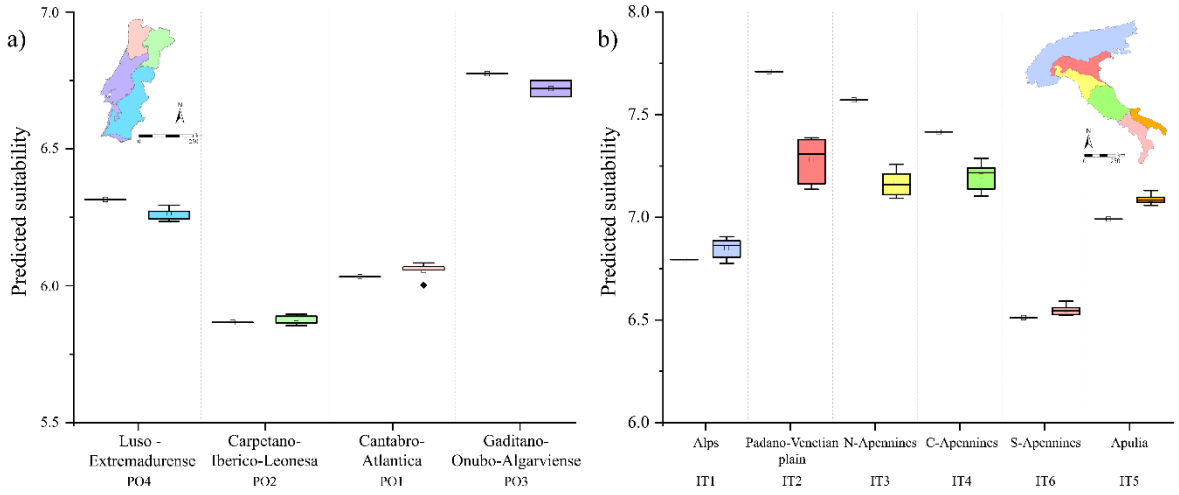


Fig. 5. (a) Current (thin line) and averaged future (boxplot) weighted suitability mean scores for Protected Areas falling within Portuguese and (b) Italian biogeographic sectors.

Discussion

The recolonization of territories by the Eurasian beaver is a today a fact; however, one must remember that this event basis its success on reintroduction programs (Halley et al. 2012). Reflecting the IUCN guidelines, where a strong indication of ceased pressures and threats on the target species is recommended to proceed with the reintroduction (IUCN/SSC 2013), these in fact succeeded. Starting from the legal protection of the species (which, for instance, cannot be hunted as in the past), and following genetic and territorial assessment, country-scale actions were accomplished (Halley et al. 2021). Indeed, the local dimension of the activities carried out since now could represent a limitation for future conservation strategies aiming at halting possible range variations triggered by the ongoing global change.

Notwithstanding the great importance of the Eurasian beaver in terms of ecosystem services-related conservation issues (Nummi et al. 2021; Thompson et al. 2021), an overview of suitability projections for future scenarios was currently missing for the Europe. Moreover, considering that Eurasian beaver populations develop on a watershed-scale (Hartman 1994), we managed to combine the general view with this spatial data.

In our research, the model calibrated on current conditions mirrors the Eurasian beaver known distribution, indicating not only its climatic suitability, but also representing its other ecological requirements (topography and habitat), thus narrowing the climate-based predictions to more specific territories. Also, the current model highlights some patches where the species is not reported, where it is likely to spontaneously recolonize, or where reintroduction plans are proposed (Treves et al. 2020; Halley et al. 2021). For this last case, the Italian peninsula and Wales are the two areas where our results could support specific planning for future management, especially for the future scenarios, in which the currently-suitable areas are predicted to shrink by our models. If considering the Balkans' countries, a growth of suitable territories is instead predicted (even though with a slight high-suitable patches decrease), thus Bosnia and Herzegovina and Serbian stakeholders should pay special attention in the ongoing 'establishment' phase of the former country and expected population increase for the latter (Halley et al. 2021). About the main European River, the Danube, we found its basin showing a low environmental suitability, since the river itself is unsuitable for the creation of dams and burrows for beavers, considering its size and flow, and man-made modifications. However,

high values of environmental suitability are found in the tributaries of the Danube almost along its entire length. Thus, we can consider the Danube itself as unsuitable for creating core areas for the Eurasian beaver, but still important for its movement and connectivity, confirming the spatial and populational observations recently published (Halley et al. 2021). In contrast, Spain, where beavers' reintroduction in the past led to a medium-sized population currently expanding (Halley et al. 2021), should take preventive conservation actions, as a suitability decrease is predicted by our models for the areas currently inhabited by the Eurasian beaver population.

An important remark must be done for the territories which acted as refugia (following Halley et al. 2021) during the years when the Eurasian beaver suffered declines, where we found a decrease of the watershed-based suitability. The Russian and Belarusian patches resulted in the highest suitability decrease. The territories where the Norwegian refugia occurs are predicted to keep high suitability in future scenarios, while the German and French ones are predicted to reduce both in size and suitability. This is an alarming result if one considers the importance of these areas in terms of their historical role, as well as for the possible ecological functionality persisted (Thompson et al. 2021) which may be rapidly lost, as well as for the genetic bottlenecks there occurring (Halley et al. 2021).

A separate mention concerns Finland, where the Eurasian beaver coexists with the North American beaver (*Castor canadensis*) which was erroneously reintroduced in the past when the taxonomic status was still uncertain (Parker et al. 2012). Finland has high values of environmental suitability, but in this case the expansion of the Eurasian beaver is hindered by the presence of the North American beaver. This latter often seems to come out as the winner of ecological competition (Parker et al. 2012), even though there are opposite cases, such as for Austrian and Polish ones (Halley and Rosell 2002; Danilov 2009). The eradication of the North American beaver, considered an invasive species in Finland, would support the expansion process of the Eurasian beaver, in a territory bearing large highly-suitable patches.

Recent research state that, generally, Eurasian beaver population are expected to slow its increase in the next future and become stable in the next decades (Wróbel 2020; Halley et al. 2021). The rapid populations' growth was observed to be a consequence of natural recolonization or reintroductions (Halley et al. 2021), a phenomenon which deserves attention for countries which want to successfully reintroduce this species. As studied in our case, Italy and Portugal (which are the only two southwestern European countries where the species occurred in the past) should address robust plans if they want to achieve a proper recolonization process. Protected areas play a key role in the management of the territories they cover, and usually support conservation at the forefront; indeed, in the case of Italian and Portuguese ones, the general status is rather complex.

For instance, Italy currently hosts the overall highest suitability within the Padano-Venetian plain protected areas, where these are scattered and suffer from a severe fragmentation caused by the greatest urbanization of the whole Italian peninsula. The only beaver occurrence known site falls within the Northern Apennine biogeographic sector, for which a future decrease in suitability is predicted, and where protected areas are dispersed in wide landscapes. A slightly lower suitability results for Central Apennines, which instead are not currently recolonized, but where highly-suitable and interconnected patches occur. Going southwards, the other sectors (Southern Apennines and Apulia) seem not to be colonizable, as the basins' suitability drastically lowers, with corresponding lowering of the protected areas occurring there. A more

complex scenario is predicted for Alps' sector, where a general low suitability resulted for its protected sites. If analyzing in detail, one can note an eastern and western "polarization": in fact, the central Alps basins result not suitable, while the ones at the farthest are not only suitable, but near the other European populations (French, and Austrian-Slovenian ones). This may support a natural recolonization, or reintroduction programs, such as the one studied for the Piedmont region (Treves et al. 2020).

On the other hand, Portugal still does not have any Eurasian beaver occurrences within its borders, thus possible reintroduction programs could take advantage of the present research. Environmental suitability is generally low, except for some protected areas where average suitability values are found (in the Gaditano-Onubo-Alsarviense sector). However, these areas appear fragmented and poorly connected to each other. Conversely, greater proximity between protected areas is present in the Luso-Extremadurense sector, but only a few protected areas have good suitability values. The Carpetano-Iberico-Leonesa sector has low suitability values but is a relevant region because it borders the Spanish populations of Eurasian beaver. This leads to believe that, as things stand at present, a natural recolonization of Portugal is unlikely in the next years, and a highly-informed reintroduction is the only possible option.

The Eurasian beaver is a key species primarily due to its role as an ecosystem engineer, and can produce diverse ecosystem services, capable of services worth millions to hundreds of millions of US dollars (USD) per year. Concrete examples concern the provision of habitat and biodiversity (estimated at USD 133 million), and the sequestration of greenhouse gases (estimated at USD 75 million) (Thompson et al. 2021). Other ecosystem services provided by the Eurasian beaver include water purification, moderation of extreme events, nutrient cycling, recreational hunting and fishing, water supply, and non-consumptive recreation (Brazier et al. 2021; Thompson et al. 2021).

The ability of the beaver to restore habitat can help improve the ecological status of rivers, especially through some actions that the beaver carries out in rivers: maintenance of levees through a dynamic of their creation / destruction (Campbell-Palmer et al. 2016); spreading plants through foraging (Campbell-Palmer et al. 2016); replication of small dams in addition to the construction of dams (Pollock et al. 2014); increase habitat heterogeneity, forming different microhabitats, such as ponds and wetlands (Law et al. 2017). For Portugal in particular, the restoration actions of the beaver in rivers could reduce the costs of post-fire human interventions, carried out between 2018 and 2020 to reduce flood events and their risks, estimated at around 11.43 million € (https://sniambgeoviewer.apambiente.pt/GeoDocs/geoportaldocs/Docs/APA_Relatorio_Incendios2017_RCM11A2018.pdf). Some of the central areas of Portugal, where some protected areas with medium suitability have emerged, could benefit from the presence of the beaver. Also, further fire-related impacts may be partially mitigated by the Eurasian beaver, as dams formed by beaver (in this case, *Castor canadensis*) improve fire resistance of riparian vegetation (Fairfax and Whittle 2020). In Portugal, in 2017, fires in the central regions of the country caused the loss of 40–60% of the forested areas of some districts (DGAPPF, 2017); in fact, it should be remembered that Portugal is among the countries of the European Union most affected by fires, which burned an annual average of 147,000 hectares of land between 2000 and 2018 (San-Miguel-Ayanz et al. 2019). Reintroduction projects in these areas could contribute to improve the ecological status of rivers, partially solving the problem of fires, and

adding further ecosystem services, not only for Portugal (as reported in this specific case) but also for any historically-colonized territory.

The beaver is a species that can also increase wildlife tourism, as demonstrated by the case study in Otter, England, where the beaver has been reintroduced (Auster et al. 2020). The reintroduction in this river has resulted in an advantage for local businesses, with the magnitude of the benefit depending on the commercial initiatives that have exploited the opportunity (Auster et al. 2020). Other forms of beaver-centered tourism are "beaver safaris" (Halley et al. 2012).

In view of a possible reintroduction of the Eurasian beaver in Italy or Portugal, it is necessary to consider also the possible presence of other species that may interact with it. The beaver is in fact a prey for many mammals widely present in the western Palearctic, such as the grey wolf (Canis lupus) or the fox (Vulpes vulpes) (Kile et al. 1996). In addition to predation, the presence of the beaver can also be the cause of competition events with a species partially occupying a similar niche, such as the coypu (*Myocastor coypus*), an invasive species in Europe. Studies in central Italy reported an intermediate overlap in the activity pattern between the newly-found beavers (Pucci et al. 2021) and coypu, with the latter having more diurnal habits (Mori et al. 2022). However, slight ecological differences occur between the two species, in terms of feeding behavior (Mori et al. 2022) and habitat needs (Ruys et al. 2011).

Another important factor halting beaver expansion is the presence of man-made dams, which hinder river connectivity. In fact, given that a natural water regime is necessary for the survival of beavers (Nolet & Rosell, 1998), man-made dams can alter it, preventing individuals from dispersing. Also, beavers' food availability, supplied by intact riparian forests (Nolet & Rosell, 1998), diminishes when man-made dams occur. Thus, where populations are present in areas affected by artificial dams, it is important to evaluate technical measures to guarantee the connectivity of the river system, such as adopting naturalistic engineering alternatives.

Finally, in a reintroduction context, one should consider the topics of diseases and parasites. In fact, the relationship between coypu and beaver is concerning also considering the possible transmission of pathogens. Indeed, coypu is an intermediate host for Echinococcus multilocularis, one of the most pathogenic parasitic zoonoses in central Europe. Several cases of Echinococcus multilocularis in beaver have been reported in Switzerland, Austria, and Great Britain (Janovsky et al. 2002; Cronstedt-Fell et al. 2010; Barlow et al. 2011). Therefore, the choice of possible reintroduction sites also depends on the co-occurrence of coypu, which thus represents, among other species, both as a direct competitor and as a possible source of pathogens. About Italy, where the coypu already occurs, appropriate measures must be taken; in Portugal and Spain, the suitable habitats of coypu are predicted to expand in the future (Schertler et al. 2020), thus specific actions should be addressed to achieve successful reintroductions (for the former country) or to preserve existing populations (for the latter).

Conclusion

Our study modelled for the first time the European beaver suitable habitats at a continental scale, allowing to draw important considerations on the future of a species in the past close to extinction, but which today is once again spreading. Although the Eurasian beaver is a generalist and adaptable species, a difficult future is predicted in the southernmost areas of the western Palearctic, while in central Europe and in Scandinavia, populations may persist. In Italy (even in the future) large areas suitable for reintroduction will remain, especially in the

Central Apennines, while for Portugal only a few protected areas would be suitable. Further studies are needed to understand the feasibility of reintroductions of the Eurasian beaver in Portugal, or the persistence/colonization/reintroduction of this species in Italy. Despite the small population occurring in Central Italy being the result of illegal reintroduction, we recommend keeping and protecting it, following the Spanish case, where a similar situation occurred recently and the beavers have been protected, adopting the provisions of the Habitat Directive. Moreover, given the evidence of reproduction, it is possible that in the near future this population could spread more in Central Italy. Therefore, we recommend maintaining populations after carefully monitoring their spatial range and concurrently examining and sensitizing public opinion. It is also important to evaluate the potential ecological impact of the species in the basins where it occurs, taking into account the fauna currently present and its possible interactions.

Given the continuous populations' growth and the expansion of the range, it is likely that the beaver will be able to naturally recolonize all its historical areal. Therefore, reintroductions would favor this process, which in the case of Italy is already taking place. In the case of reintroductions, monitoring programs will be needed, as the beaver tends to move widely when colonizing a watercourse to find its ideal habitat. The benefits linked to the beaver activity are different and would allow direct gains (wildlife tourism) and savings from the beaver activity in waterways (construction of dams, creation of wetlands, resistance against fires).

Supporting Information

All supporting information are accessible on https://link.springer.com/article/10.1007/s10531-023-02587-x#Sec11

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Case Study II: A shifting carnivore's community: habitat modeling suggests increased overlap between the golden jackal and the Eurasian lynx in Europe

Introduction

Despite the increasingly severe effects of climate change, land use alterations, and habitat degradation, biodiversity is not spatially declining evenly: there are several cases of species that expanded their ranges (Nolet and Rosell, 1998; VerCauteren, 2003; Arnold et al., 2012; Deinet et al., 2013; Chapron et al., 2014; Halliez et al., 2015; Carvalho et al., 2018; Pacifici et al., 2020; Wehr, 2021) or managed to survive by adapting to new environmental conditions, which also involve the human presence (Basille et al., 2009; Chapron et al., 2014; Bouyer et al., 2015; Ražen et al., 2016; Fenton et al., 2021). Of course, these processes did not occur alone, but together with successful conservation actions which allowed many species to recover or survive (Hoffmann et al., 2010; Deinet et al., 2013).

This is the case of Europe, where the Living Planet Index, reports a slow decline rate linked both to conservation successes (Hoffmann et al., 2010; Chapron et al., 2014) and to the natural adaptability and recolonization capacity of some species (Ledger et al., 2022). Also, a meta-analysis noted increases in species richness and abundance in many bioregions of Northern and Eastern Europe (Pilotto et al., 2020).

Although Europe is one of the least wild continents, considering the human footprint which led (and continues to lead) to the loss of ecosystems (Williams et al., 2020) and the declining trend of some species (Inger et al., 2015; Warren et al., 2021), many species appear to be able to adapt, or in general, to persist. We are witnessing the comeback of various species of mammals, including the European bison (*Bison bonasus*), the elk (*Alces alces*), the Eurasian beaver (*Castor fiber*), the southern chamois (Rupicapra pyrenaica), and the alpine ibex (*Capra ibex*) (Deinet et al., 2013; Ledger et al., 2022). Also, the main European predators, such as the brown bear (*Ursus arctos*), the grey wolf (*Canis lupus*), and Eurasian lynx (*Lynx lynx*) are expanding their ranges (Chapron et al., 2014).

From a conservation perspective, the recovery of these species and their range expansion is particularly relevant, as predators require large spaces to survive and can easily come into conflict with local communities. It should not be forgotten that their return is linked to a series of factors such as an increase in forest cover, a decrease in human population densities, protective legislation, acceptance by public opinion, and the use of measures that allow coexistence with humans (Chapron et al., 2014; Cimatti et al., 2021). Preserving this delicate equilibrium between apex predators and human activities is thus important since not far as a hundred years ago these have been hunted and persecuted, and their decrease has facilitated the expansion of mesopredators (Prugh et al., 2009; Ripple et al., 2013; Newsome et al., 2017).

In Europe, the golden jackal (*Canis aureus*), represents an excellent example of this phenomenon; it is currently an expanding species, whose growth was initially favored by the absence of the wolf (Krofel et al., 2017). The European distribution of this medium-sized canid species was once limited to the Balkan area (Kryštufek et al., 1997), and saw a decline until 1950 caused by human persecution (Spassov, 1989) which reduced it to a few populations among Former Yugoslavia, Bulgaria, Turkey, and Greece (Spassov, 1989; Giannatos, 2004;

Spassov, 2007). Then, two waves of expansion, the first occurred around the 1950s, and the second from the 1980s, also favored by the legal protection (in Bulgaria from 1962) led to a north- and westward expansion (Trouwborst et al., 2015; Krofel et al., 2017); in the following years, the jackal colonized most of the countries of central and southern Europe. More recently, a small population has established in the Baltic countries (Pyšková et al., 2016). Dispersing individuals have also been observed in northern Europe (Sørensen and Lindsø, 2021; Rykov et al., 2022), and central Europe (Hatlauf et al., 2016; Böcker et al., 2023), and its presence has been reported in 33 European countries, 10 of them in the last decade (Hatlauf et al., 2021).

The golden jackal is a generalist species with opportunistic feeding habits, with its prey spanning from ungulates to rodents (the most common prey), also comprising invertebrates, vegetables, and anthropogenic resources, including waste and carcasses (Markov and Lanszki, 2012; Aleksandra and Duško, 2015; Ćirović et al., 2016; Lange et al., 2021). The ecological plasticity of the golden jackal also emerges in the choice of habitat: the most used one is a mixture of shrub and herbaceous vegetation, including mesophilic woods or riparian habitats (Lapini et al., 2011; Šálek et al., 2014; Spassov and Acosta-Pankov, 2019), but sometimes it may also be attracted by human settlements (Lapini et al., 2011). However, the habitat choice of the golden jackal is highly influenced by the wolf presence (Krofel et al., 2017), and climatic-based models predict its change for the next future (Cunze & Klimpel, 2022).

The changing distribution of a species, such as in the case of the golden jackal which is currently expanding its range, can lead to new biotic communities, and new interactions with other species that find themselves coexisting for the first time (Gilman et al., 2010; Pecl et al., 2017). In the case of the golden jackal, it is exceptional the recent observation of kleptoparasitism towards the Eurasian lynx (Krofel et al., 2022), another predator expanding in Europe.

The Eurasian lynx is a European top predator that was intentionally eradicated from many parts of Europe between the 19th century and the beginning of the 20th century (Breitenmoser, 1998). Only four populations survived, in Scandinavia, the Carpathians, the Baltic area, and in the southwestern Balkans (von Arx et al., 2004). The species recolonized parts of its former range thanks to several factors, from legal protection and reintroductions to an increase in prey availability and greater public acceptance (Linnell et al., 2009), and is now slowly recovering (9–10,000 individuals estimated in Europe) (Chapron et al., 2014). This species is a predator specialized on roe deer (Capreolus capreolus) (Jędrzejewski et al., 1993), but the diet varies regionally and may include other species, from hare (Lepus europaeus) and chamois (Rupicapra spp.) to red deer (Cervus elaphus), also including livestock (Okarma et al., 1997; Stahl et al., 2001; Odden et al., 2006). The Eurasian lynx is associated with forest habitats with good environmental heterogeneity for hunting (Belotti et al., 2013) and many hiding places to rest (Podgórski et al., 2008). However, the species can select also more open habitats, especially at night (Filla et al., 2017) adapting to them by generations (Nagl et al., 2022). Also, it can adapt to habitats with moderate human activity if prey abundance is elevated and refuges are available, seeking a compromise between human avoidance and prey hunting (Basille et al., 2009; Bouyer et al., 2015; Oeser et al., 2023). The overlap between the golden jackal and Eurasian lynx ranges was scanty until the mid-20th. Indeed, the recent expansion of the jackal, especially since 2011, caused an increase in this overlap, currently estimated at 13% (Krofel et al., 2022). Considering the expansion of the golden jackal and the recovery of the Eurasian lynx, this overlap is likely to increase, even though no information is available to date.

Moreover, considering the positive trends of the wolf populations, and their influence on the golden jackal (Krofel et al., 2017; Newsome et al., 2017), it could be also important to assess whether the range changes of both golden jackal and Eurasian lynx would increase in areas where the wolves are well-established, or where is predicted an expansion in the future.

To lay the foundation for the study of this ecological issue, we infer the areas of potential current and future overlap between the two target species, as they may indicate the zones where the interactions are more likely to occur. To achieve this result, we take advantage of the most up-to-date Ecological Niche Modeling techniques and post-modeling GIS spatial analyses. The use of Ecological Niche Models for the management of expanding species and the understanding of their dynamics has increased in recent years (De Marco et al., 2008; Jiménez-Valverde et al., 2011; Maiorano et al., 2011; Barbet-Massin et al., 2012a; Barbet-Massin et al., 2012b; Dawe and Boutin, 2016; Iannella et al., 2019; Rodríguez-Rey et al., 2019; Serva et al., 2023). Also, Ecological Niche Models can be refined through a post-modeling phase, converting them into more precise Species Distribution Models (SDMs), in a process which increases the predictive performances and allows the creation of more realistic models (Iannella et al., 2021).

Given the ongoing range changes observed for both the Eurasian lynx and the golden jackal, and the recently observed interactions between them, we build SDMs for these two species under current and future conditions. Then, we use those SDMs to analyze their possible range overlap under both current and future scenarios, using for these latter the areas predicted to remain stable and the ones predicted to be gained. We finally use these zones to highlight the areas where possible interaction may occur. Moreover, given the great influence of the wolf on the golden jackal, we build environmental niche models (ENMs) to estimate the current and the future predicted suitable areas for the wolf, to understand if the predicted overlap areas of the Eurasian lynx and golden jackal would overlay with this other large European carnivore.

Materials and methods

Target species and study area

The target species are represented by the Eurasian lynx, a top predator, and the golden jackal, a mesopredator. Secondly, we focused on the grey wolf, another European apex predator.

The Eurasian lynx is classified as Least Concern by the IUCN and is included both in the Bern Convention (Appendix III except for the Balkan lynx balcanicus, listed in Appendix II) and in the EU Habitats Directive (Annexes II and IV, except for some countries where it is included in Annex V and excluded from Annex II). The golden jackal is also classified as Least Concern by the IUCN, and it is included in Annex V of the Habitats Directive. However, the protection of the golden jackal in Europe has been under discussion, since some countries reported it as an alien species, and the Habitats Directive imposes distinct limitations on national policies and national management options (Trouwborst et al., 2015). Indeed, currently, both populations of the target species are increasing (Arnold et al., 2012; Deinet et al., 2013; Chapron et al., 2014; Spassov and Acosta-Pankov, 2019). Similarly, the grey wolf is increasing in Europe, and is classified as Least Concern by the IUCN. Like the Eurasian lynx, the grey wolf is protected both by the Bern Convention (Appendix II) and the EU Habitats Directive (Annex II and IV), even if there are some local derogations.

The area selected for our study is the western Palearctic, a region where the golden jackal is expanding and co-occurring with the lynx.

Environmental predictors

To encompass as much as possible the ecological needs and the factors influencing the two target species' distribution, we used climatic, topographic, habitat, hydrographic, human disturbance and biotic predictors, each of which is described below.

The climatic aspect was assessed through the 19 bioclimatic variables available on WorldClim (version 2.1, 2.5 arc-min, Supplementary Document 1) (Fick and Hijmans, 2017) downloaded for current and future (2050 and 2070) conditions. For each future scenario, we selected the shared socio-economic pathways (SSP) 2.45, 3.70, and 5.85 to involve all the different possible trajectories except the most optimistic one (SSP 1.26) (Riahi et al., 2017). Since the use of a single General Circulation Model (GCM) in future projections is shown to produce variable predictions (Stralberg et al., 2015), we selected and managed three different GCMs, namely the BCC-CSM2-MR (Wu et al., 2019), the IPSL-CM6A-LR (Boucher et al., 2020) and the MIROC6 (Tatebe et al., 2019) for all future models' forecasts.

We collected elevation data from the ASTER NASA database (https://asterweb.jpl.nasa.gov/gdem.asp), deriving the slope raster map at the same spatial resolution (2.5 arc-min) ('Slope' function, Spatial Analyst in ArcGIS Pro), because the slope is considered as a relevant variable for the ecology of both the Eurasian lynx (acting as a proxy for resting sites) and the golden jackal (Filla et al., 2017; Spassov and Acosta-Pankov, 2019; Hočevar et al., 2021).

About the habitat predictors, we took advantage of the 100-m resolution Global Corine Land Cover map of the Copernicus repository (https://land.copernicus.eu/global/products/lc), containing a discrete classification with 23 classes according to the UN-FAO Land Cover Classification System (Buchhorn et al., 2020).

To incorporate the human influence over the two target species, we considered the influence of roads, since they represent a major limit to the dispersal of lynx and jackal, and are capable to alter movement behavior, increase direct mortality and lower patches' connectivity (Kramer-Schadt et al., 2004; Lapini et al., 2011; Heurich et al., 2018). For these reasons, we downloaded the roads data from the "World Roads" Layer Package managed by ESRI (ESRI Inc, 2022) and divided them into major roads and highways. To use this information as a modeling predictor, we calculated the distances from those, classifying them into four intervals (0–500 m, 500–1,000 m, 1,000–5,000 m, 5,000–20,000 m). To further account for human disturbance, especially important for the Eurasian lynx (Ripari et al., 2022), we also downloaded the GHSL SMOD data (Global Human Settlement Layer, available at https://ghsl.jrc.ec.europa.eu/) at ~1 km resolution: this map takes into account both population densities and built-up area densities, in a unique spatial data (Pesaresi et al., 2019).

Also, we used three other predictors for golden jackal modeling only: the average snow cover map (since snow cover was used in previous studies and could partially limit its suitable habitat) (Ranc et al., 2015; Spassov and Acosta-Pankov, 2019; Männil and Ranc, 2022), the river network (as riverine habitats are known to be important dispersal corridors; Arnold et al., 2012; Spassov and Acosta-Pankov, 2019) and the grey wolf current range (since this species is

known to be a major limiting factor for the jackal, especially through intraguild predation; Krofel et al., 2017; Ranc et al., 2018; Spassov and Acosta-Pankov, 2019).

Specifically, for the snow cover information we used the MODIS data (Terra Snow Cover Monthly L3 Global, ~5 km resolution, available at https://nsidc.org/data/MOD10CM; Hall and Riggs, 2021) averaging each month from 2010 to 2020.

The rivers' network information were first obtained from the HydroRIVERS dataset (https://www.hydrosheds.org/products/hydrorivers; Lehner and Grill, 2013) and then processed through the 'Euclidean distance' tool in ArcGIS Pro 10.3 (ESRI Inc, 2022), to obtain distance intervals form each watercourse, with the following intervals: 0–1 km, 1–2 km, 2–3 km, 3–10 km, > 10 km. Finally, the grey wolf current range was obtained at a resolution of 10 km from the work of Kaczensky et al. (2021), giving a different weight to the cells in which the presence of the wolf is permanent, compared to the cells in which the presence of the wolf is sporadic.

Ecological niche modeling

The occurrence datasets were obtained from the GBIF repositories for both golden jackal (GBIF, 2022a) and Eurasian lynx (GBIF, 2022b). Two filters were applied, namely a temporal (selecting the occurrences 1970–current only) and a spatial (coordinate uncertainty < 5 km) one. Moreover, we added occurrence data from recent reports in literature of both the golden jackal and the Eurasian lynx (Supplementary Tables), comparing the final datasets with the known distributions of the species. For the purposes of the modeling process, we processed the GBIF-filtered records so as to obtain a comparable spatial resolution between the occurrences and environmental predictors (Sillero and Barbosa, 2021), moreover reducing the spatial autocorrelation. In order to do that, we used the 'Spatial rarefy' tool of SDMtoolbox (Brown et al., 2017).

To better explore the potential expansion of the golden jackal in the future, we decided to keep the records from dispersing individuals (~19% of the total occurrences), given that these individuals are likely to form stable population, considering his ongoing expansion pattern. The records belonging to dispersing individuals can be noted in Supplementary Figure 1, together with the core areas for each population. However, to assess possible biases caused by the inclusion of dispersing individuals in the species distribution models or related to the nature of the dataset (mainly composed of citizen-science-derived data), we repeated the analysis (building ENMs) using only records from the dataset of Ranc et al. (2022) selecting only the cells where golden jackal is reported as "permanent" or "high confidence presence" (expert-based ENMs).

To model the grey wolf predicted distribution for the current and future projections, we relied on to the dataset of Kaczensky et al. (2021), considering only the cells where the species is reported as "permanent". Then, we assessed the multicollinearity of the 19 bioclimatic variables by measuring the Variance Inflation Factor ('vifstep' algorithm of the 'usdm' R package (Naimi, 2015), threshold = 10); we included the ones both not exceeding this threshold and being important for the species' ecology (Brandt et al., 2017). To minimize the variation caused by the use of individual General Circulation Models (GCMs) in future projections (Stralberg et al., 2015), we used during the modeling process the three different GCMs, namely the BCC-CSM2-MR (Wu et al., 2019), the IPSL-CM6A-LR (Boucher et al., 2020) and the

MIROC6 (Tatebe et al., 2019), and the three SSPs mentioned before for future projections (2.45, 3.70, and 5.85).

To build the ENMs we used the 'biomod2' package (Thuiller et al., 2016) in R (R Core Team, 2016). The advantage of this package is that allows to create ensemble models, which are the result of the combination of individual algorithms' outcomes, corresponding to different modeling techniques. We generated five sets of 1,000 pseudo-absences each (for the wolf, five sets of 10,000 pseudo-absences) using the Surface Range Envelope algorithm (quantile = 0.05) (Barbet-Massin et al., 2012a). We parametrized the single models through the 'BIOMOD_ModelingOptions' as follows: GLM: type = "quadratic", interaction.level = 3; GBM: n.trees = 10,000, interaction.depth = 3, cv.folds = 10; GAM: type="s_smoother", interaction.level=3; RF: n.trees=10,000, bag.fraction = 0.75, shrinkage = 0.001. Then, the 'BIOMOD_Modeling' function was used to calibrate the single models, and the 'BIOMOD_EnsembleModeling' algorithm was finally run to obtain the Ensemble models, using as input only single models with high performances (AUC >0.8 and TSS >0.7). To merge the single models, we use the 'wmean' algorithm, that averages models into the Ensemble one based on a weighted mean function, in which weights are the discrimination scores (Thuiller et al., 2016). Finally, we projected to future scenarios with the 'BIOMOD_EnsembleForecasting' function.

For each projection of the same future scenario (i.e., keeping as fixed the year/SSP combination, for instance the 2050 SSP 3.70), we reduced the uncertainties deriving from the calibration performed on each GCM as follows. We first checked for model extrapolation (i.e., the dissimilarity from the calibration conditions) by assessing the Multivariate Environmental Surface Similarity (MESS) (Elith et al., 2010), computed through the function 'mess' of the 'dismo' package (Hijmans et al., 2016). The MESS maps so obtained were then included in the Multivariate Environmental Dissimilarity Index (MEDI) algorithm (Iannella et al., 2017), a form of weighted raster average which down-weights extrapolation based on projections and MESS, thus reducing the uncertainties in future projections. We finally used those MEDI-corrected future projections as baseline models for all the following analyses.

Weighted overlay process and post-modeling analyses

To obtain a more informative and robust models, we applied the 'Weighted overlay' framework of Iannella et al. (2021) to both target species. This procedure permits to refine Ecological Niche Models into more precise Species Distribution Models, incorporating, in a post-modeling GIS environment, the information not included during the Ecological Niche Modeling process, also increasing predictive performances (Iannella et al., 2021). Thus, we included in this process all the predictors mentioned above except the climatic ones, which were included in the ENM calibration and projection. The information about slope, habitat, population density, snow cover, and wolf range was extracted in occurrence localities for both species through the 'Extract multi values to points' tool in ArcGIS. Then, relative frequencies were calculated for each predictor/occurrence localities and converted into absolute frequencies, on a 1-to-10 scale, to make them comparable with the ENMs. The only exception we made is the conversion into the 1-to-10 scale of the roads and rivers distance categories, deduced from literature (roads information for Eurasian lynx model referring to Dobbert et al. (2021); rivers data for the golden jackal modeling referring to Spassov and Acosta-Pankov (2019) and thus not obtained through the occurrences' frequencies).

Specifically, we used as input into the weighted process on current conditions the ENMs, habitat, population/built areas density, slope, distance from roads and rivers, snow cover, and wolf range predictors to model the distribution of the golden jackal; about the Eurasian lynx, we used the ENMs, habitat, population/built areas density, slope, and distance from roads ones.

For the projections to future scenarios, we kept all the predictors as fixed, except the ENMs; when needed, weighted models were binarized using as a threshold the 10th percentile value (Iannella et al., 2021). Subsequently, the 'BIOMOD_RangeSize' function of the 'biomod2' package (Thuiller et al., 2016) was applied to calculate the areas predicted to be lost, remaining stable, or gained from the two target species in the future scenarios. Considering the presence-only nature of the data, we assess the predictive performance of the weighted models (as well as for the ENMs presented above) through the Boyce index (Hirzel et al., 2006; Leroy et al., 2018).

To evaluate areas where sympatry between the two species may occur, we assessed the overlap of their respective "gain + stable" areas for both the present and the future (considering all the SSPs for this latter case).

Wolf ENMs were binarized through the 10th percentile; we overlap the predicted suitable areas with the zones where future sympatry between golden jackal and Eurasian lynx is predicted to occur.

Results

Ecological Niche Models

After the presence localities filtering processes, we obtained 2,164 occurrences for the Eurasian lynx, and 564 for the golden jackal within the study area (Figures 1A, B). These datasets are roughly comparable to current distributions of the target species, even if they show some gaps, especially for the golden jackal in the core distribution areas.

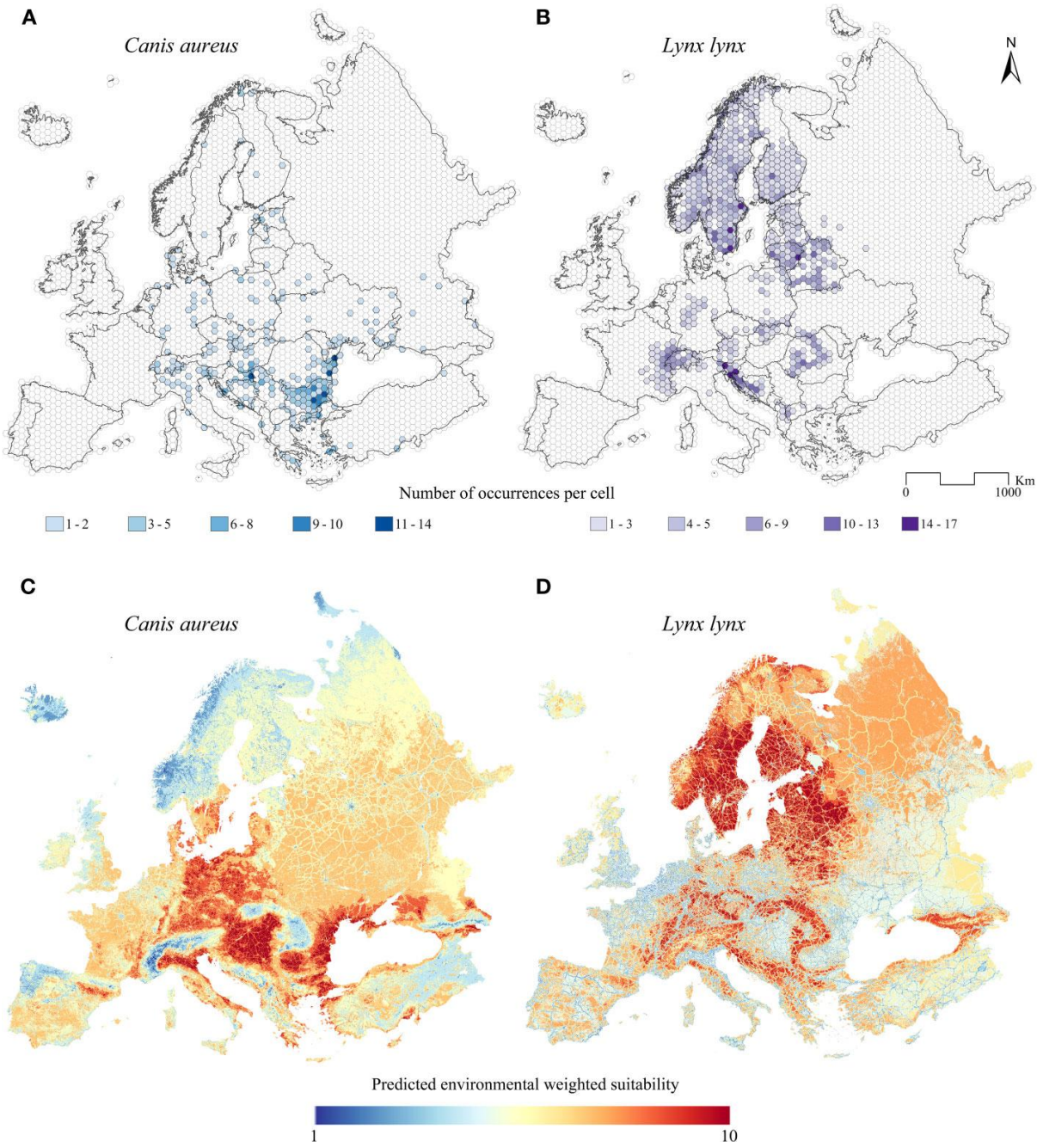


Figure 1. Current and predicted distribution. Current European distribution of (A) the golden jackal (*Canis aureus*) and (B) the Eurasian lynx (*Lynx lynx*). Predicted species distribution model for (C) the golden jackal and (D) the Eurasian lynx, ranging from low (blue) to high (red) suitability.

Considering the results of the VIF analysis and the ecological characteristics of the species, we kept ten bioclimatic variables for the modeling of the golden jackal: BIO1 (Annual Mean Temperature), BIO2 (Annual Mean Diurnal Range), BIO4 (Temperature Seasonality), BIO6 (Min Temperature of Coldest Month), BIO8 (Mean Temperature of Wettest Quarter), BIO9 (Mean Temperature of Driest Quarter), BIO14 (Precipitation of Driest Month), BIO15 (Precipitation Seasonality), BIO18 (Precipitation of Warmest Quarter), BIO19 (Precipitation of Coldest Quarter), and ten for the modeling of the Eurasian lynx: BIO1 (Annual Mean Temperature), BIO2 (Annual Mean Diurnal Range), BIO4 (Temperature Seasonality), BIO8 (Mean Temperature of Wettest Quarter), BIO9 (Mean Temperature of Driest Quarter), BIO11

(Mean Temperature of Coldest Quarter), BIO14 (Precipitation of Driest Month), BIO15 (Precipitation Seasonality), BIO18 (Precipitation of Warmest Quarter), BIO19 (Precipitation of Coldest Quarter). About the wolf, after the VIF analysis, we kept eight bioclimatic variables: BIO1 (Annual Mean Temperature), BIO2 (Annual Mean Diurnal Range), BIO4 (Temperature Seasonality), BIO8 (Mean Temperature of Wettest Quarter), BIO9 (Mean Temperature of Driest Quarter), BIO15 (Precipitation Seasonality), BIO18 (Precipitation of Warmest Quarter), BIO19 (Precipitation of Coldest Quarter).

The ENMs for the Eurasian lynx, the golden jackal, and the wolf resulted in high predictive performances, scoring a Boyce index value of B = 0.897, B = 0.869, and B = 0.921 respectively. The models calibrated on current climatic conditions reveal a wide, highly suitable territory in central Europe, between Germany and Poland, in the Pannonian basin, and the Po valley in Italy, for the golden jackal (Supplementary Figure 2A). Also, some minor and highly suitable patches appear in southern France and eastern Iberian peninsula, in the Northwestern coasts of the Black Sea, and Caucasus (Supplementary Figure 2A). Regarding the future predictions, a great expansion of the climatically-suitable areas is inferred (Supplementary Figures 3A–F). In general, a northeastern suitability gain is observed, as well as an increase in Germany and France, for all the future scenarios (Supplementary Figures 3A–F). The expert-based ENM for the current condition concerning the golden jackal shows similar habitat suitability compared with the prediction obtained with the first ENMs, exception made for a minor suitability between Poland and Germany, and southern Sweden (Supplementary Figure 4). The future habitat suitability maps obtained from expert-based ENMs indicate an analogous pattern of increase in habitat suitability towards the northernmost part of the study area (Supplementary Figures 5A–F). However, a slight difference is observed in Finland and among Ukraine and Russia (Supplementary Figures 3G–L, 5A–F). Regarding the Eurasian lynx, two highly suitable areas emerge, namely the main European mountain systems (Pyrenees, Alps, Apennines, Dinarides, Carpathians, and Caucasus) and the central and northern European territories, with the latter being vaster than the former (Supplementary Figure 2B). In future scenarios, the climatic suitability is generally predicted to massively decrease from all the aforementioned territories, especially in the central and northern European ones (but excluding the Scandinavian peninsula) (Supplementary Figures 3G–L).

Species' frequencies in non-climatic predictors

The extraction of the information about slope, habitat, population density, snow cover, and wolf range performed in occurrence localities for both species highlighted different trends between the species.

About the habitat information (Supplementary Figure 6A), 40% of the occurrences of the golden jackal fall into the "Cropland" habitats, with the lynx reaching only 10% of its occurrences in this category. On the other side, the "Closed forests" resulted to be the most preferred habitat for the Eurasian lynx (~52%), while the golden jackal occurred in 27% of its total occurrences. The "Open forest" category had similar percentages for the two species: 11.4% for the Eurasian lynx and 11% for the golden jackal. Finally, the "Herbaceous vegetation" category is more used by the lynx (21.4%) compared with the golden jackal (6.4%).

Regarding slope, the golden jackal highly prefers low values of it (53.9% of occurrences in the 2% slope category, followed by 17.8% in the 3% slope one), while the Eurasian lynx uses

territories both with low (32.5% for the 2% category, 16.6% for the 3%) and medium (10% of slope used in the ~5% of the occurrences) slopes (Supplementary Figure 6B).

Another result from the frequency of occurrence emerges from the ones falling into territories where human presence occurs. The golden jackal is mainly found in human settlements classified as low-density rural or rural clusters (78% and 13%, respectively), while the Eurasian lynx, when occurring in those settlements, is mainly found in low-density rural patches (89%) (Supplementary Figure 6C).

Weighted suitability models and overlap analyses

The weighted models obtained starting from the ENMs and from the frequency of occurrence of the two target species into the non-climatic predictors are reported for current (Figures 1C, D) and future (Figures 2A–L) conditions. The predictive performance resulted in B = 0.988 for the Eurasian lynx and B = 0.943 for the golden jackal.

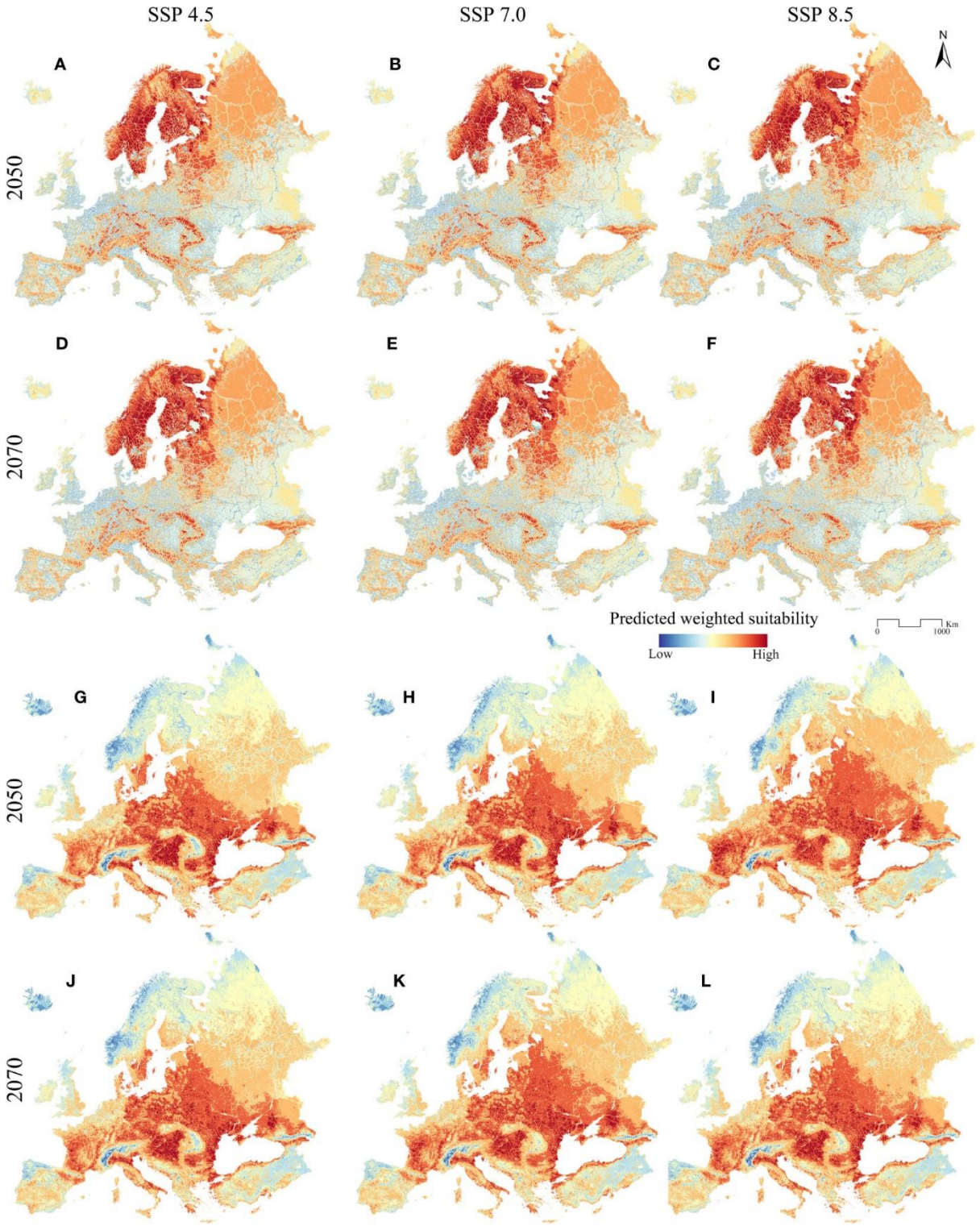


Figure 2. Future suitability predictions (low to high on a blue-to-red scale) for (A–F) the Eurasian lynx and (G–L) the golden jackal, for each different Shared Socio-economic Pathway and projection year considered.

The current weighted map resulted for the Eurasian lynx (Figure 1D) emphasized the high-suitability areas which are compliant with the current distribution of the species (Figure 1B), except for the suitable territories in the Apennines. In contrast, the golden jackal current weighted suitability map (Figure 1C) shows high values in areas from which the jackal is expanding, such as southern and eastern Europe. On the other side, areas where the jackal is

currently extending its range (e.g., Baltic countries, Finland, and Norway) show lower environmental suitability.

About future weighted scenarios, the Eurasian lynx is predicted to face a reduction in its environmental suitability. The greatest reduction is observed for the 2070_SSP8.5 scenario, where only some clusters in central and southern Europe persist with medium-high values of environmental suitability (Figures 2A-F). Similarly, all the other projections in other year scenarios report similar trends, indicating that all the southern populations of the Eurasian lynx (the ones occurring in the Alps, Dinarides, Balkans, and Carpathians) could face a decrease in habitat suitability in the near future. Specifically, a clear decrease in suitability is observable in all future projections, and it is highlighted the fragmentation effect of the road network, especially in the Alps and the Balkans, resulting in a patchy mosaic of suitable areas separated by these infrastructures. By contrast, Scandinavia, the Baltic area, and northern Russia's suitability remains stable at high values, even though the road network heavily influences those areas.

The future scenarios for the golden jackal, on the other hand, report an increase in its environmental suitability in the entire study area, except for the Atlantic coast of Scandinavia and northern Russia (Figures 2G–L). This can be observed across central Europe and in the Baltic States. Also, Italy, France, Balkan countries, and southern Sweden are predicted to be more suitable, with the greater increment represented by scenario 2070_8.5, where also Finland appears to be environmentally suitable for the golden jackal.

When binarizing the weighted predictions (10th percentile threshold = 7.6 for the Eurasian lynx, Figure 3A, and threshold = 6.4 for the golden jackal, Figure 3B) and subsequently assessing the current potential overlapping territories for the two species, we find that this is mainly limited to areas where mountain systems are not present (Figure 3C).

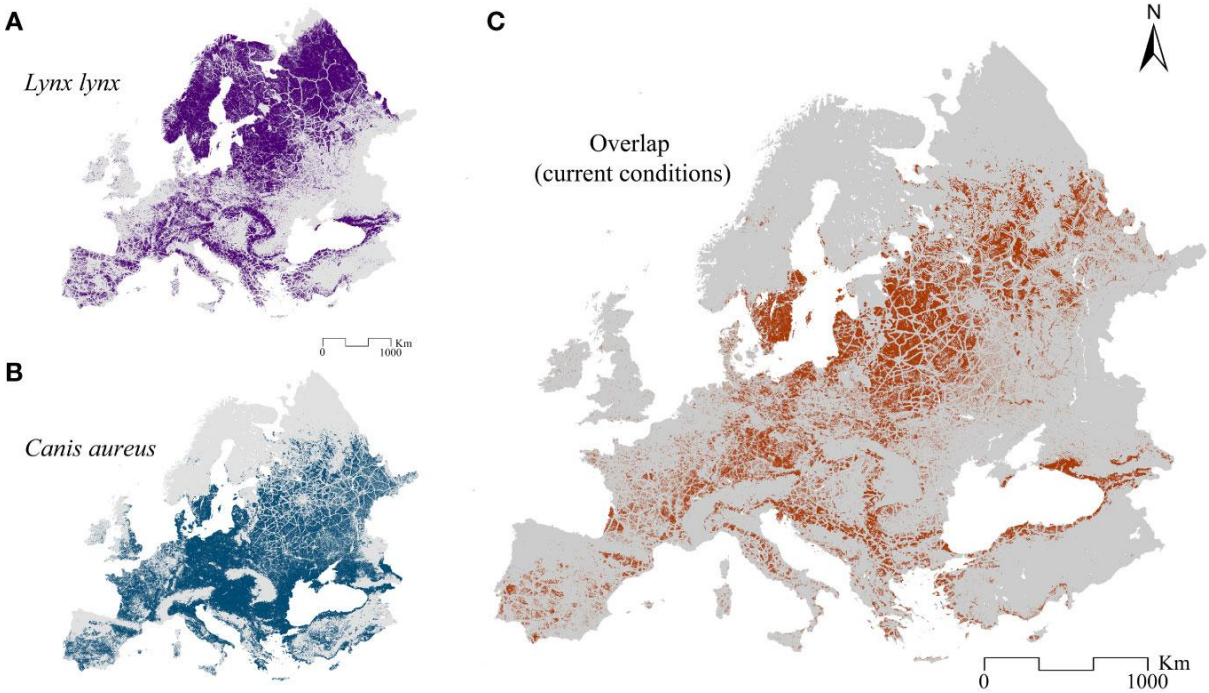


Figure 3. Binarized predictions and corresponding overlap. The binarized weighted suitability model for (A) the Eurasian lynx, (B) the golden jackal, and (C) the shared areas between the two models, obtained by overlapping them.

Future sympatry areas and overlap with grey wolf distribution

In the future, an evident trend emerges: the overlap between the two species gradually shifts towards northeastern Europe, concurrently decreasing in southern Europe (Supplementary Figure 7). When comparing these trends with the range shifts analyses (Supplementary Figure 7), we find that this pattern is driven both by the expansion of the environmental suitability of the golden jackal towards the north-east, and by the reduction of the environmental suitability of the Eurasian lynx in the southwest.

In particular, sympatric areas gradually increase in Finland, southern and eastern Sweden, and Russia, especially in the scenario 2070_8.5.

A slight increase in overlap arises on the slopes of the Carpathians Mountains, in the Balkan area, and in the Dinaric range, where both species occur. Also, along the Apennines, it emerges an increase in the overlapping ranges, where however the Eurasian lynx is not present and the golden jackal sporadically occurs.

Comparing these results with the current wolf-predicted suitable areas, most of the current sympatric areas appear to be overlapped (Figure 4). These mainly occur in the Carpathians Mountains, the Dinaric range, and various zones between Bulgaria, Albania, Macedonia, and Greece (Figure 4). Moreover, the current overlapping areas from the Baltic area to those in central Europe are also suitable for the grey wolf (Figure 4), which occur in some of these countries with stable populations. Similarly, between Italy and France, the predicted sympatric areas for the golden jackal and the Eurasian lynx are eligible for the wolf, which is recently spreading in these countries. Thus, considering the current wolf suitable areas, the potential sympatric areas for the golden jackal and Eurasian lynx (lacking wolf suitable areas) are only a few, located in the Pannonian Basin, Germany, Slovenia, and Russia (Figure 4).

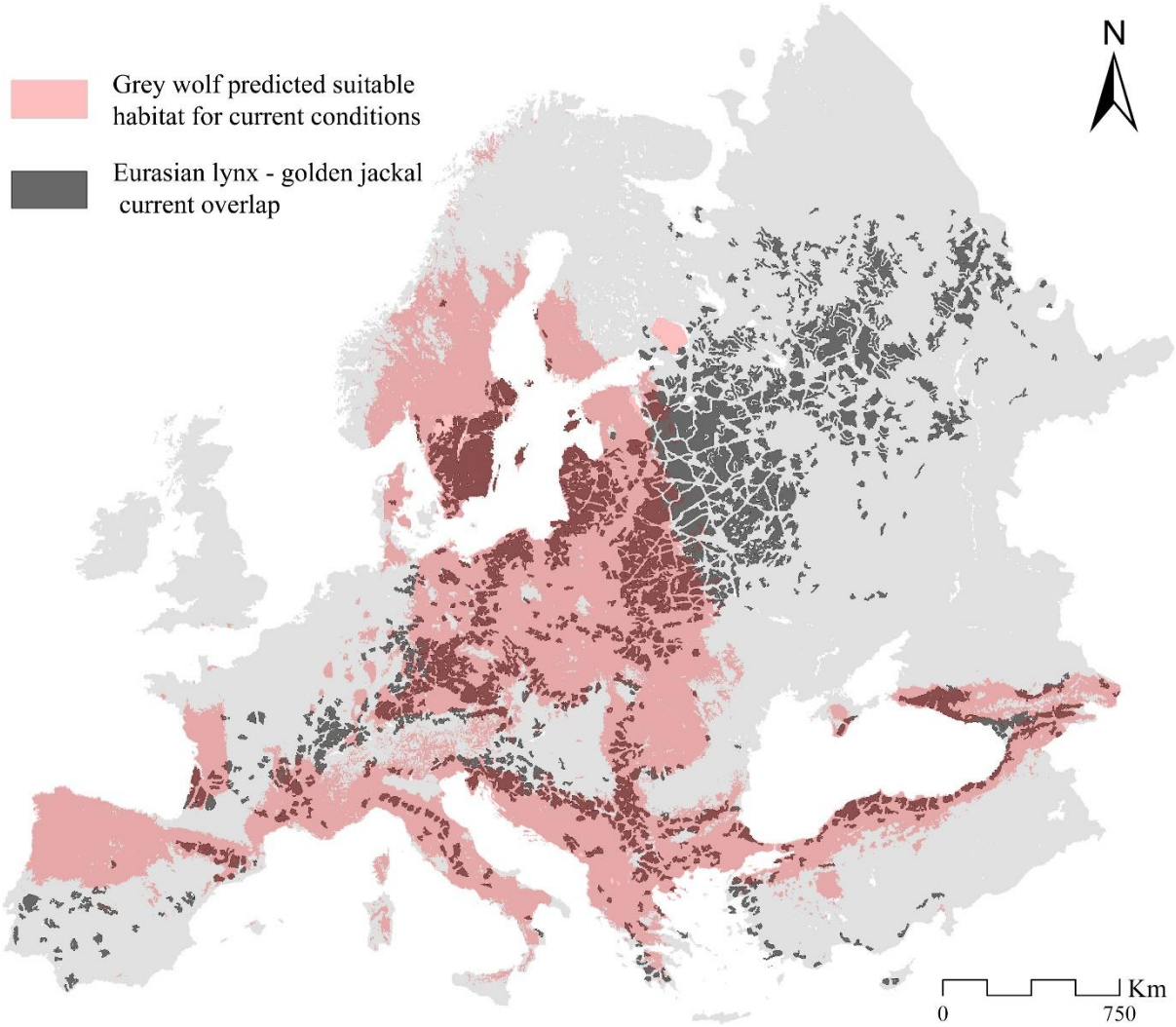


Figure 4. Predicted current overlap between the Eurasian lynx and the golden jackal (dark grey areas) and the grey wolf predicted suitable areas as inferred from the ENMs built on current climatic conditions.

Concerning the future predicted sympatric areas between the golden jackal and the Eurasian lynx, it is shown a gradual increase towards the northernmost part of the study area (Figure 5). Sympatric areas expand across the Baltic area, Russia, and Scandinavia. On the contrary, sympatric areas remain stable or decrease elsewhere in future scenarios (Figure 5). However, considering the future predictions for the wolf distribution, the great majoring of the predicted sympatric areas in Scandinavia and the Baltic area are covered by suitable areas (Figure 5). Thus, considering the predicted expansion of the wolf in these countries, it is unlikely that the golden jackal could spread significantly. A different situation could occur in central and southern Europe. In fact, the future predictions for the wolf show that its suitable areas will increase between France and Italy, and between France and Germany, but reduce in eastern Europe, with suitable areas kept only in the Carpathians, Balkans, and Dinaric range (Figure 5). Then, sympatric areas between the golden jackal and the Eurasian lynx in these areas could expand, such as in some zones in central Europe, between Germany and Poland (Figure 5).

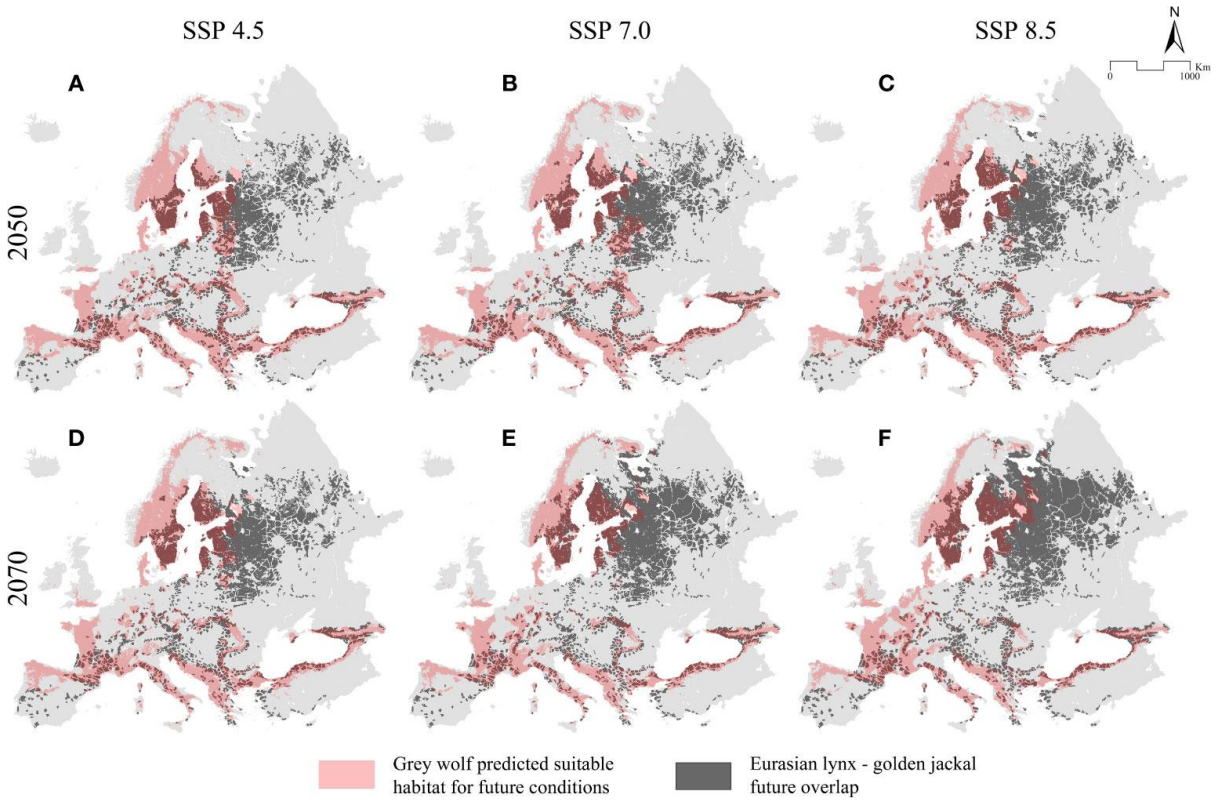


Figure 5. Predicted future overlap (A–F) between the Eurasian lynx and the golden jackal (dark grey) and the binarized predicted suitable range, inferred for future climatic scenarios, of the grey wolf.

Discussion

Europe is seeing a great return of some wildlife species in recent years (Deinet et al., 2013; Ledger et al., 2022), despite the effect of climate and land use changes. While these may favor the expansion of some species, for others they represent a threat that makes their future uncertain (Pacifici et al., 2020; Ledger et al., 2022), as also our results suggest (Figures 2A–L).

Indeed, the expansion of the jackal is favored by several factors: deforestation and land use changes (Šálek et al., 2014), additional anthropogenic trophic resources, the absence of competitors (such as the wolf) (Pyšková et al., 2016; Krofel et al., 2017; Spassov and Acosta-Pankov, 2019). In addition to these elements, climate change may also favor the expansion of the jackal. While in the past it was believed that deep snow could act as a limiting factor for the golden jackal, recent findings proved that the species is able to adapt even in areas with stable snow cover, such as in the boreal ecoregion. Although, in the Baltic states, it was reported that the golden jackal tends to avoid zones with permanent snow cover, preferring coastal areas without snow (Männil and Ranc, 2022). In our results, the greatest expansions are observed in the scenarios with the greatest impact of climate change, especially in the northern part of the study area (Figure 2G–L). The same expansion process affects not only higher latitudes but altitudes as well. In fact, the Range Shift analysis shows a growing rise of "gains" in the main mountain ranges of the study area. The strength of our results is highlighted by the fact that they are in line with those recently obtained (Cunze and Klimpel, 2022) for a similar area, with the important difference that in our analysis we used not only climatic predictors but also non-climatic parameters.

The redistribution of a species can lead to the appearance of new interactions with the fauna already present (Pecl et al., 2017). Changes in the dynamics of predation, herbivory, competition, and mutualism can all have substantial impacts at the community level (Gilman et al., 2010). The expansion of the golden jackal may change these dynamics, particularly interspecies competition, as observed from interactions with the red fox (Vulpes vulpes), where the golden jackal is dominant (Giannatos,

2004; Stoyanov, 2012). On the contrary, with the grey wolf, the cases of competition are few, and the golden jackal is usually defeated (Krofel et al., 2017). Competition is also possible with the European badger (Meles meles), pine marten (Martes martes), and stone marten (Martes foina) (Stratford, 2015). Data about the interactions between golden jackals and other large European predators are scant, but recently it has been observed a case of kleptoparasitism toward the Eurasian lynx (Krofel et al., 2022).

The recovery of the Eurasian lynx has been linked to a series of factors: various measures of legal protection, greater acceptance of this species by the population, reintroductions and recent population reinforcements in many European countries, the return of ungulate species that have expanded the availability of prey (Breitenmoser, 1998; Linnell et al., 2009). The modern expansion of this species is also associated with reduced human population density and increased forest cover (Cimatti et al., 2021). The current suitability map shows that there are large suitable zones in the study area where the species does not occur even if it could survive (e.g., in the Alpine range). The current environmental suitability is comparable with that obtained in a previous study (Dobbert et al., 2021). Our spatially explicit results are in line with those obtained from previous studies which explore lynx habitat selection at European scale (Ripari et al., 2022; Oeser et al., 2023). In fact, our maps of environmental suitability show that at the landscape scale, lynx tend to avoid human-modified areas and human infrastructures network, with habitat suitability remaining clustered in forested areas and/or zones associated with moderate slopes. But the future of this iconic predator is likely to be worse: our results of environmental suitability for the future show clear reductions, particularly around the Alps, in the Carpathian Mountains, and the Balkan area, with the suitability remaining high only in Scandinavia and northwestern Russia (Figures 2A–F; Supplementary Figure 4). Despite these reductions, the Eurasian lynx is a plastic species, especially regarding climatic conditions, and is able to survive even in warmer and drier habitats (Fležar et al., 2023).

In addition to these reductions, there are also some areas with increases in habitat suitability. In particular, beyond the Scandinavia and the Baltic area, good environmental suitability will be maintained in the Alps. Considering these predictions, it is essential to encourage conservation measures for the populations of Eastern Europe (such as the Balkan population and the Dinaric population), but it is also important to improve connectivity along the Alpine range to favor the expansion of the Alpine population. Our overlap analysis shows that in the future the two species could have much more than the current 13% overlap between the ranges, as currently found by Krofel et al. (2022): this increase is mainly linked to the predicted expansion of the golden jackal throughout Europe, especially in the area between Russia, Baltics States and Scandinavia (Figures 2G–L; Supplementary Figure 4). In the same countries, Eurasian lynx suitability is expected to increase, so it could become an area of sympatry in the future. However, considering that these areas host stable populations of wolves, and that habitat suitability is predicted to increase in the future (Figure 5), it is unlikely that the golden jackal could expand significantly in the future, or at least his expansion will be restrained only in areas where the wolf is less abundant.

From a conservation point of view are interesting the overlap dynamics in the Carpathians, the Balkan area, and the Alpine area. Although our maps show future losses for the Eurasian lynx, some suitable patches will be maintained, and for the Alps, some increases are predicted. However, “gains” are also expected in the same areas for the golden jackal, therefore it is probable that in the future the slopes of these mountain ranges may also become areas of sympatry between the two species. But in the same mountain ranges the wolf is also expanding, and habitat suitability is predicted to increase (Figure 5). Thus, even in this case, the predicted sympatric areas between the golden jackal and the Eurasian lynx could be limited by the wolf’s presence. However, even considering the wolf’s presence, interactions between these species can’t be excluded a priori. And the consequences of this coexistence, not only between the golden jackal and Eurasian lynx but involving the grey wolf and the brown bear as well, must be deepened, especially considering that the lynx populations of Alpine, Balkan, and Dinaric areas

are the focus of several conservation efforts, such as translocations and reintroductions (Topličanec et al., 2022).

A previous sympatric occurrence between the golden jackal, grey wolf, Eurasian lynx, and brown bear, was reported in a dense forest in Slovakia (Kysucké Beskydy Mountains), demonstrating the capacity of the golden jackal to coexist even in the presence of other large carnivores (Guimãraes et al., 2021). Thus, the adaptability of the golden jackal could led to different interactions with these large carnivores, beyond the ones reported. Observing future scenarios, the greatest overlap among the ranges is observed in the 2070 scenario with SSP 8.5, a projection where is observed the greatest expansion for the golden jackal, especially in the northernmost areas of the study area. Despite the reduction in habitat suitability for the Eurasian lynx in future scenarios (especially 2070), the overlap between the ranges remains high because the "losses" of the lynx are balanced by the higher "gains" of the golden jackal (Supplementary Figure 4). The results of the Point Sampling tool underline the known differences in the habitat preference between the Eurasian lynx and the golden jackal: while the jackal tends to prefer suburban rural environments, such as cropland, the lynx tends to select preferentially dense forests. Although, this does not exclude interactions, as both species may select the other's preferred habitat. In fact, the golden jackal can select woodland habitats to search for burrows and reproduce, and its ecological plasticity allows it to use even more closed forests, especially when any apical predators are absent (Krofel et al., 2017). Still, Eurasian lynx select more open habitats (Belotti et al., 2013), even if close to humans, if they have high prey densities (Basille et al., 2009; Filla et al., 2017). Ungulates often are abundant near human infrastructures because they find protection from predators due to the proximity of man, a process known as the "human shield effect" (Berger, 2007). However, given that the golden jackal habitat selection is strongly influenced by the presence of wolves (Krofel et al., 2017), where sympatry may occur between the species (Figures 4, 5), the golden jackal habitat selection would probably change significantly.

After being the most widely distributed large terrestrial predator in the northern hemisphere, wolves went to a severe decline mainly due to human persecution (Ripple et al., 2014). Recently the species is recolonizing Europe: expanding both from its permanent range in Italy and Spain, and from the Dinaric-Balkan, Carpathian, and Polish lowland populations, recolonizing central Europe and Scandinavia, and expanding in eastern Europe (Boitani and Linnell, 2015; Hindrikson et al., 2017). Several studies prove the wolf's strong influence on the golden jackal through intraguild predation (Mohammadi et al., 2017), and the wolf's absence is considered one of the main causes of golden jackal expansion (Krofel et al., 2017). Our predicted sympatric areas for the golden jackal and the Eurasian lynx show that most of them overlap with current wolf-predicted suitable areas. In these areas it is more probable that the golden jackal could exploit different resources, like anthropogenic food sources, using more human-modified habitats and more open habitats. Consequently, the interactions with the Eurasian lynx would be significantly reduced. Moreover, it should not be forgotten that Europe hosts other populations of a large predator (i.e., brown bear) and mesopredators, like the red fox. For example, the Eurasian lynx suffers kleptoparasitism from the red fox, which feeds on lynx prey (Krofel et al., 2019), and similarly, there are also cases of brown bears feeding on the prey hunted by the lynx (Krofel et al., 2012). Future studies will be needed to fully understand the outcomes of the interaction between the golden jackal and the Eurasian lynx, an interaction already real, but which our study shows would be much more frequent in the future. Furthermore, future research will also have to better consider possible interactions, apart from kleptoparasitism, with other species of predators.

A possible limitation of our study could be linked to the dataset used, especially for the golden jackal, because we retained the records from dispersing individuals (i.e., out of the current core areas), and the main part of the dataset is obtained from the GBIF repository, known to be possibly spatially biased due to differences in data-sharing between countries and the consequent unequal effort of sampling (Beck et al., 2014). This could have led to an inflated effect on the environmental suitability in the northernmost part of the study area, even though the robust design of the modeling methods we used,

together with the limited number of the dispersing individuals' occurrences, buffer this issue. To check possible biases in the models' output, we repeated the ecological niche modeling process by using only records reported as "permanent" or "high-confidence presence" from an expert-based dataset. Comparing these modeling outputs (Supplementary Figures 2–5), only some subtle differences are noted, resulting in similar habitat suitability values, both for current and future conditions. Thus, this interesting finding proves that for some specific contexts (i.e., modeling habitat suitability of a generalist species at the landscape scale), the use of citizen-science data could be as useful as data from expert-based datasets. However, considering the small differences in the northernmost part of the study area between the two different ENMs (the ones built with our dataset and the one obtained from the expert-based dataset), we recommend considering this aspect when exploring our maps. However, the future availability of more robust and expert-based datasets would surely improve the quality of ecological modeling studies, and for species in rapid expansion, these datasets are also urgently needed.

In this complex context of large carnivores expansion through the European landscapes, is important to improve measures that could bring the conservation of the entire biocenosis: for example, regulating hunting activities, especially of wolves and ungulates, in order to reduce possible competition between large predators. Other measures could include the coverage increase of protected areas, which have favored the expansion of large carnivores in the past, together with an increasing public acceptance (Dressel et al., 2015), especially in areas where these species are making a comeback after some time. The use of economic compensation for any damage by predators can also help improve the public acceptance of these species (Dickman et al., 2011).

In conclusion, our results can support conservationists by identifying which areas these two carnivores could coexist in the future. Both in areas already occupied by both species and in those where sympatry is expected in the future, further studies will be needed to better understand the effects of this coexistence and any interactions.

Supporting Information

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1165968/full#supplementary-material

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Chapter 6

Case Study I: Don’t stop it now: functional and structural habitat connectivity assessment suggests further expansion in Southern Europe for the Eurasian beaver

Introduction

After being widespread in Europe, the Eurasian beaver (*Castor fiber*) was reduced to 1200 individuals at the beginning of the 20th century, mainly due to overhunting (Nolet and Rosell 1998; Halley and Rosell 2002). These individuals were divided into eight relict populations, five of them occurring in Europe (Halley et al. 2012). Following legal protection, hunting restrictions, and several translocation programs, the species started a recovery, gradually recolonizing much of its former habitat (Nolet and Rosell 1998), and the more recent estimate now indicates a population of approximately 1,200,000 individuals in Europe (Wróbel 2020).

Legal protection started in the 18th and 19th centuries in most European countries, while the first reintroduction occurred in Sweden in the 1920s (Nolet and Rosell 1998). Subsequent reintroductions concerned Norway, Finland, Russia, Estonia, Latvia, Lithuania, Poland, Netherlands, Germany, Switzerland, France, Austria, and the Czech Republic, initially motivated by the aim of reintroducing the species for hunting purposes (Nolet and Rosell 1998). Even if some reintroductions failed, most of them resulted in the establishment of stable populations (Nolet and Rosell 1998). Among the factors that favor its recovery, are the habitat availability and the ecological plasticity of the species, capable of using various food sources and selecting even sub-optimal habitats (Haarberg and Rosell 2006; John et al. 2010; Krojerová-Prokešová et al. 2010; Swinnen et al. 2017).

Similar to the situation in other parts of Europe, the Eurasian beaver in Italy and Spain was hunted extensively for meat, fur, and castoreum, a secretion produced by peri-anal glands used by humans for medical purposes (Nolet and Rosell 1998). In Italy, the species appeared in the Early Pleistocene, with fossils found in both Northern and Central Italy (Barisone et al. 2006). Late Pleistocene fossils have been found predominantly in Northern Italy (Salari et al. 2020). Similarly, most of the Holocene records of the species came from Northern Italy, Lombardy, and North-Eastern Italy, with fewer numbers from Central Italy (Salari et al. 2020). The extinction of the Eurasian beaver in Italy is dated between the 15th and 16th centuries, with a specific extinction date in 1541 (Halley et al. 2012). Regarding the Iberian Peninsula, the beaver has been present since the Pliocene, with its first appearance in the Early Pleistocene, followed by population fluctuations during subsequent periods (Cuenca-Bescós et al. 2021). The extinction in Spain is dated to the 17th century (Halley and Rosell 2002), while no historical information is available for Portugal.

In 2003, eighteen beavers were illegally reintroduced in Spain within the Ebro basin (Ceña et al. 2004). Attempts to remove the individuals failed, and the species subsequently expanded its range, establishing a permanent presence in the Ebro basin (Halley et al. 2021). Currently, there are more than 1000 individuals, spanning approximately 300 km along the Ebro River and its primary tributaries (Halley et al. 2021). Following the derogation from the Habitats Directive which allowed the Spanish authorities to remove the species, in 2018 a letter from the European

Commission Environment Directorate reversed the position, affirming beavers as a historically native species, and once again extending protection under the Habitats Directive. More recently, the species was reported in the western Iberian Peninsula, bordering Portugal, in the Douro basin, as a result of a probable unauthorized release (Calderón et al. 2022).

Only recently, the Eurasian beaver reappeared in north-eastern Italy (Friuli Venezia Giulia region), with a natural recolonization right from one of the reintroduced populations in Austria (Pontarini et al. 2018). Another individual was observed in Alto Adige in 2020 (Pucci et al. 2021). Since then, the species has been noted in different disjointed areas in Central Italy, probably because of multiple illegal reintroductions (Pucci et al. 2021). Currently, the Eurasian beaver in Italy occurs in Friuli-Venezia-Giulia (Tarvisio forest), Alto-Adige, Tuscany (Tevere, Arno, Merse and Ombrone river basins), Emilia Romagna (Reno river basin), Umbria (Tevere river basin), Latium (Tevere river basin), Abruzzi (Aterno river basin), between Molise and Campania (Volturno river basin), and in Piedmont (Po and Toce river basin) (Mori et al. 2021; Pucci et al. 2021; Capobianco et al. 2023).

While the return of the Eurasian beaver in Northern Italy may be attributed to natural recolonization from the populations from Austria, the occurrences from Central Italy are likely the result of multiple illegal reintroductions, like the ones occurred in the western Iberian Peninsula (Pucci et al. 2021; Calderón et al. 2022; Capobianco et al. 2023). In this context of rapid beaver expansion, it is of paramount importance to assess where the species could further expand next. Furthermore, considering the abundance and environmental impacts, of the dams settled in the European rivers (Belletti et al. 2020), it is relevant to identify the specific barriers that should be targeted for mitigation or management actions to reduce river's fragmentation for the Eurasian beaver.

Previous ecological modeling studies have indicated that both the Italian and Iberian Peninsulas retain several suitable patches for the beaver, particularly in Central Italy, Northern Spain, and Central Portugal (Serva et al. 2023a). Thus, further waves of natural expansions from the reproductive populations in Central Italy can be expected, as well as for the populations in the Ebro basin. In fact, this process is still ongoing as demonstrated by the recent new occurrences in both countries. To assess how the Eurasian beaver could expand, structural and functional connectivity is critical. In recent years, several techniques have been developed to evaluate functional connectivity. Circuit theory is among the most popular techniques, and Circuitscape is the reference software (McRae et al. 2008; Dickson et al. 2019). Circuitscape is based on the random-walk assumption (i.e., individuals moving across a landscape have no knowledge of surrounding habitat patches (McRae et al. 2008; Dickson et al. 2019). The Omniscape algorithm, applies Circuitscape in 'advanced' mode, iteratively, by using a moving window with a user-specified search radius, to evaluate omnidirectional connectivity in the landscape without considering source/destination areas (McRae et al. 2016; Landau et al. 2021). Both were recently used for semi-aquatic species (Dertien and Baldwin 2023; Falaschi et al. 2023; Leoncini et al. 2023). To explore structural and functional connectivity only considering each river where it has reported the presence of the Eurasian beaver, we also used the recently developed R package 'riverconn' (Baldan et al. 2022). The package is based on graph theory and allows the user to calculate different metrics of connectivity and fragmentation within each river (at reach-level), prioritizing the barriers present (Baldan et al. 2022).

In this study, we first aim to model functional connectivity in Italy and in the Iberian Peninsula, using circuit-theory techniques. Moreover, we apply the 'riverconn' R package to explore the functional and structural connectivity inside each river where the beaver presence is reported, and to highlight the potential barrier to the beaver's expansion.

Material and Methods

Target species and study areas

The target species is the Eurasian beaver, among the larger rodents on Earth, listed as 'least concern' on the IUCN Red List. The species is protected under Annex II and IV of the European Habitats Directive, as under the Federal Act for the Protection of Nature. We focus on two different study areas, the Italian and the Iberian Peninsulas, two regions where the beavers are now expanding, after having been illegally reintroduced recently.

Environmental predictors

A resistance surface was generated as a layer, to describe the relationship between landscape structure and the Eurasian beaver movement. In this resistance surface, each pixel is assigned a value reflecting the resistance to the movement of the target species (Adriaensen et al. 2003). Considering the ecology of the Eurasian beaver, we integrated six environmental variables: Corine Land Cover, the hydrographic network, the distance from the hydrographic network, the Profile Curvature (which acts as a proxy of acceleration or deceleration of water flow, following Bernabò et al. (2022), the Tree Cover, and the position of dams.

The CORINE Land Cover layer was obtained from the Copernicus repository (https://land.copernicus.eu/pan-european/corine-land-cover/clc2018), the hydrographic network data from the HydroSHED dataset (https://www.hydrosheds.org/hydroatlas), the dams shapefile from OpenStreetMap, and then compared to other existing dams' datasets (https://www.globaldamwatch.org/), while the Tree Cover was accessed from the Copernicus repository (https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density). We used the 'Euclidean Distance' tool available in ArcGIS Pro (Inc 2023) to calculate the distance from the river network, and the 'Surface Parameters' function to obtain the Profile Curvature layer, starting from a Digital Elevation Model (downloaded from the Copernicus repository, European Digital Elevation Model, EU-DEM, version 1.1 https://land.copernicus.eu/imagery-in-situ/eu-dem). All the raster layers were processed at a 100 m resolution. Each variable was reclassified to a common scale, ranging from 1 (indicating the lowest suitability, and maximum resistance) to 10 (indicating the highest suitability and minimum resistance), with the 'Reclassify' tool in ArcGIS Pro. We opted for an expert-based approach to assign a resistance value to each pixel, and the such-obtained results were finally compared to published literature. This method was chosen because using inferential data applied to peripheral or new areas of a species' expanding range might not effectively distinguish between suitable and unsuitable patches, as such areas may not yet be utilized as pathways (Clevenger et al. 2002). Moreover, expert-based opinion is among the most used approach to estimate resistance to movement (Zeller et al. 2012).

Given the semi-aquatic nature of beavers, the hydrographic network was assigned the lowest resistance value. Different resistance values were applied based on the Strahler order of rivers (higher resistance for rivers with Strahler order equal to 1, indicating torrential flow and unsuitability for beaver dams with a higher probability of running dry). We reclassified the

distance from the hydrographic network following the reported terrestrial distances preferences (Haarberg and Rosell 2006; Graf et al. 2016; Swinnen et al. 2017), with different intervals: 0–50 m (lower resistance), 50–100 m, 100–200 m, 200–400 m, 400–20,000 m (higher resistance).

Considering the habitat selection of the beaver (Pinto et al. 2009; John et al. 2010; Smeraldo et al. 2017; Swinnen et al. 2017; Alakoski et al. 2020), we reclassified the Corine Land Cover (see Table S1 in Online Resource 1 for full details) assigning higher resistance values to artificial sites, marine waters, arable land, permanent crops and open space with little or no vegetation. Medium resistance values to pastures, heterogeneous agricultural areas, and shrub or herbaceous vegetation associations. Lower resistance values to forest areas, inland waters, and inland wetlands. The Tree Cover layer was reclassified linearly, i.e., from 1 to 100 to 1 to 10, according to beaver's habitat preferences (Pinto et al. 2009; Smeraldo et al. 2017; Swinnen et al. 2017). We chose to use Profile Curvature, rather than Slope alone, as a predictor: this layer reports the acceleration and deceleration of the water flow and is useful to identify areas where slow- (or fast-) flowing water-adapted species may occur. We reclassified the Profile Curvature layer, following the beaver's preferences (Pinto et al. 2009; Steyaert et al. 2015), giving low resistance values for areas with low acceleration/deceleration, thus indicating flat areas, and high resistance values for areas with high acceleration/deceleration values.

Finally, the dams' layer was assigned a unique value of 1 (highest resistance), giving their potential role as a barrier for beaver dispersal (Nolet and Rosell 1998).

Resistance surface

We combined the predictors through the 'Weighted Overlay' tool in ArcGIS Pro. This tool lets the user combine different layers that share the same scale of values, assigning to each a specific percentage weight. We deliberately excluded the dam layer from this process to avoid modifying the effect (i.e., the resistance value) of these artificial barriers. Instead, we added the dams' information after merging the other layers through the 'Mosaic to New Raster' function in ArcGIS Pro. Then, we transformed the final habitat suitability layer into a resistance layer, using a negative exponential transformation function (Keeley et al. 2016):

$$R = 1{,}000 - 999 \times \frac{1 - \exp(-c \times h)}{1 - \exp(-c)}$$

In this function, R represents the final resistance value of a pixel, h is the habitat suitability value for the same pixel, and c represents a constant factor determining the curvature of the negative exponential function. Previous studies have demonstrated that moderate values of the constant factor, c, provide the best performance (Keeley et al. 2016). The resistance layer expresses the degree to which a grid cell facilitates or impedes movement of the target species (Spear et al., 2010), a technique already employed in previous connectivity studies (Iannella et al. 2021a).

This transformation assigns high resistance values to the lowest habitat suitability values, and it has been shown to be a more accurate representation of landscape resistance, considering that habitat suitability may not be correlated with movement probability and landscape permeability (Keeley et al. 2016; Zeller et al. 2018). We finally compared the resistance layer so obtained with the suitability maps found in Serva et al. (2023a) and Falaschi et al. (2023).

Omniscape analysis

We used Omniscape v.0.5.8 in Julia to compute landscape connectivity (Landau et al. 2021). Omniscape calculates omnidirectional connectivity using circuit theory, by using as input a resistance surface (McRae et al. 2016; Landau et al. 2021). This software operates iteratively within a moving window framework, with a user-specified search radius, where the center pixel is used as the destination and is set to 'ground', while pixels within the moving window are the sources where the current is injected, and the user could decide whether to use all the pixels as sources or only those with certain resistance values (Landau et al. 2021). Once defined the target pixel and the sources, Omniscape applies Circuitscape in "advanced" mode (Landau et al. 2021). These steps are repeated for every potential target pixel. As with other circuit theory software, the computed current is comparable to the probability of movement of the target species, in this case, the Eurasian beaver. Omniscape generates three different outputs: cumulative current flow, potential current flow, and normalized current flow. We set the search radius of the moving window to 25 km, as it is reported to be the maximum distance dispersal for the beaver (Mayer et al. 2017).

Connectivity toward current suitable patches

Considering that further beaver expansion in the Italian and Iberian Peninsulas is plausible (Halley et al. 2021; Serva et al. 2023a), we took advantage of the suitable patches in those areas identified by Serva et al. (2023a), to perform Circuitscape (v5.13.1, in Julia) runs in 'advanced' mode (Hall et al. 2021). Circuitscape requires as input a resistance layer and some source/target locations (i.e., the nodes). In the 'advanced' mode, users can select multiple sources (i.e., where current is injected) and destinations (i.e., where current exits the system) across a landscape, and they are activated simultaneously. We designated the basins with the highest suitability values and treated them as destination nodes. The areas where the beaver's presence is confirmed (Halley et al. 2021; Mori et al. 2021; Pucci et al. 2021; Calderón et al. 2022; Capobianco et al. 2023) were used as sources. The resulted connectivity map represents the expected net probability of an organism moving from the nodes to the destinations.

Circuitscape analysis

Even though, within the two study areas, the beaver occurs only in a few territories, we decided to model a directional connectivity assessment, by using Circuitscape with the 'pairwise' mode. The main difference compared to Omniscape is that in this case, the software produces a connectivity assessment between source/destination nodes, i.e., a directional connectivity. In contrast to other connectivity analyses which produce only one path, Circuitscape produces multiple paths between nodes. The resistance map is read as an electric circuit, where the current flows between nodes, and the pixel value represents the passage cost of a 'random walker' (McRae et al. 2008). In the 'pairwise' mode, each node is both the source and the destination, and a current map is calculated iteratively for every pair of nodes, with a cumulative final map for all nodes representing the expected net probability of an organism to move between nodes.

Structural connectivity assessment

To assess structural connectivity within the river systems where the Eurasian beaver has been reported, we employed the recently developed 'riverconn' R package (Baldan et al. 2022). This package allows user to calculate different indices related to connectivity and fragmentation, at catchment or reach scale, distinguishing between structural (resulting from the physical

structure of the river network) and functional connectivity (Baldan et al. 2022). The river network is treated as a graph (Erős et al., 2012), with an assemblage of edges and vertices, with edges representing either barriers or confluences between reaches, and vertices representing reaches. Reaches are river sections placed either between two confluences or between two barriers (Baldan et al. 2022). Furthermore, it is possible to prioritize the main barriers (such as the dams in this case) and include in the indices' calculation additional data relevant to the target species (Baldan et al. 2022). We opted to include in those the tree cover density, as tree abundance is a critical factor for the expansion process of the Eurasian beaver and in defining whether a habitat will be occupied (Pinto et al. 2009; John et al. 2010; Swinnen et al. 2017). Specifically, we decided to calculate the following indices: DCI (Dendritic Connectivity Indices) where n ode weights are reaches lengths, IIC (Integral Index of Connectivity) also with uniform weights, and PCI (Population Connectivity Indices) both normal and with weighted usable length, associating the Tree Cover data. All the analyses were conducted in R software (R Core Team 2023), and the required shapefiles were managed in ArcGIS Pro (Inc 2023).

Results

Omniscape cumulative current map

The resistance layers (Fig. 1a) generally show the importance of the hydrographic network as corridors for the Eurasian beaver expansion, especially in flat areas and with medium-high tree density.

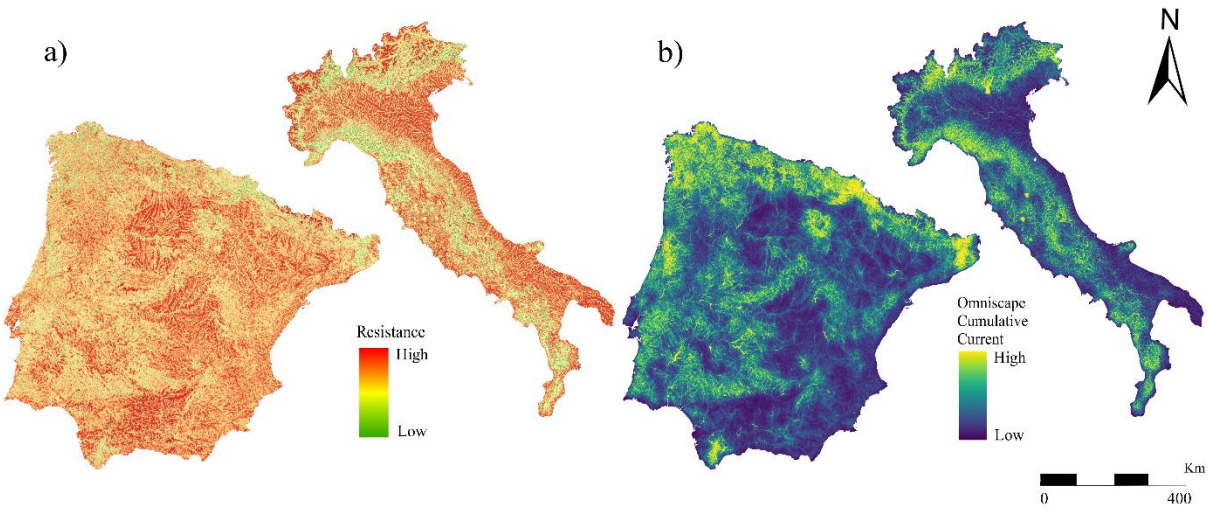


Figure 1. (a) Resistance surfaces for the study areas and (b) current landscape connectivity obtained from Omniscape cumulative current map

In Italy there is a generally robust connectivity network, particularly in the Northern Apennines and the regions surrounding Garda, Como, and Maggiore lakes (Fig. 1b). In the proximity of the latter (Toce river) the presence of the beaver has been confirmed, and from this area, the Ticino River basin shows favorable connectivity values extending towards the Po basin (Fig. 1b). High connectivity values are also evident in the western Po basin, where the presence of beavers is verified. In Central Italy, an area in which the Eurasian beavers are found, a general high connectivity is found, although exceptions should be made. For instance, the occurrences found in the Tevere basin in the Umbria Region and the ones in the Aterno basin (Fig. 1b).

In the Iberian Peninsula, the highest connectivity values occur in the northwestern regions (Fig. 1b). In the Ebro basin, where beavers have been present since 2003, connectivity is generally lower, with higher values in the northern tributaries of the Ebro and the southern tributaries leading towards the Sistema Iberico (Fig. 1b). The recent occurrence from the Douro basin is more connected southwards, possibly through the Huebra river (Fig. 1b).

At the basin level, the Omniscape current mean map for the Iberian Peninsula reveals greater connectivity in the northern areas and the northern side of the Ebro basin, where beavers occur (Supplementary Figure S1 in Online Resource 1). A similar pattern is observed in the Omniscape current mean map for the Italian Peninsula at the basin level (Supplementary Figure S1 in Online Resource 1), highlighting high connectivity values in the Northern Apennines and in the proximity of major northern lakes. For Central Italy, this analysis indicates that most of the occurrences are situated in basins with medium to high levels of connectivity (Supplementary Figure S1 in Online Resource 1).

Connectivity toward current suitable patches

When considering the connectivity derived from Circuitscape in 'advanced' mode towards the currently suitable patches, it becomes evident that in Italy, the northern occurrences in Piedmont and Alto-Adige have the potential to make the Eurasian beaver expand southwards through the Piave and Tagliamento rivers, even considering that the presence in the Po River is in close proximity to various suitable patches (Fig. 2). In Central Italy, there are several corridors, with a notably stronger connection originating from the Tevere and Volturno basins (Fig. 2). Furthermore, from the Ombrone and the Aterno basins, there are good connectivity values linked to the same patches well-connected to the Tevere and Volturno basins (Fig. 2). From these projections, it is very likely that these patches could become areas of stable presence in the near future. This pattern of connectivity is highlighted also from the connectivity map obtained from Circuitscape in 'pairwise' mode, where high connectivity is found in Central Italy, between the Tevere and the Ombrone basins, and between the Aterno and the Volturno basins (Supplementary Figure S2 in Online Resource 1).

Regarding the Iberian Peninsula, numerous corridors establish connections between the Ebro occurrences and nearby suitable patches in both northern and southern directions (Fig. 2). In addition, the Douro occurrence is well-connected to the suitable eastern patches across the Tormes river, but with the important barrier of the Almendra dam (Fig. 2). From the connectivity map obtained from Circuitscape in 'pairwise' mode great connectivity values occur in the Ebro basin, with important corridors toward the west and south, especially in the Esla river, which could potentially link the occurrence in the Douro basin (Supplementary Figure S2 in Online Resource 1).

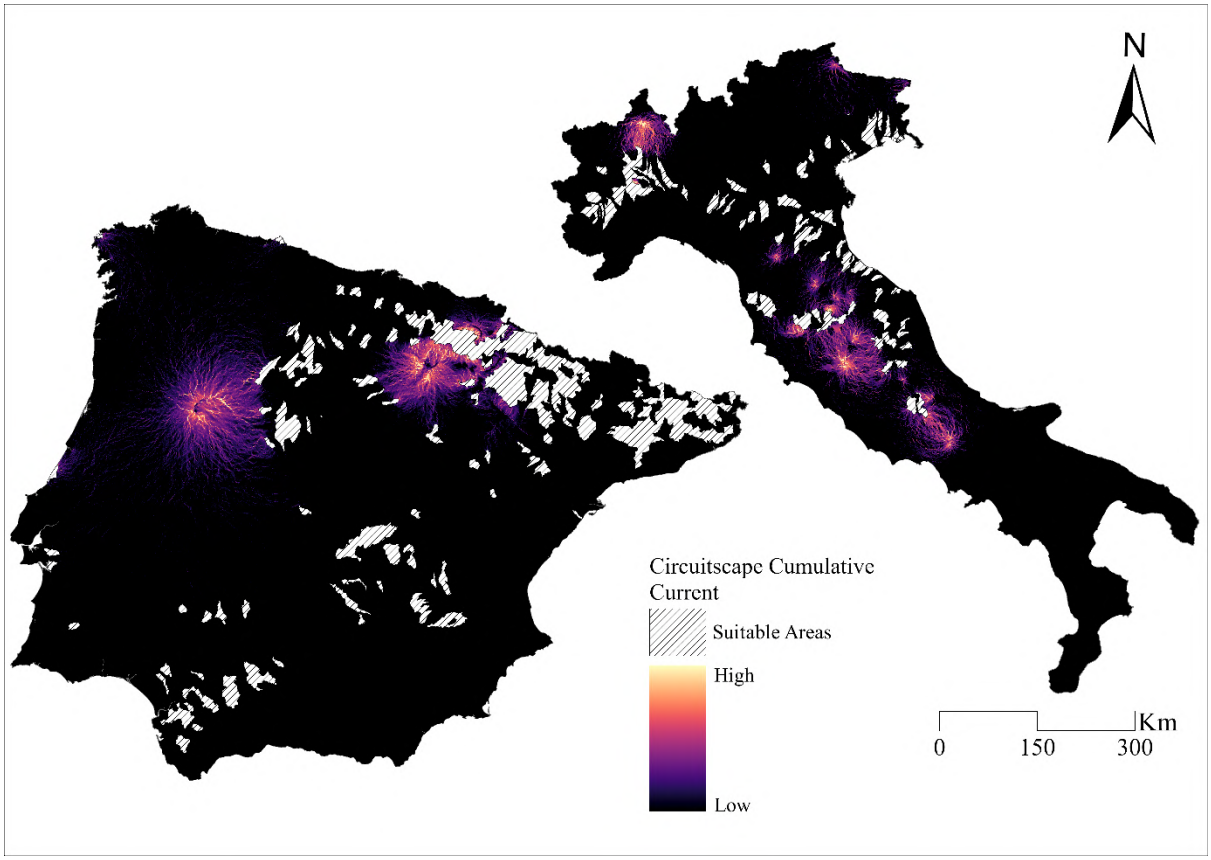


Figure 2. Circuitscape cumulative current map using advanced mode for both Peninsulas, with beaver occurrences as sources and suitable patches as destination nodes. In the Iberian Peninsula, the recent occurrence from the Douro basin is well-connected eastward, while the occurrences in the Ebro basin are in proximity with several suitable northern patches. In Italy, higher connectivity values occur in the Tevere basin, and from Volturno and Toce rivers.

Connectivity assessment within PAs

Among PAs, high connectivity values occur in the Po basin, as for the Alto Garda Bresciano Natural Park (In Fig. 3 indicated as AGB), or in the Val Grande National Park (VG) and neighboring PAs, and in the Northern Apennines, as in the Val Boreca Monte Lesina Special Protection Areas (VB-ML), in the Antola Regional Natural Park (An) and in the Aveto Regional Natural Park (Av) (Fig. 3a). Connectivity remains high across the Apennine range up to the Site of Community Importance (SCI) Forests of the upper Arno basin (UAB). In the Eastern Alps Basin, high connectivity values are found in two SCIs, Rio Bianco di Taipana and Gran Monte (RBT-GM), and in the Middle Tagliamento Valley (MTV). In Central Italy, high connectivity values are found in fewer PAs, such as the Alto Merse and Val di Farma Nature Reserves (AM-VF), or in the lower Valnerina and in the Boschi di Terne Special Protection Areas (LV-BT) (Fig. 3a).

In the Iberian Peninsula, the highest connectivity values are found in some protected areas in the northern area of the peninsula, such as the Urbasa y Andía (UA) or Robledales de Ultzama y Basaburua Natural Park (RUB), the Gorbeia Natural Park (Go) and towards the west through the Redes Natural Park (R) up to Ancares - Courel (A-C) site (Fig. 3a). Furthermore, in the Catalonian basin there are great connectivity values from the Garrotxa Natural Park (Ga) to the

Montseny Natural Park (M), and between the Ebro and Douro basins, in the Sierra de la Demanda (SD) natural park there are good connectivity values (Fig. 3a).

At the basin scale, higher connectivity values occur in the Arno in Italy, and in the Cantabrian-Miño and Mondego basins in the Iberian Peninsula (Fig. 3b). The lowest connectivity values in the Andalusian basin are mainly due to climatic factors: this basin hosts the hottest and driest conditions in the Iberian Peninsula. Overall, PAs have slightly higher levels of connectivity when compared to the basin itself, especially in the Northern Apennines and the Volturno basin in Italy, while in the Iberian Peninsula PAs have higher values only in the Catalonian and Cantabrian-Miño basins (Fig. 3b). Therefore, as regards the state of connectivity, the PAs of the Iberian Peninsula in general have lower values when compared to their catchment area (Fig. 3a).

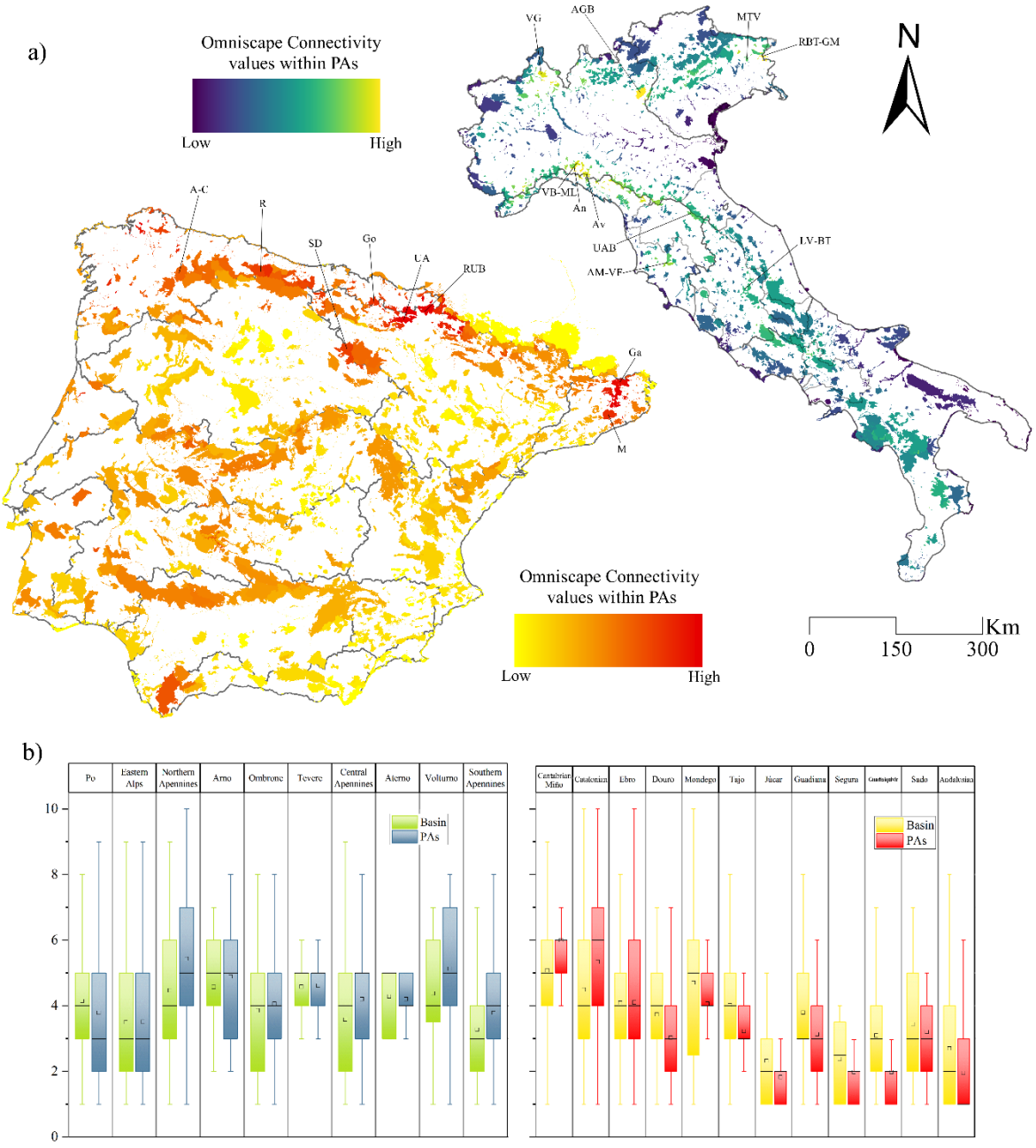


Figure 3. Omniscape connectivity values (a) within PAs for both peninsulas, and (b) mean connectivity values for Italian and Iberian Peninsulas at basin level, and only for the PAs occurring in each basin.

Riverconn connectivity assessment

In Fig. 4, we consider four hydrographic basins within the Italian Peninsula, along with the two basins where beaver presence has been reported in the Iberian Peninsula, introducing the results of the IIC and PCI indices only for the sake of brevity. Indeed, all the calculated indices for each individual basin can be found in Online Resource 1 (Figs. S4-S11), accompanied by prioritization rankings for reaches and dams.

In the Iberian Peninsula, the Ebro basin shows a high concentration of dams, contributing significantly to fragmentation in both the northern and southern tributaries, particularly when considering the PCI index (Fig. 4a). Conversely, the primary segment of the Ebro demonstrates

higher fragmentation according to both indices, even though the prioritization of reaches indicates good connectivity (Fig. 4a). It is important to note that most of the northern dams with high fragmentation due to PCI index in the Ebro basin are near some PAs (Fig. 4a). In the Douro basin, higher connectivity values at the reach level are observed mainly on the eastern side, whereas the other rivers exhibit more significant fragmentation (Fig. 4a). Despite a lower abundance of dams, they still contribute significantly to the fragmentation of the Douro, especially in the southern portion of the basin (Fig. 4a).

Turning to the Italian Peninsula, the prioritization of dams reveals that all four considered basins (ordered from north to south: Arno, Ombrone, Tevere, and Aterno) have at least one dam contributing to fragmentation when both indices are considered, with the Tevere basin being the most impacted one (Fig. 4b). The dam's PCI index shows higher fragmentation, while the IIC indices reports the fragmentation only in the Tevere and Ombrone basins (Fig. 4b). When prioritizing reaches in Italy, the central sections of the Arno and Ombrone rivers, as well as the southern section of the Aterno river, exhibit high connectivity when both indices are considered, while the Tevere basin displays greater fragmentation, especially in its tributaries (Fig. 4b). Additionally, in the southern Tevere basin, connectivity is hindered in the Aniene river and the Salto river, the latter being due to the presence of the Salto dam (Fig. 4b).

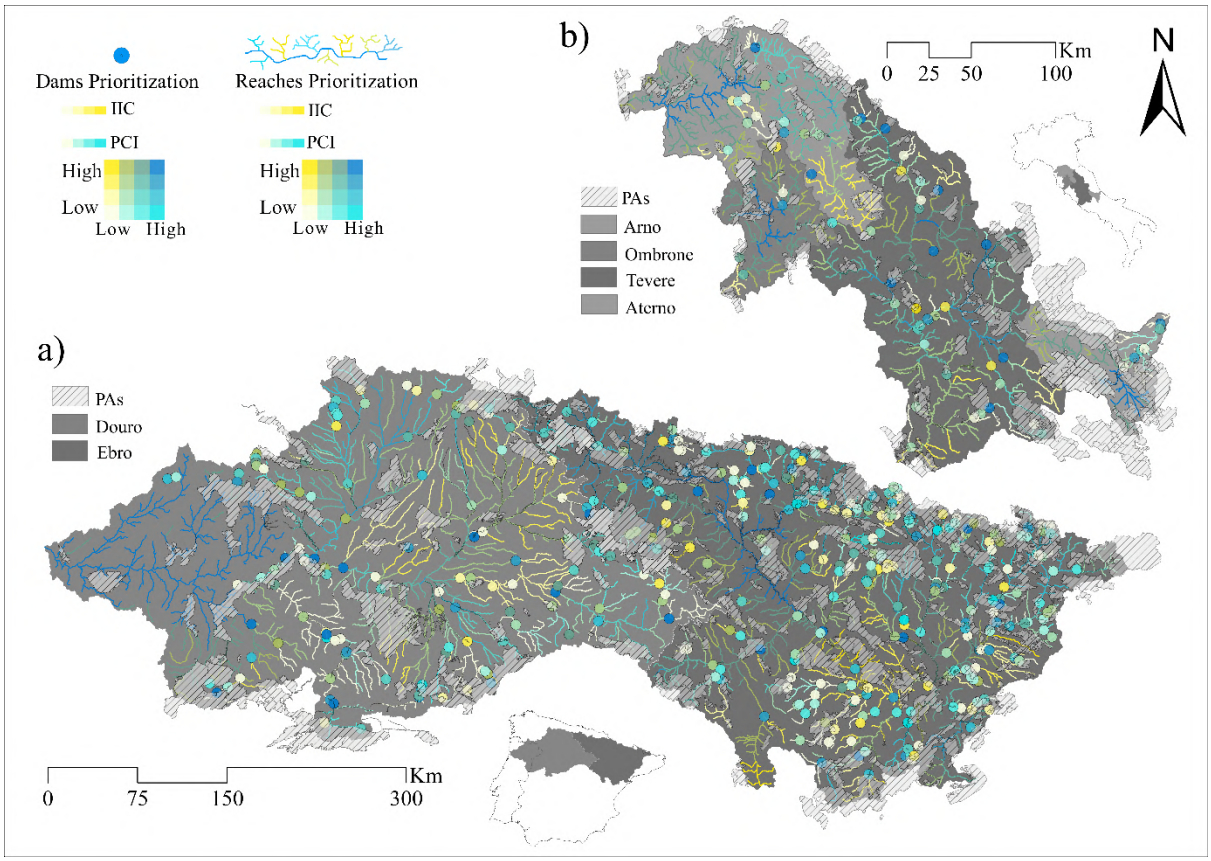


Figure 4. Habitat and barriers prioritization using 'riverconn' package: a for the basin in the Iberian Peninsula where the Eurasian beaver occurs, and b for the basins in Central Italy where the species is recently expanding. Classification was made using PCI (for functional connectivity) and IIC (for structural connectivity) indices. The Iberian Peninsulas appear as the more impacted, considering the greater number of barriers, especially in the Ebro basin. In Italy, important barriers for the beaver occur mainly in the Tevere basin.

Discussion

In this study, we explored the functional and structural connectivity of the Eurasian beaver in the Italian and the Iberian Peninsula, two areas where the species is expanding, both through natural recolonization and through illegal reintroductions (Mori et al. 2021; Pucci et al. 2021; Calderón et al. 2022; Capobianco et al. 2023). After being close to extinction in the last centuries, the species is recovering and recolonizing much of its formal range (Halley et al. 2021). Moreover, it is probable that this expansion will continue in the future. A prior study utilizing species distribution models at the European scale has shown that several suitable areas in Southern Europe remain unoccupied (Serva et al. 2023a). Our connectivity models, together with predicted suitable areas (Serva et al. 2023a), highlight areas where the beaver may undergo further expansion in the near future, allowing management actions to be focused on these. The EU biodiversity strategy aims to reconnect 25,000 km of European rivers by 2030. However, the alterations to river flow resulting from historical human activities, primarily due to the presence of barriers, especially dams, pose a significant challenge, with an estimated 0.74 barriers per kilometer (Belletti et al. 2020). Therefore, it is important to know what barrier management actions focus on to restore river connectivity. Our results on barrier prioritization allowed us to identify the ones with the most severe effects on the Eurasian beaver.

For both study areas, higher connectivity is detected for areas with high tree cover, broadleaved forests, and flat terrains, including valleys within the Apennine range, the Cantabrian Mountains, and the Basque range (Fig. 1b).

In Italy, the Omniscape cumulative current map reveals elevated current values along the Apennines, particularly in the northern segment, and in the vicinity of the larger lakes located in the northernmost part of the study area (Fig. 1b). Some well-connected patches emerge in the Po basin, primarily in its western reaches (Fig. 1b). Despite this good connectivity, a natural expansion from the northern occurrences (Alto Adige and Friuli-Venezia-Giulia Regions) to the central ones, seems not viable, even considering the dispersing capacity of the beaver and the long-distance traveled per year, up to 70–80 km (Fustec et al. 2001; Smeraldo et al. 2017), capable to swim for 20 km at night (Nolet and Rosell 1994). Furthermore, the considerable distance between the central Italian occurrences could also be linked to the Eurasian beaver's spatially discontinuous dispersal pattern, which tends to favor optimal sites further from less suitable ones located closer by (Nolet and Rosell 1994; John and Kostkan 2009).

Considering the occurrences in Central Italy, both Omniscape cumulative current and Circuitscape pairwise current show that these occurrences are well-connected, and the barriers present (i.e., man-made dams) do not seem to significantly impede the corridor's accessibility (Figs. 1b and 2, Supplementary Figure S2 in Online Resource 1). It is possible that for the Eurasian beaver, some artificial dams could be a tangible threat to movements (Nolet and Rosell 1998). Although, in some cases, dams occur near the springs, where the steep slopes made the habitat unsuitable for the beaver, thus not influencing the connectivity, as also found from Leoncini et al. (2023). For dams located in valleys, there may exist multiple aquatic and terrestrial routes that compensate for their presence, a phenomenon similar to what has been reported for the otters (Lutra lutra) (Leoncini et al., 2023). In the context of possible expansion toward the suitable patches, most of them are in close proximity to the current beaver occurrences (Fig. 2). Consequently, it is highly probable that the species could reach these areas in the near future. Thus, these regions merit special attention.

In the Iberian Peninsula, the Eurasian beaver was reintroduced in 2003 in the Ebro basin (Ceña et al. 2004). In this basin, an expansion of approximately 15 km per year has been calculated, thus considering the new occurrence in the Douro basin of anthropic origin (Calderón et al. 2022). This is supported by the fact that no signs attributable to beaver activity were found between the two sites of presence. Our connectivity models support this scenario, even if the connectivity map obtained from Circuitscape in the 'pairwise' mode finds a corridor in the Esla river northward, and in the Douro river eastward (Supplementary Figure S2 in Online Resource 1). Our analysis of habitat connectivity demonstrates that specific parts of the Iberian Peninsula are both connected as well as suitable (Serva et al. 2023a). The higher connectivity values detected from Omniscape in the Iberian Peninsula, such as those in the Cantabrian and Mino basins are mainly due to the higher values in tree cover. From the well-established Ebro basin population, there is a potential southward expansion path toward the Júcar basin (Fig. 1b). Instead, from the recent occurrence in the Douro basin, the beaver could expand southwards to the near Mondego basin, in Portugal, or to the Tajo basin, between Spain and Portugal (Fig. 1b). The greater connectivity towards the northern Iberian Peninsula is accompanied by the presence of suitable patches in proximity to the occurrences from the Ebro basin (Fig. 2). Still, some smaller suitable patches occur also southwards and westwards, being well-connected despite the long distance from the Ebro river. Additionally, some suitable patches are located between the Ebro and Douro occurrences, aligning with the rivers highlighted by Circuitscape (Fig. 2, Supplementary Figure S2 in Online Resource 1).

PAs are of crucial importance for biodiversity conservation (Pacifici et al. 2020; Chen et al. 2022), and it has been estimated that without those, the rate of extinction for vertebrates could have been 20% higher (Hoffmann et al. 2010). Despite in some basins PAs maintain higher connectivity values compared to unprotected areas, in other basins, such as Po and Aterno in Italy, and Douro and Tajo in the Iberian Peninsula, PAs host low connectivity values. Additionally, some PAs are affected by the presence of dams that could hinder structural ecological connectivity. Consequently, management measures should prioritize addressing the impact of these barriers within PAs, given their significance in facilitating biodiversity dispersal movements (Santini et al. 2016).

The analysis of barriers and habitat prioritization conducted through the 'riverconn' package highlights the reaches most fragmented and the primary barriers contributing to this fragmentation (Baldan et al. 2022). These metrics can serve as valuable tools in the restoration of river connectivity, pinpointing the specific sites where interventions are necessary. In the Tevere basin, the major barriers are situated in its central part, both to the east and west (Fig. 3b). Interestingly, these barriers, primarily dams, do not appear to significantly impede beaver connectivity (Fig. 1b). However, to enhance river connectivity in the Italian Peninsula, efforts should be focused between the Arno and Ombrone basins, and between the Arno and the upper Tevere basin. Conversely, the Ebro basin exhibits strong structural connectivity values in its main channel, with tree cover playing a more significant role in the northern parts of the basin (Fig. 3a). However, the high structural connectivity at reach level detected in the Ebro, despite the high presence of dams, is linked to the 'passability' (a parameter of the 'riverconn' package) of the barriers, considering the semi-aquatic ecology of the beaver (Baldan, 2023 pers. comm.). The barriers identified to the north could account for the limited beaver expansion into these suitable areas (Figs. 1b and 3a). Thus, to restore connectivity in the Ebro, specific measures should focus on the northern dams, and to the southern tributaries, while considering the Douro

basin, efforts to improve connectivity should primarily focus on the Meseta Central area, where several barriers contribute to its fragmentation.

Recently, in Europe several species are making a comeback (Nolet and Rosell 1998; Chapron et al. 2014; Ledger et al. 2022; Serva et al. 2023b). The return of the Eurasian beaver to Italy and its expansion in the Iberian Peninsula could potentially lead to conflicts with human activities (Auster et al. 2021). These conflicts are primarily due to plantation damage, alteration of artificial channels, and inundations (Taylor and Singleton 2014; Swinnen et al. 2017). A prior study in Italy found that, while local communities, in general, do not perceive the beaver as a threat, some express concerns about its presence due to certain impacts, such as flooding and damage to crops and local species (Viviano et al. 2023). However, we must not forget that the Eurasian beaver is a protected species in most European countries, and its presence is generally associated with positive effects on the ecosystem and biodiversity (Puttock et al. 2017; Brazier et al. 2021), especially in the context of climate change which is negatively impacting on ecosystem services (e.g., De Simone et al. 2020; Iannella et al. 2021b). In fact, beavers can increase local species richness by increasing riparian habitat, and improving the hydrogeological safety of rivers, helping in preventing floods (Rosell et al. 2005; Puttock et al. 2017). Furthermore, beaver activity contributes to creating various habitats used by other species, including taxa of conservation concern (Dalbeck et al. 2007; Nummi et al. 2019). These different habitats contribute to increased environmental heterogeneity. Despite the major positive effects across multiple levels of biodiversity, some negative effects could be observed for some taxa (Rosell et al. 2005; Stringer and Gaywood 2016). Among invertebrates, Trichoptera and Plecoptera could be negatively influenced by the transition to lentic habitat (Stringer and Gaywood 2016), while for amphibians, some salamanders preferring fast-flowing, highly-oxigenated waters could not utilize beaver ponds (Dalbeck et al. 2007). For what concerns mammals, a previous meta-analysis comparing the effects of beaver activity, reported mainly positive effects; though, some negative impacts occur, such as for bats (Stringer and Gaywood 2016). Semiaquatic mammals, like otters (Lutra lutra), benefit from beaver ponds, which provide stable water levels and prey abundance (Rosell et al. 2005). Furthermore, also ungulates generally profit from the presence of beavers due to the greater availability of vegetation (Rosell et al. 2005). Beavers cut down trees and some trees die from flooding events, becoming attractive for woodpeckers (Grover and Baldassarre 1995), and other ecosystem engineers, due to the use of their holes by a range of secondary cavity-nesting species (Robles and Martin 2014). Negative effects have been observed only for some bird species, such as horned grebe (Podiceps auritus, which, however, does not occur in the study areas) and common whitethroat (Curruca communis) (Elmeros et al. 2003; Kuczynski et al. 2012). Especially for the Iberian Peninsula, the Eurasian beaver presence could help in preventing fires, as beaver dams (in this case *Castor canandensis*) enhance the fire resistance of riparian vegetation (Fairfax and Whittle 2020). In particular, Portugal is among the countries of the European Union most affected by fires, which burned an annual average of 147,000 hectares of land between 2000 and 2018 (San-Miguel-Ayanz et al. 2018).

Therefore, the best strategy is to prevent and limit conflicts with human activities. For instance, given that beaver activity is concentrated near the water's edge, restoring a small width zone of riparian habitat could be sufficient to limit some damages to plantations (Nolet and Rosell 1998), even if could not be realistic in more urbanized landscapes. Informing local stakeholders about the Eurasian beaver's presence is another tool that can help maintain local support

(Swinnen et al. 2017). Predicting the areas that the Eurasian beaver could colonize is an important tool for monitoring signs of presence and damage, as well as for implementing any necessary management measures.

Though the robustness of both the algorithms used for our analyses and the corresponding high performances, it is important to make some considerations about our results and the datasets used. Considering the scale of the study areas and the accessibility of published data, we relied on the use of the Corine Land Cover map from Copernicus at 100 m precision, buffering some possible forest cover-limitations also including the Tree Cover layer in the dataset preparation. The HydroRIVERS dataset does not contain rivers with less than 10 km2 catchment area and/or river flow less than 0.1 m3/s. However, we did not consider this an important limit considering the target species studied. Similarly, the HydroBASINS dataset is available at a resolution of ~ 500 m. All this considered, studies on smaller study areas, as well as research on peculiar territories, should include finer-scale predictors to obtain more specific outcomes. Also, higher-resolution datasets are urgently needed to improve ecological modeling studies.

We did not incorporate a road layer into the resistance surface, as roadkill is not a significant risk for the Eurasian beaver, with a very low number of individuals being road-killed (Balčiauskas et al. 2022). Furthermore, in some cases, beavers might be attracted to roads, likely due to the presence of herbaceous roadside vegetation (Forman and Alexander 1998; Steyaert et al. 2015; Ciach et al. 2023). The low effect of anthropic environments is also corroborated by other studies that have shown the Eurasian beaver's tendency not to avoid urban areas, demonstrating its capacity to survive even in urbanized environments (Dewas et al. 2012; Korbelová et al. 2016).

In Italy the colonization process is still in its initial phase, considering that it takes about 30–50 years (Hartman 1995; Halley and Rosell 2002), while in the Iberian Peninsula, where beavers have been present for 20 years, the colonization process has led the species to spread almost only in the Ebro basin, and further expansion is therefore probable.

Conclusion

The ability to move without barriers is a necessary condition for animal species to disperse, reproduce, and survive (Turner et al. 2001; Nathan et al. 2008). Increasingly, ecological connectivity is limited by the presence of human structures that contribute to habitat fragmentation (Haddad et al. 2015). In our study, we analyzed habitat connectivity on multiple levels, for the Eurasian beaver in two areas where the species has been expanding recently. Despite the presence of some barriers, particularly dams, which can negatively affect the beaver, we found good connectivity values, especially in areas associated with good forest cover and flat relief. Furthermore, despite the great distance, the occurrences in Central Italy are still well connected through the hydrographic network. In the near future, it is plausible that there will be a further expansion of the species in these countries, considering the suitable patch available (Serva et al. 2023a). Identifying key barriers in watersheds where beaver presence has been reported can help mitigate the impact of these barriers on beaver expansion. Our results may help predict further expansion of the beaver into the Italian and Iberian peninsulas, helping to understand this recolonization process, regardless of the initial causes of the return of this keystone species.

Supporting Information

This is the link to the electronic supplementary material: https://link.springer.com/article/10.1007/s10980-024-01859-3#Sec17

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Case Study II: Functional connectivity and the current arrangement of protected areas show multiple, poorly protected dispersal corridors for the Eurasian lynx

Introduction

Despite the historical reduction in large carnivores' population size (Dirzo et al., 2014; Ripple et al., 2014), some recoveries have been recently documented in Europe (Chapron et al., 2014; Ingeman et al., 2022).

The reasons encompass different aspects: first, coordinated legislation shared by many European countries (Habitat Directive 92/43/EEC; Bern Convention), as well as some context-specific management measures, such as economic incentives for livestock protection, practices that permit a coexistence between human activities and large predators (Dickman et al., 2011), and a more favorable public opinion towards those (Chapron et al., 2014). Another important factor that led the large carnivores to recover is the rural-area abandonment (Ustaoglu and Collier, 2018), which in turn favored the increase of wild ungulates' population densities across Europe (Linnell et al., 2020).

In this context, the Eurasian lynx, a top predator once widely distributed across Europe and Asia (Sommer and Benecke, 2006), came close to extinction in the last centuries due to human persecution, loss of ungulate prey, and habitat changes (Breitenmoser, 1998), indeed now recovering (Chapron et al., 2014). Historically in Europe (by the mid-20th century), the species managed to survive only in four areas (i.e., in Scandinavia, Carpathian Mountains, Southern Balkans, and east-Baltic drainage (Von Arx et al., 2004)), but after recent recoveries, current estimates place the number of Eurasian lynx individuals at about 8.000–9.000 (Von Arx, 2020).

Despite this recovery, some subpopulations (in accordance with von Arx, 2020), are still ‘endangered’ and ‘critically endangered’, especially the reintroduced ones, with a small number of individuals (von Arx et al., 2021). One of the main problems concerning the Eurasian lynx conservation regards the isolation of the small subpopulations in Central and Eastern Europe, and of the larger Carpathians population (Lucena-Perez et al., 2020). In fact, this isolation led to the high genetic differentiation observed nowadays between subpopulations (Gajdárová et al., 2023), and to the very low genetic diversity among them, especially in the reintroduced ones (Mueller et al., 2022). This low genetic variability is due to the low exchange of individuals between subpopulations. Indeed, Europe is among the continents most modified by man (Williams et al., 2020), due to the high anthropization and the high population density, which lead to an elevated level of habitat fragmentation. Habitat fragmentation could cause large gaps that limit both the potential population size and the natural expansion (Zimmermann and Breitenmoser, 2007). This evidence is also noted in some Eurasian lynx subpopulations, which despite the availability of suitable habitat, struggle to expand (Molinari-Jobin et al., 2010; Müller et al., 2014). Moreover, large carnivore conservation necessitates large spatial requirements (Gittleman, 2001), and the consequent problem is whether there is enough suitable habitat for viable and ecologically functional subpopulations (Packer et al., 2013).

Finding the key corridors to favor connectivity between and within lynx subpopulations is of crucial importance for their conservation. In particular, the main conservation strategy's objective would be to create a functional viable metapopulation across West and Central Europe that would prevent future genetic erosion (Mueller et al., 2022).

The existing network of the European Protected Areas (EPAs, after Staccione et al. (2023)) could favor an exchange of individuals between subpopulations. EPAs connectivity is necessary to facilitate large-scale ecological processes and to favor the persistence of viable populations (Saura et al., 2018). Previous studies showed the importance of EPAs as source areas for the Eurasian lynx, with the probability of presence decreasing drastically outside these areas (Müller et al., 2014). However, for what concern the Eurasian lynx, previous analysis shows that lynx's habitat is mostly protected in Sweden, Finland, and Romania (Santini et al., 2016). In recent years several theoretical and technical studies have been published to restore and support landscape connectivity (Correa Ayram et al., 2016; Ersoy et al., 2019; Iannella et al., 2021). Various software applications and algorithms can model ecological corridors. Circuitscape and Omniscape use electronic circuit theory to assess connectivity in a heterogeneous landscape (McRae et al., 2008; Landau et al., 2021). These approaches treat the landscape as a resistance surface, where the "current" flows between nodes across the resistant surface, following different modeling options (McRae et al., 2008). Circuit-theory techniques gained more support and popularity among conservationists and ecologists because they are not limited by the "route-selection" assumption (i.e., random-walk theory) (Dickson et al., 2019).

The aims of this study were: (1) to address the ecological connectivity between the European subpopulations of Eurasian lynx to identify the potential ecological corridors; (2) to evaluate the ecological connectivity of the EPAs with reference to lynx ecology; (3) to assess the measure in which protected areas could facilitate lynx dispersion and movements, both in the current arrangement and considering an expansion of EPAs' surface in accordance with the European Union's Biodiversity Strategy for 2030.

Material and methods

Target species and study area

The target species is the Eurasian Lynx *Lynx lynx*, a predator widely distributed from Europe to Central Asia up to Siberia, overall classified as "Least Concern" by the IUCN Red List. In this study, we refer to the European subpopulations some of them reported as 'Critically Endangered' (i.e., Balkan, Bohemian-Bavarian-Austrian (BBA), Vosges-Palatinian subpopulations) and 'Endangered' (i.e., Alpine and Jura subpopulations) (von Arx, 2020). For the purposes of the present research, we gathered occurrence data from the work of Serva et al. (2023) (Supplementary Material Table A1). To get the populations' range, we applied a buffer (10 km radius) around each occurrence with the "Buffer" tool on ArcGIS Pro managed by ESRI (ESRI Inc, 2023), refining the polygons when needed. The subpopulation ranges obtained were then compared to the reported ones (Kaczensky et al., 2021) (Supplementary Fig. A1).

We focus on European subpopulations of Eurasian lynx; thus, the main study area is Europe, including all the countries for which a biogeographic contiguity occurs, even at the farthest borders (e.g., Belarus and western Russia).

Populations' connectivity modeling in Circuitscape and connectivity change index

For the aims of the present study, we inferred the landscape connectivity through the Circuitscape application implemented in Julia language (v1.6.7) (Hall et al., 2021). This software, which results in great performances when computing large landscapes' connectivity, takes advantage of the circuit theory models, which are proven to have better performance than other approaches (Anantharaman et al., 2019; McClure et al., 2016). The inputs that Circuitscape requires are a resistance (or conductance) layer, and some source/target locations

(i.e., nodes) (McRae et al., 2008). Using this data, it produces a current map that reflects the landscape connectivity as the expected net probability of an individual to move between two nodes (McRae et al., 2008).

Since Circuitscape requires those inputs, we use the Species Distribution Models (SDMs) from Serva et al. (2023) as the conductance raster. Briefly, to obtain those SDMs, a "couple and weigh" framework (Iannella et al., 2021) was applied after the climatic modeling. Thus, different types of predictors relevant to the Eurasian lynx were used, namely some climatic, topographic, human disturbance, and habitat-related ones (Serva et al., 2023). These SDMs are comparable to others recently developed for the current scenario (Oeser et al., 2023b), confirming their reliability.

To deepen the precision of our analyses, we further refine the so-obtained conductance raster, by applying target species' specific connectivity information. In fact, we used the function 'Mosaic to new raster' in ArcGIS Pro 3.1 (ESRI Inc, 2023) to merge the weighted SDMs to the road's spatial information (highways and major roads), incorporating these as barriers, as recent research demonstrated them to be the most relevant variable limiting the dispersal of Eurasian lynx (Mueller et al., 2022; Ripari et al., 2022). We repeated the same process to incorporate the built-up areas as barriers (Ripari et al., 2022). Moreover, we added lakes and bigger rivers, setting these barriers as less constraining than anthropogenic barriers. We then transformed the resulting conductance layer with a negative exponential function following the approach of Keeley et al. (2016) setting the c factor to 4.

We ran Circuitscape selecting the 'pairwise' option: in this mode, connectivity is evaluated between each pair of nodes (in this case, the subpopulation's ranges), so that each pair is both the source and the destination node (McRae et al., 2008). Setting this parametrization ensures that also barriers inside the subpopulation ranges are considered. We infer the connectivity for different scenarios, the current, 2050, and 2070, based on respective SDMs obtained from Serva et al. (2023).

The connectivity maps obtained for the different scenarios were then compared using the Standardized Connectivity Change Index (SCCI) (Iannella et al., 2021). This index returns values ranging from loss (−1) and gain (+1) of connectivity, summarizing the effect of future changes on the inferred landscape corridors.

EPAs' connectivity assessment for the Eurasian lynx

To complement Circuitscape analysis, we used ArcGIS Pro's 'Optimal region connections' (ORC) tool. ORC identifies optimal least-cost paths between input points by converting conductance layers into cost surfaces. Then, for the least-cost corridors of the European study area, we used the EPAs centroids as input features. We applied it to identify least-cost corridors within the study area, using EPAs centroids larger than 40 km2 (approximating the minimum home range for the Eurasian lynx) that intersected subpopulation ranges (Suppl. Fig. A1). The tool lets the users define an input barrier feature, which is completely impassable. Built-up areas from the Corine Land Cover (https://land.copernicus.eu/en/products/corine-land-cover) map were designated as impassable barriers, given their significance as disturbances for Eurasian lynx (Mueller et al., 2022). We decided to use the EPAs centroids as input for the least-cost path given the great importance of the input features for the analysis and considering the possible limitations of the dataset (built upon citizen science data, literature records, and data from national repositories). Thus, the resulting least-cost corridors are not affected by the species movement, leading to a fixed pattern of connectivity. Corridors were generated for both present and future projections to detect variations. To assess these differences, we devised a dedicated index, presented in its formula:

$$ORC\ CostChange = \log\left[\left(\frac{Cost\ current - Cost\ future}{Cost\ current + Cost\ future}\right) \cdot relative\ dist\right],$$

$$\text{where } relative\ dist = (dist\ /\ \max dist) \cdot 100$$

The formula is designed to normalize spatial data, allowing for comparison across different territories. ORC generates linear outputs with varying costs and geographies for each line segment. As these outputs change over time, it's challenging to spatially compare current and future ORC results, necessitating the normalization of data to a range of −1 to +1. Thus, the overall assessment of variation between scenarios is possible by calculating the distance between each of the two ORCs' segments, also assessing their cost every time. Again, to give normalized values, we use a relative distance standardization to have the possibility of comparing changes from small to great landscapes (and their respective connectivity). Finally, since there may be great variation in each landscape/timeframe, we use a log normalization.

To better assess the connectivity between the EPAs, considering their importance for the lynx (Müller et al., 2014; Heurich et al., 2018), we used the Omniscape connectivity algorithm (McRae et al., 2016). Since its development, Omniscape is gaining more popularity and it has been used in various contexts and at different scales (Jennings et al., 2020; Choe et al., 2021; Belote et al., 2022; Cameron et al., 2022). This software produces maps of omnidirectional connectivity, and it is based on circuit theory. Omniscape applied iteratively the Circuitscape "advanced" mode algorithm, with a moving window with a specific radius, based on species dispersal ability (Landau et al., 2021). We used the same resistance layer applied in Circuitscape, but selecting EPAs greater than 40 km2 (reported as the minimum home range detected for the Eurasian lynx, following Breitenmoser-Würsten et al. (2007)) as sources. In this way, we obtained a connectivity assessment of EPAs with reference to the Eurasian lynx.

Quantitative and qualitative EPAs' assessment

To check whether the current EPAs could work as an ecological network to connect the different European lynx populations, we evaluate the quantitative coverage of the critical corridors, and the qualitative characteristics of the EPAs considering the main aspects that could influence the Eurasian lynx's habitat selection.

We identified the crucial corridors for the Eurasian lynx movement between subpopulations using the 90th percentile values of our Circuitscape model. Then, we used the 'Pairwise Intersect' tool of ArcGIS Pro to identify the overlapping areas, i.e., critical corridors protected by EPAs. Moreover, considering the Target 1 of the Biodiversity section of the Agenda 2030, i.e., legally protect a minimum of 30 % of the EU land's area, integrating ecological corridors, we applied a buffer to every EPAs to increase its extension by ~34 %. Thus, we repeated the intersect analysis with these 'increased' EPAs.

To assess whether protected areas meet the most important requirements to protect the movement of the Eurasian lynx (Ripari et al., 2022; Oeser et al., 2023a), we select three main variables inside the EPAs: forest cover (FC), human footprint index (HFI), and terrain ruggedness index (TRI) (as a proxy of the availability of refuges).

Indeed, we download the FC data at a precision of ~30 m (Hansen et al., 2013). As a measure of human disturbance, we downloaded the recent global HFI layer (Mu et al., 2022) at a resolution of ~1 km. Finally, the TRI was obtained from the work of Amatulli et al. (2018), at a resolution of ~1 km. We resampled the Forest Cover layer (FC) (Hansen et al., 2013) in order to match the other raster's resolution, and then we performed the 'Zonal Statistic' tool in

ArcGIS Pro to calculate the mean value of each layer inside each EPA polygon before and after the increased surface.

To assess if the EPAs are in general more suitable for lynx movements, we compared the values of the above-mentioned layers inside the EPAs, with the values outside the EPAs, extracted with random points generated at a minimum distance of 1 km, through the tool 'Extract multi-values to Points' in ArcGIS Pro. We first selected the EPAs inside the minimum convex polygon that encloses all the subpopulations. We then performed in R studio (R Core Team, 2023) a t-test (after checking for normality and homoscedasticity of data) to check for significant differences ($p = 0.05$) between Circuitscape connectivity values resulting inside and outside EPAs.

Results

Circuitscape results

Starting from 2164 total occurrences, we obtained the subpopulation ranges that reflect the real situation of the Eurasian lynx in Europe (Fig. 1a).

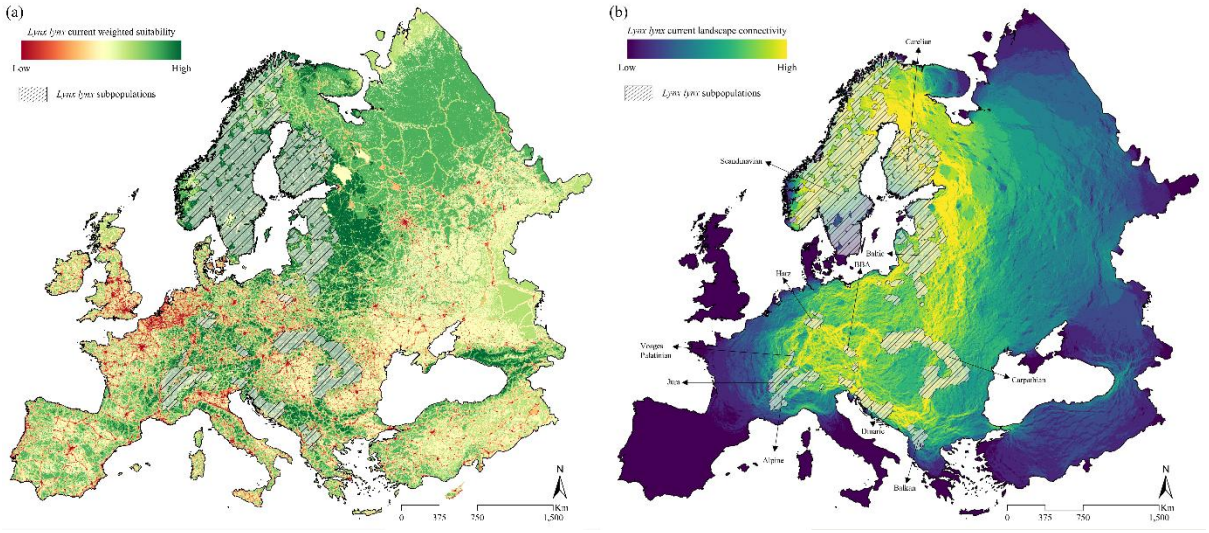


Figure 1. (a) The final conductance map obtained from the habitat suitability map from Serva et al. (2023) merged with the built-up areas, the main roads, and the water features, and (b) the cumulative current map obtained from Circuitscape in the 'pairwise' mode for the current scenario. In transparency the subpopulation ranges obtained from the occurrences.

The resistance layer shows the best conditions in the main European mountains' ranges, and in the northern part of the study area, while Central and Southern Europe shows a more fragmented landscape with higher resistance to movements, mainly due to the high density of human infrastructures (Fig. 1a).

The raster correlation performed between the conductance layer and the cumulative current map shows a little correlation ($r = \sim 0.34$). The corridor network obtained from Circuitscape for all the European subpopulations of Eurasian lynx in the current scenario shows higher connectivity in Northern Europe, where some large corridors link the Karelian, the Scandinavian, and the Baltic subpopulations (Fig. 1b). In contrast, in Central and Southern Europe there is generally lower connectivity. Despite this, some key corridors able to connect the central European subpopulations of lynx are highlighted (Fig. 1b). Thus, good connectivity values are noted between the Dinaric and Alpine subpopulations, in the southwestern part of Slovenia, and between the subpopulation in the Harz range and the BBA subpopulation, despite the distance of ~250 km. A slight connectivity is noted between the Carpathian and Bohemian-

Bavarian-Austrian subpopulations, and a longer strip of connectivity links the Carpathian and the Harz subpopulations (Fig. 1b). In contrast, between the Jura and Alpine subpopulations, despite the short distance, there is low connectivity (Fig. 1b), and the same process affects the Vosges Palatinian subpopulations, linked with only two corridors with the Jura subpopulations (Fig. 1b). In Eastern Europe, Carpathians, Dinaric, and Balkan subpopulations are connected by various corridors between Kosovo, Montenegro, and southern Serbia (Fig. 1b).

The future corridor networks computed with Circuitscape show some differences compared to the current one (see Supplementary Material Figs. A2, A4 for maps detail). In both future scenarios, bigger increases in landscape connectivity concern Alpine, Jura, Dinaric, and Balkan subpopulations (Figs. 2a and c), but connectivity increase also between Alpine, Dinaric, and Balkan subpopulations for 2050 projection (Fig. 2b) and between Scandinavian and Carelian subpopulations for 2070 (Fig. 2d). Within subpopulations, a major decrease concerns the Carelian, Harz, Scandinavian, and Baltic subpopulations (Figs. 2a and c), where the current connectivity is high. At between subpopulations level, there are some decreases in both future projections between Baltic States and Finland, and between Harz, BBA, and Vosges Palatinian subpopulations (Figs. 2b and d). Overall, the two future scenarios are similar to each other and show only very small differences.

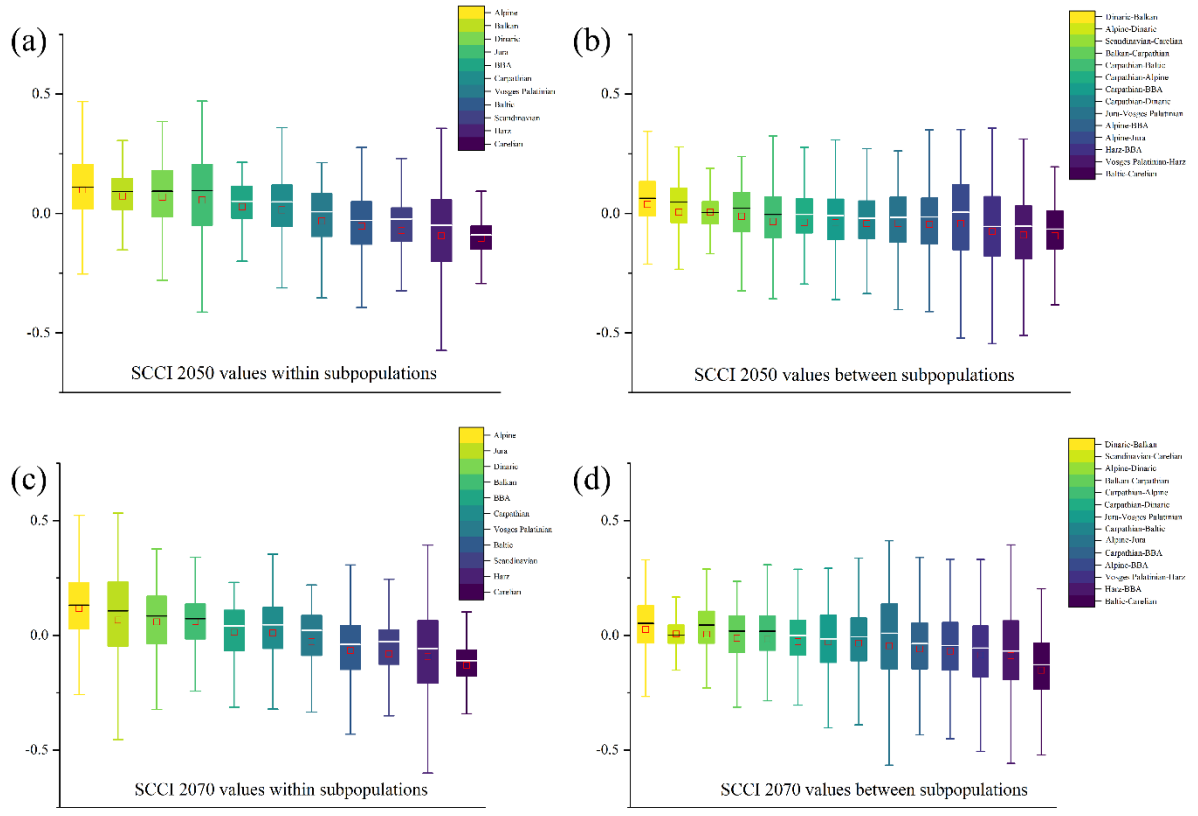


Figure 2. Circuitscape SCCI values for future scenarios: a) SCCI values within subpopulations for 2050 scenarios. b) SCCI values between subpopulations for 2050 scenarios. c) SCCI values within subpopulations for 2070 scenarios. d) SCCI values between subpopulations for 2070 scenarios.

Landscape connectivity obtained from Omniscape

The cumulative current map obtained from Omniscape using the EPAs as sources shows great amount of current in Central Europe, between Germany and Poland, in the Pyrenees, and in Greece (Fig. 3a). While the last ones are of less interest for the Eurasian lynx conservation, the first ones are more important, with a patch matching the Harz subpopulation, and with some

areas with moderate-high connectivity towards the BBA and Vosges-Palatinian subpopulations (Fig. 3a). The Alpine subpopulation appears to be connected to the Dinaric one, but corridors to the nearest Jura subpopulations are missing (Fig. 3a). Still focusing on Central Europe, the normalized current map shows a possible ecological network connecting the Harz and the Carpathian subpopulations, through the BBA subpopulation (Fig. 3b). Furthermore, the good connectivity highlighted from Circuitscape between the Dinaric and Alpine subpopulations is confirmed (Figs. 1b and 3b).

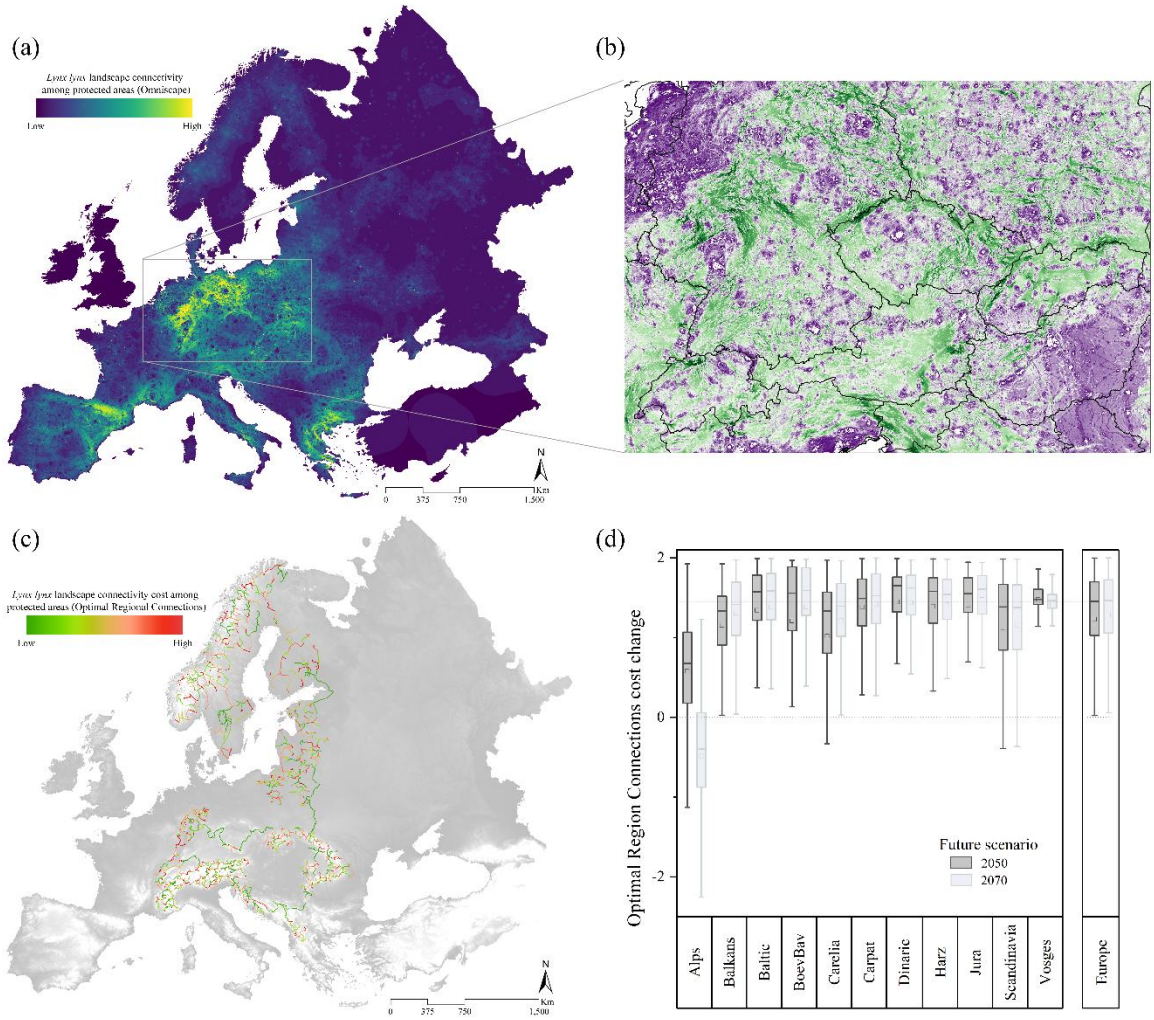


Figure 3. Landscape connectivity between EPAs for the Eurasian lynx. a) The cumulative current map between EPAs obtained from Omniscape. b) The inlay for Central Europe of the normalized current map from Omniscape: green zones are the areas with a channelized flow, i.e., possible corridors. c) The least-cost corridors obtained from the Optimal Region Connections in ArcGIS Pro between the EPAs inside the subpopulation's ranges. d) The least-cost path cost change for all the European subpopulations of Eurasian lynx in the future scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Least-cost corridors obtained from ArcGIS Pro

The least-cost corridor analysis for all the Eurasian lynx subpopulations in the current scenario shows a complex pattern of corridors (Fig. 3c). Within each subpopulation, there are generally cheaper corridors, while the corridors between subpopulations appear to be expensive, especially those connecting western and eastern subpopulations in Central and Southern Europe (Fig. 3c). The future cost changes of the least-cost corridors show a general increase for all the subpopulations, especially for the 2070 scenario, except for the Alpine subpopulation

(Fig. 3d). Thus, indicating the possibility of a decrease in EPAs' connectivity for the Eurasian lynx.

Qualitative and quantitative assessment of EPAs for Eurasian lynx movements

When comparing the considered variables' asset (HFI, FC, TRI) inside and outside the EPAs enclosed by the Minimum Convex Polygon obtained by the lynx subpopulations, we found a significant increase in FC inside the EPAs ($p = 0.05$) (Fig. 4a). Furthermore, considering the current EPAs network, the crucial corridors obtained from Circuitscape (Supplementary Material Fig. A6) are covered for 179,652 km2 (~21 % of all crucial corridors). Currently, a lack of protection to the crucial corridors occurs between the Dinaric and the Balkan subpopulations in Eastern Europe, and between the Carpathian and the BBA subpopulations in Central Europe. An increase in the surface of the EPAs following the European Union's Biodiversity Strategy for 2030 would cover 533,725 km2 (~62 % of all crucial corridors) of the crucial corridors for the Eurasian lynx. The increase of the EPAs' surface would keep similar conditions considering the HFI and TRI, but with a different amount of the FC (Fig. 4b). The data of connectivity maps relative to the 'inside and outside' assets of the EPAs within the minimum convex polygon of all the subpopulations (Supplementary Material Fig. A7) showed normal distribution and homoscedasticity. The t-test performed over those data shows that inside the EPAs there is greater connectivity than outside (with a significance level of 0.05) (Fig. 4c). To better summarize the spatial asset of the analyses reported above, we report in Fig. 4d a scheme.

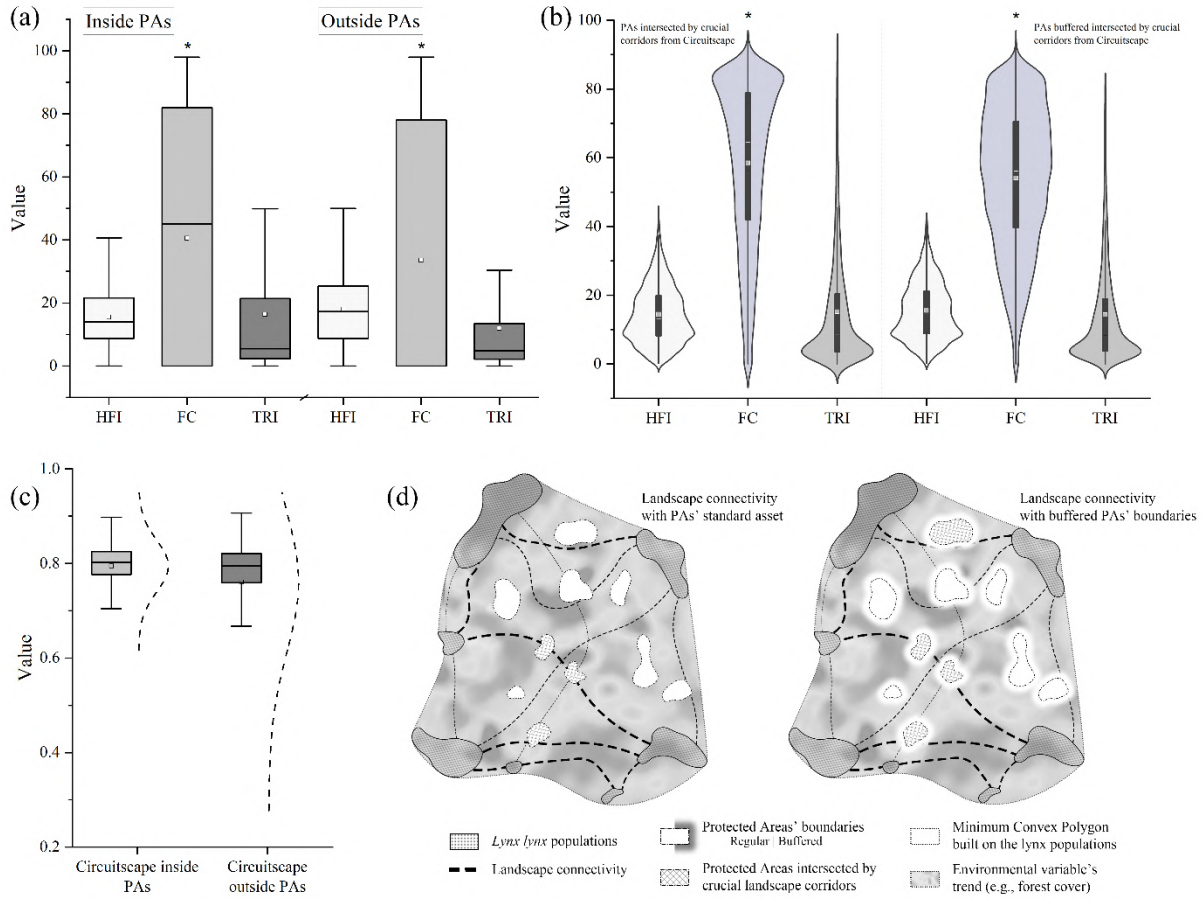


Figure 4. Qualitative assessment of EPAs for the Eurasian lynx. a) The values of the Human Footprint Index (HFI), Forest Cover (FC), and Terrain Ruggedness Index (TRI) inside and outside the EPAs intersected from the minimum convex polygon enclosing all the subpopulations. b) The values of HFI,

FC, and TRI, between current EPAs intersecting the crucial corridors for the Eurasian lynx, and the same EPAs with an increased surface of ~34 % (following Agenda 2030 objectives). c) The value of the cumulative current map obtained from Circuitscape (normalized to a 0–1 scale), inside and outside EPAs. d) The protected areas to which we refer in the previous figures: on the left, the current structure of the EPAs included within the minimum convex polygon that enclosed all the populations (Supplementary Material Fig. A7); right, buffered EPA with ~30 % surface area increase. The filled EPAs are those intersected by corridors crucial for the Eurasian lynx.

Discussion

Recognizing the importance of landscape connectivity as a crucial conservation strategy effectively reduces the negative consequences of habitat loss and fragmentation (Fletcher et al., 2016). Connectivity enhances individual movement, supporting dispersal, migration, and gene flow, thereby promoting population recolonization or establishment in previously unoccupied areas (Hilty et al., 2012). Additionally, connectivity is pivotal in sustaining viable metapopulations and contributes to the demographic rescue of small, isolated populations (Haddad et al., 2015). The Eurasian lynx, known for thriving in human-dominated landscapes, serves as a conservation model for large carnivores at a landscape scale (Carter and Linnell, 2016). Recent findings indicate low genetic diversity and high inbreeding rates in reintroduced lynx populations (Huvier et al., 2023; Mueller et al., 2020, Mueller et al., 2022), emphasizing the need to enhance connectivity both between and within subpopulations. This study takes the initial step towards establishing a functional metapopulation of Eurasian lynx in fragmented landscapes of Eastern and Central Europe by assessing landscape connectivity at these two levels.

Regarding European corridors identified by Circuitscape, a key distinction emerges between the northern subpopulations, including Scandinavian, Karelian, and Baltic lynx subpopulations, and others. Our findings reveal strong connectivity among these northern subpopulations through multiple corridors, which are expected to persist in future scenarios (Fig. 1b). In contrast, central and western European subpopulations exhibit lower current connectivity in the present scenario, with predictions of increased connectivity only for some subpopulations in future projections. However, a clear connection between the Dinaric and the south-eastern Alpine area appears, confirmed by the least-cost corridors and the Omniscape outputs (Fig. 1 b, Fig. 3 a, and c), consistent with findings from previous studies (Favilli et al., 2023). These corridors are crucial for establishing a viable lynx population within the Alps. To achieve this, it is essential to establish functional corridors connecting the Alpine subpopulation with the BBA and the Jura subpopulations. Despite their spatial proximity, our current predictions indicate only a few corridors, and while others may emerge in the future (Supplementary Material Figs. A3, A5), these subpopulations face significant barriers linked to human infrastructures, and limited protected areas (Supplementary Material A6). The BBA subpopulation plays a vital role in linking Alpine, Harz, and Carpathian lynx subpopulations, making it crucial for Eurasian lynx conservation in Central Europe (Heurich et al., 2018). Effective habitat preservation measures can facilitate natural expansion from BBA subpopulations due to good habitat connectivity (Magg et al., 2016). Furthermore, to support this expansion, efforts are needed to combat illegal killings, a major threat stagnating this subpopulation (Heurich et al., 2018).

Given the recent evidence of extremely low genetic diversity in the Jura subpopulation (Huvier et al., 2023), urgent individual exchange is required. Between Alpine and Jura subpopulations, approximately 80 km apart, we find a viable corridor between the Upper Jura Regional Nature Park and the Bauges Prealps, even if various barriers separate these subpopulations, such as roads, large urban areas, and lakes.

The Harz subpopulation shows good connectivity with the BBA subpopulation, with corridors maintained in all future projections (Figs. 1b, 2b, and d). Despite moderate human disturbance, effective conservation measures can establish a vital link with the BBA subpopulation, essential for Harz subpopulation conservation (Mueller et al., 2020). For example, considering the anthropogenic disturbance between these subpopulations, and the concomitant presence of unprotected areas, new protected stepping-stones areas would be important to favor an exchange of individuals. These actions are needed especially considering the impact of illegal hunting on the BBA subpopulation (Palmero et al., 2021). On the contrary, the network between the Alpine, Jura, Vosges Palatinian, and Harz subpopulations does not seem to be viable, due to artificial habitat fragmentation (Gimenez et al., 2019). The critically endangered Balkan subpopulation is connected to the Dinaric population by corridors poorly covered by EPAs, and a natural connection is improbable, even if moderate connectivity occurs (Fig. 1b). In Central Europe, the larger Carpathian population shows moderate genetic diversity (Mueller et al., 2022) and has the potential to serve as a source for other subpopulations, particularly the isolated BBA subpopulation (Gajdárová et al., 2023). Although two main potential routes appear with relatively high predicted connectivity between these subpopulations, still they are not actually connected (Gajdárová et al., 2023). Thus, additional protected areas are needed to ensure the effectiveness of these routes, especially considering that these potential corridors are mostly unprotected (Supplementary Material Fig. A6). So far, there is only one report of the dispersal of a male from the Carpathians close to the BBA subpopulation, demonstrating such long-distance dispersal for the lynx (Gajdárová et al., 2021), so appropriate management actions could enhance a more conspicuous individuals' flow.

Protected areas play a vital role in the survival and stable reproduction of the Eurasian lynx, as complete protection within them enhances survival probabilities (Müller et al., 2014; Palmero et al., 2021). Our connectivity results from Omniscape align with findings by Saura et al. (2018), indicating higher connectivity in Germany, Poland, and France, compared to EPAs in the northern and eastern European regions (Fig. 3a). These great differences in the connectivity analysis between subpopulations range are also related to the Omniscape analysis itself, in which the higher connectivity between EPAs detected in Central Europe is partly related to their higher abundance, i.e., higher number of input nodes for the connectivity analysis, despite the higher habitat fragmentation. Similarly, the lower connectivity in Northern Europe, despite the lower anthropogenic impact, is partly related to the lower numbers of EPAs. These good connectivity values between protected areas of Central and Western Europe for the Eurasian lynx, combined with its dispersal capacity, with individuals capable of moving almost 170 km (i.e., from the Harz subpopulation to the vicinity of the BBA subpopulation) (Gajdárová et al., 2021), indicate that there is the possibility of gene flow between these subpopulations, if proper management actions are provided. Thus, it is essential to enhance permeability in unprotected areas between EPAs for lynx conservation. Additionally, lynx suitable habitat is more protected in Sweden and Finland, followed by Romania, where the species has a ‘favorable’ status (Santini et al., 2016), even if the connectivity among the EPAs is low. This underscores the need to bolster habitat protection in Central and Eastern Europe, especially in corridor-affected regions. Given the lynx's sensitivity to human disturbance (Ripari et al., 2022), relying solely on EPAs is insufficient to ensure subpopulation connections.

Various factors, including roads, particularly highways, act as barriers that impede the Eurasian lynx's movement, leading to population separation on a small scale (Zimmermann et al., 2007). Some of the identified corridors intersect with highways and major roads, necessitating specific management actions. Thus, our results offer valuable insights for prioritizing mitigation measures, such as overpasses, to reduce the effect of these barriers on the lynx's movements.

The limited size of certain EPAs in Central Europe poses a challenge due to the Eurasian lynx's extensive spatial requirements, making long-term subpopulations health unsustainable (Palmero et al., 2021). Expanding EPA's coverage in line with the European Union's Biodiversity Strategy for 2030 is a crucial initial step, ensuring enhanced protection for corridors, particularly in Central and Eastern Europe. Our results indicate that a random expansion of EPA's surfaces could lead to increased forest cover. However, it is important to note that our circular buffer approach may not accurately represent the real expansion for all EPAs. As an alternative strategy, other conservation measures could include the establishment of new, peculiar EPAs acting as stepping-stones in areas where high connectivity between subpopulations is predicted (Fig. 1b).

Concerning natural or human-mediated connectivity, as a tool to ensure the long-term survival of the Eurasian lynx subpopulations in Eastern and Central Europe, it is important to consider the current evolutionary significant units (ESU). Actually, there are six lineages, three of which are in Europe: the Northern lynx (L. l. lynx), the Carpathian lynx (L. l. carpathicus), and the Balkan lynx (L. l. balcanicus) (Kitchener et al., 2017; Lucena-Perez et al., 2020; Mueller et al., 2022). Thus, it is important to favor connectivity among the subpopulations that belong to the same ESU (Schmidt et al., 2011). Considering the Balkan subpopulation, previous studies have demonstrated the similarity with the Carpathian lynx present in the Dinaric area, which could therefore be used as a source to favor the exchange of individuals between these populations (Bazzicalupo et al., 2022; Melovski et al., 2022).

The analysis of ecological connectivity is crucial for designing effective ecological networks and evaluating the efficacy of protected areas. Nonetheless, overcoming the obstacles that impede the integration of connectivity into conservation planning, including the validation of connectivity models and enhancements in field data collection and sharing among researchers, is essential (Correa Ayram et al., 2016). Meta-analyses by Fletcher et al. (2016) and Resasco (2019) have shown that ecological corridors positively impact movement across diverse species and organizational levels, reinforcing the notion that investing in corridor creation and maintenance is beneficial for biodiversity conservation.

Previous studies that validated circuit-theory algorithms with empirical data demonstrated their effectiveness in the identification of dispersal corridors (McClure et al., 2016). The recent findings of individuals belonging to Baltic, Harz, and Carpathian subpopulations, in the vicinity of the BBA subpopulation (Gajdárová et al., 2021), partly support our landscape connectivity models' outcomes. Moreover, our connectivity results have been confirmed from other sensitivity analyses repeated with different input data (Supplementary Material Figs. A8, A9).

Given the Eurasian lynx's dispersal ability, especially in Central Europe (Mueller et al., 2020; Gajdárová et al., 2021), and its adaptability (Filla et al., 2017), establishing dispersal corridors is a viable management option to enhance the conservation status of isolated and endangered subpopulations. Previous studies have shown that even a small number of individuals can increase genetic diversity in small populations (Bull et al., 2016). Furthermore, the BBA subpopulation case-study indicated that full protection, sufficient food supply and suitable permeable habitat supported population recovery (Gajdárová et al., 2023). Our approach, which assesses connectivity using various techniques and considers both the target species and protected areas, offers utility for species with similar spatial requirements. In conclusion, our findings can inform conservation and management strategies at multiple scales, potentially aiding the creation of a functional metapopulation in Central Europe and preserving the small and isolated populations of Eurasian lynx. Moreover, these results can support managing existing protected areas, which are essential for promoting Eurasian lynx expansion. However,

effective conservation requires tackling poaching and illegal killing outside protected areas, and given the species' extensive mobility, international cooperation is imperative.

Supporting Information

Supplementary Data can be accessed at the following link: https://www.sciencedirect.com/science/article/pii/S0006320724000594#s0075

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Chapter 7

Case study I: Coupling habitat modelling, functional connectivity, and individual-based models to assess the theoretical feasibility of Eurasian lynx reintroduction in the Apennines

Introduction

Historically, many large carnivores have faced population declines and range contractions due to habitat loss, fragmentation, persecution, and reduced prey abundance (Linnell et al., 2009; Ripple et al., 2014). Despite historical declines, populations of Eurasian lynx (*Lynx lynx*; hereafter 'lynx'), brown bear (*Ursus arctos*), and grey wolf (*Canis lupus*) have increased in Europe over the past few decades, returning to areas where they previously went extinct (Cimatti et al., 2021). This conservation success stems from coordinated legal protection, specific management measures, rural abandonment, favorable public opinion, and reintroduction/translocation programs, the latter particularly relevant for the lynx (Cimatti et al., 2021).

Reintroductions and translocations are key components of biodiversity conservation efforts (Seddon et al., 2014). Despite reintroductions may lead to unexpected ecological dynamics, decisions regarding when, where, and how to reintroduce are often based on non-existent or limited empirical data. To partially counter data deficiency, ecological models informed with available knowledge about species' ecology have been applied to predict the possible outcomes of reintroductions before investing in the latter (Bellis et al., 2021; Finn et al., 2024). In most cases, this approach relies on species distribution models (SDMs) to identify suitable areas for reintroduction. Nonetheless, standard SDMs do not consider factors like functional connectivity and dispersal capability (Hunter-Ayad et al., 2020). The need for mechanistic models, which simulate processes like dispersal, demography, and evolution, stimulated the development of individual-based models (IBMs), rapidly implemented in evaluations of alternative reintroduction scenarios (e.g., Ovenden et al., 2019).

Reintroducing large carnivores poses significant challenges, particularly concerning public acceptance (Linnell et al., 2009). For example, lynx predation on livestock and hunters' concerns about its impact on ungulate populations can lead to conflicts and illegal killings (Breitenmoser-Würsten et al., 2007; Vandel et al., 2006). However, apex predator's reintroductions can benefit ecosystems by restoring trophic interactions, reducing densities of herbivores and/or mesopredators, supporting biodiversity, and enhancing ecosystem stability (Bakker & Svenning, 2018; Ritchie & Johnson, 2009). Additionally, large carnivores offer economic and ecosystem services, influencing scavenger subsidies, disease dynamics, carbon storage, crop production (Ripple et al., 2014), and providing ecotourism opportunities (Penteriani et al., 2017). Despite increasing success in translocation of large carnivores, only 66% of individuals survive the first six months, and 37% reproduce (Thomas et al., 2023). Application of habitat modelling has potential to further improve the decision-making when choosing optimal release locations, thus contributing to the success of reintroduction programs.

Reintroductions have been key to the lynx's recovery in Europe, with some subpopulations fully reconstituted (Linnell et al., 2009). Once widespread across Eurasia (Werdelin, 1981), the lynx went extinct in much of Europe due to habitat changes, persecution, and prey loss (Breitenmoser, 1998). Historically, only the Scandinavian, Eastern Baltic, Carpathian, and Balkan populations survived. The recovery of other European populations required reintroductions over the past 50 years, as natural recolonization was unlikely due to limited

ecological corridors (Linnell et al., 2009). Despite some unsuccessful reintroductions due to poor planning, several populations have become established, such as the Dinaric, Alpine, Bohemian-Bavarian-Austrian, and Jura populations (Linnell et al., 2009).

The lynx likely reached Europe from Asia during Middle-Late Pleistocene (Werdelin, 1981), but precise timing of colonization of Italy is unknown. In Italy, it currently occurs only in the Eastern Alps on the border with Slovenia with few individuals belonging to the Alpine population. Beside the Alps, the lynx in Italy historically also inhabited the Apennines, as indicated by paleontological and cultural evidence (Cherin et al., 2013; Ghezzo et al., 2015). While exact timing of the lynx extinction in the Apennines remain unclear, the pattern of lynx disappearance was similar to the Alps, where the lynx was exterminated during the 18th and 19th centuries (Tassi, 2018, Breitenmoser, 1998). Previous continent-wide habitat-modeling studies on the lynx suggested potential suitability of the Apennines, which represent one of the largest suitable, but currently non-occupied areas within the species' historic range in Europe (Oeser et al., 2023; Serva et al., 2023). Thus, the Apennines could represent one of the possible sites for future lynx reintroduction to contribute to the recovery of this apex predator in the European forest ecosystems.

Here, we first aimed to assess the potential for natural recolonization of the Apennines from the Alps. Next, we analyzed the feasibility of reintroducing this large carnivore to the Apennines by: (i) assessing the main drivers of reintroduction failures (Macdonald, 2009); (ii) integrating the gained knowledge within a new coherent framework where the most important habitat requirements of the species are computed by coupling SDMs-based habitat suitability estimates with quantification of the functional connectivity among suitable areas. Finally, we used IBMs to evaluate several reintroduction scenarios, aiming to provide baseline guidance on how to establish a viable lynx population in the Apennines.

Material and methods

Study area and target species

The target study area is the Apennines, a 1200 km long calcareous mountain range crossing Italy. The Apennines feature many protected and forested areas with low human density and high wild ungulate densities, including the roe deer (Capreolus capreolus), which is the main prey for lynx in Europe. The target species is the lynx, once present in the Apennines but now limited to the Alps in Italy. Given that most reintroductions in Central Europe over the past 50 years involved individuals from the Carpathian population, we considered Southern and Central Europe (excluding regions with other subpopulations like the Scandinavian, Karelian, and Baltic) as a second study area for SDMs calibration.

The lynx, with an estimated 9,000-10,000 individuals in Europe, is classified by the IUCN Red List as "Least Concern". However, subpopulation statuses vary, with some "Critically Endangered", and others "Endangered" (Von Arx, 2020). Data on the lynx distribution included records from previous studies and additional occurrences retrieved from various sources (Supplementary Table S1).

Environmental predictors

We selected bioclimatic, topographic, human-related, and habitat-related variables previously shown to be relevant to lynx ecology (Čonč et al., 2024; Oeser et al., 2023; Serva et al., 2023). Specifically, we considered 11 candidate predictors: elevation, retrieved from a Digital Elevation Model (DEM) at 90m resolution, Terrain Ruggedness Index (TRI), Tree Cover (TC),

Human Footprint Index (HFI), Snow Cover, Mean Annual Temperature (BIO1), Precipitation Seasonality (BIO15), Forest Integrity Index (FII), NDVI, Human Impact, and Night Light. Full details on the predictors used are available in the supplementary table 2.

The candidate predictors were found to be non-collinear, after assessing multicollinearity using the Variance Inflation Factor ('vifstep' algorithm of the 'usdm' R package (Naimi, 2015), threshold = 10) (Supplementary Fig. 1a), and the 'layerCor' function (Hijmans et al., 2024) (Supplementary Fig. 1b).

All variables were resampled to a resolution of 300m using GEE and the 'terra' R package (R Core Team, 2024).

Ecological niche modeling and niche overlap

The occurrence dataset was filtered using the 'thinData' function of the 'SDMtune' R package (Vignali et al., 2020) to maintain a single occurrence per raster cell, reducing spatial autocorrelation (Sillero & Barbosa, 2021).

Species distribution models (SDMs) were generated through the 'SDMtune' R package, which permits to fit SDMs through four machine learning algorithms — artificial neural networks (ANN), boosted regression trees (BRT), MaxEnt, and random forest (RF) — and tune them by searching for the best hyperparameters with a real-time chart display (Vignali et al., 2020). To fit ANN, BRT and RF, pseudoabsences were created through the 'biomod2' R package (Thuiller et al., 2016) using the Surface Range Envelope algorithm (quantile = 0.05), generating 13,000 pseudoabsences (ratio pseudoabsences:occurrences equaling 10:1) (Barbet-Massin et al., 2012). Differently, to feed the MaxEnt algorithm, ~20,000 background points were randomly drawn from the study area. Presences and pseudoabsences were merged and split into training (80%) and testing (20%) datasets, using four folds random cross-validation.

Taking advantage of the 'optimizeModel' function from 'SDMtune', the best values (i.e., those maximizing model evaluation scores) for critical hyperparameters of each algorithm were chosen using the area under the curve (AUC) as evaluation metric. The optimized SDMs were projected across both study areas (Central and Southern Europe, and the Apennines). A final ensemble model was then generated through a weighted mean of predictions from the single SDMs, based on the respective AUC scores. Full details about SDMs' tuned parameterization are available in Supplementary Table S3.

The 'ecospat' R package (Di Cola et al., 2017) was used to assess environmental overlap between the potential lynx range (as estimated through the ensemble model) in the Apennines and in the Carpathian. Specifically, since the lynx is absent in the Apennines, we generated 300 random points within pixels with very high predicted suitability. Environmental variability within the two regions was then summarized into two orthogonal axes through a Principal Component Analysis (PCA). Finally, the 'ecospat.niche.overlap' function was used to generate kernel-smoothed grids showing density of occurrence in environmental space for each potential range, subsequently measuring the corresponding overlap through the Schoener's D index.

Connectivity analyses

A resistance layer spanning the Alpine biogeographic area, and the Italian peninsula was created by transforming the predicted habitat suitability according to the negative exponential function of Keeley et al. (2016). Barriers such as major roads, urban areas, rivers, and lakes, were assigned the highest resistance value and were later merged through the 'Mosaic to New Raster' tool in ArcGIS Pro.

Connectivity was computed using Circuitscape in Julia (version 1.9.2), a circuit-theory technique shown to perform better than other approaches (Anantharaman et al., 2019). Circuitscape requires a resistance layer and source/target locations (nodes) (McRae et al., 2008), producing a current map reflecting landscape connectivity as the expected net probability of movement between nodes, considering a random-walk scenario (McRae et al., 2008).

In the Alps, lynx occurrences were used as focal nodes. In the Apennines, where lynx does not currently occur, the most suitable areas were individuated by applying a >90% quantile classification to predictions derived from the ensemble SDM. The centroids of these suitable areas were then used as focal nodes for the Apennines: the assumption is that these areas will be the ones selected by lynx individuals in a scenario of natural recolonization. Circuitscape was initially run in 'pairwise' mode, computing current for every node pair, so that each node served as both source and destination (McRae et al., 2008). To test a different scenario, a second Circuitscape run was performed in 'advanced' mode, computing connectivity from sources (i.e., Alps' nodes) to destinations (i.e., Apennines' nodes) only.

Omniscape v.0.5.8 in Julia (Landau et al., 2021) was then used to compute landscape connectivity without the effects of focal nodes' positions. Omniscape iteratively computes connectivity within a moving window, where the center pixel is the destination and pixels within the window are sources. Users can specify whether to use all pixels as sources or only those with certain resistance values. Omniscape then applies Circuitscape in 'advanced' mode for each target pixel (Landau et al., 2021).

Lastly, Circuitscape in 'pairwise' mode was run again, this time limiting the analysis to the Apennines, to compute connectivity between potentially suitable areas based on the ensemble SDM.

Habitat functionality and potential reintroduction areas

To identify potential reintroduction sites, habitat suitability predicted by the ensemble SDM and the connectivity layer resulting from Circuitscape in 'pairwise' mode were integrated using the 'Suitability Modeler' tool in ArcGIS Pro. This tool helps find the best sites for establishment based on several user's defined criteria, each of them is transformed and weighted to produce a final layer, which serves as input for selecting optimal sites. The algorithm can be further informed with spatial requirements such as the total area needed by a target species, the number and size of sites, and their reciprocal distance.

To feed the 'Suitability Modeler', the habitat suitability layer (weight = 60%) was transformed using a simple linear function, while the connectivity map (weight = 40%) was transformed according to an MSLarge function, emphasizing large values using mean and standard deviation multipliers (Esri Inc., 2023). After obtaining the final integrated layer, defined as 'habitat functionality' sensu Van Moorter et al. (2023), the 'Locate' tool was used to identify the best release sites for the reintroduction of the lynx in the Apennines. Specifically, the tool was run considering three major scenarios: (1) minimum distance of 10 km between sites; (2) no minimum distance between sites; (3) no minimum distance but sites cannot be inside protected areas (PAs). Further, spatial patterns to identify the best sites were altered five times for each scenario, varying the total reserved area from 2,800 km² to 4,400 km², resulting in fifteen different scenarios overall (Supplementary Table S4). For each scenario, the tool identified the best 30 release sites, leading to a total of 450 release sites identified in the end, which were later merged into a single layer.

The maximum and minimum site areas imposed to the algorithm were 45 and 120 km², respectively, with an average of ~80 km², based on female lynx home-range sizes in the Alps (Molinari-Jobin et al., 2007).

Individual-based modeling and reintroduction scenarios

The 'RangeShiftR' R package (Malchow et al., 2021), based on RangeShifter 2.0 (Bocedi et al., 2021) was used to produce IBMs and subsequent Population Viability Analysis (PVA). RangeShifter is a spatially-explicit, individual-based simulation platform that model's species' range dynamics, patch connectivity, and complex local population dynamics, accounting for inter-individual variability and evolutionary processes (Bocedi et al., 2021; Malchow et al., 2021). The package is modular, allowing the users to define the Landscape settings and add parameters for Demography, Dispersal, Genetics, Initialization, Simulation, and Output modules. The ensemble SDM reclassified into ten habitat quality classes, each with specific carrying capacities and mortalities, was used as imported landscape. For the Stochastic Movement Simulator (SMS), a cost layer was provided based on the reclassified resistance layer resulting from the connectivity analyses.

Simulations were run under a patch-based model. All the patches individuated through the 'Locate' tool were initially loaded, some specific sites were delimited, and three scenarios were then explored, namely reintroductions occurring in: two regions (Northern and Central Apennines); Central Apennines only; Northern Apennines only. Species-specific parameters were set based on previous studies (Guilfoyle et al., 2023; Ovenden et al., 2019) and adjusted for the Carpathian lynx (Supplementary Table S5). For each reintroduction scenario, three simulations were performed: (1) no environmental stochasticity, (2) 'white noise' stochasticity, and (3) 'red noise' stochasticity (Malchow et al., 2021). Finally, all simulations were replicated considering enhanced mortality to make possible negative events (e.g., poaching) be reflected in the IBMs' outputs.

Results

Connectivity between the Alps and the Apennines

The final dataset after the thinning procedure contained 1373 occurrences. AUC of the fitted SDMs spanned from 0.92 of the ANN to 0.97 of RF algorithm (Supplementary Fig. S2). In all algorithms, elevation and Bio1 were the most important variables, followed by TRI and Bio15 (Supplementary Figs. S2-S3).

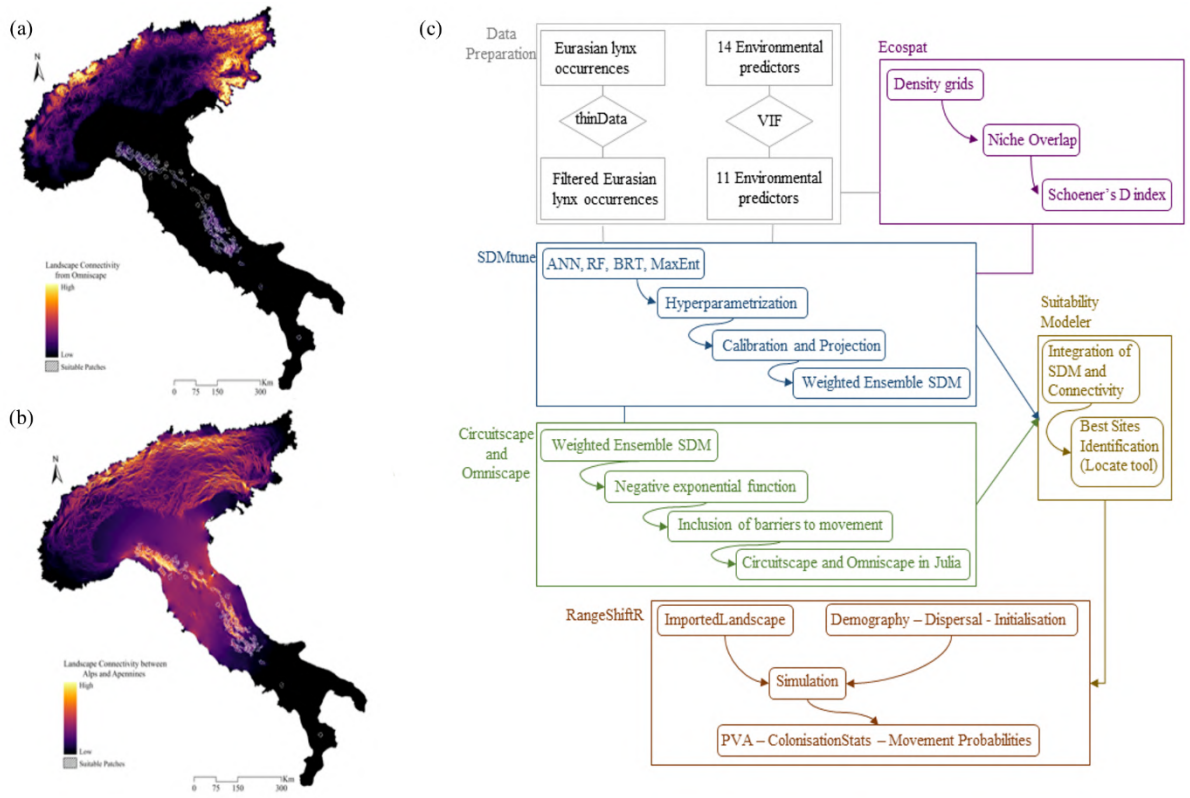


Fig. 1. Landscape connectivity for the Eurasian lynx across the Alpine biogeographic region and the Italian Peninsula, as detected from Omniscape (a), and Circuitscape in 'pairwise' mode (b), showing in both cases low connectivity between the Alps and the Apennines; (c) full workflow adopted for assessing reintroduction scenarios.

Landscape connectivity between the Alps and the Apennines was generally low, regardless of the algorithm used (Figs. 1a, b), while medium-to-high connectivity emerged within both the Alpine and Apennine regions. These results established the basis for the subsequent analysis of reintroduction scenarios, as natural recolonization of the Apennines from the Alps seems unlike in the foreseeable future (Fig. 1c).

Habitat suitability and connectivity in the Apennines

The ensemble SDM highlighted several suitable patches mainly in the Northern and Central Apennines, with several potential stepping-stones areas in between (Fig. 2a). Furthermore, most of the suitable patches in the Central Apennines at least partially overlap with larger PAs and are located in mountain areas with low human disturbance (Fig. 2a). A moderately-high niche overlap (Schoener's D index = 0.73) emerged between the potential lynx distribution in the Apennines and that of the Carpathian lynx in its current range (Fig. 2b). This niche overlap is also suggested by the relative importance estimates of the predictors used to fit the SDMs (Supplementary Fig. S5).

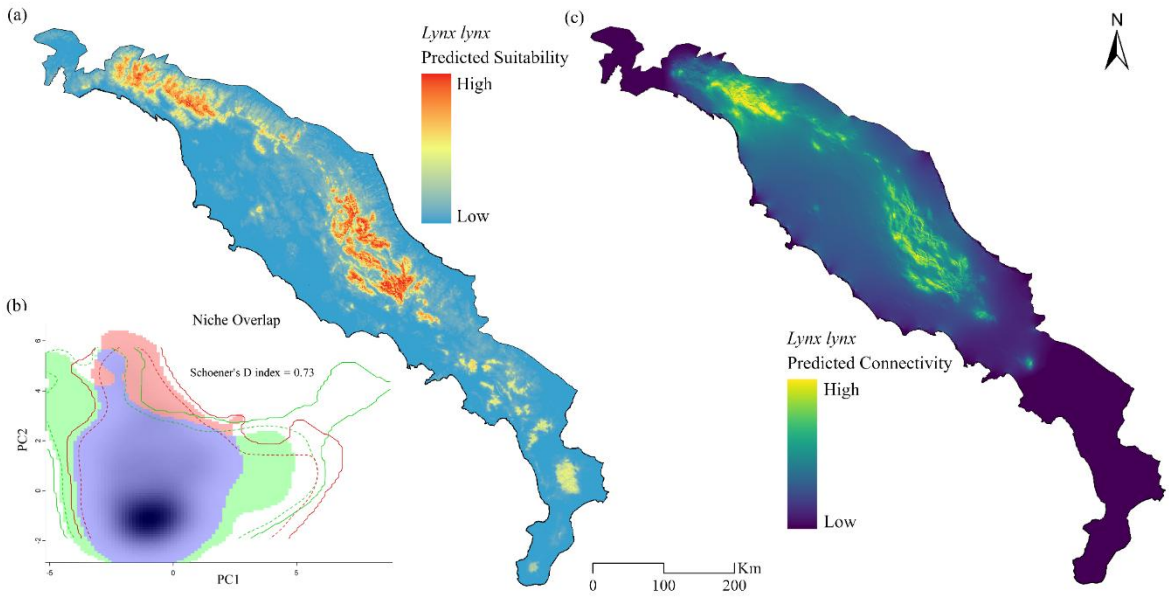


Fig. 2. Predicted habitat suitability, resulting from the ensemble SDM, for the lynx in the Apennines (a); niche overlap (blue) between potential lynx distribution (i.e., high-suitability areas) in the Apennines (red) and the Carpathian lynx range (green) (b); predicted connectivity (c), estimated using as focal nodes the most suitable areas detected from the habitat suitability layer.

Landscape connectivity in the Apennines, as estimated in Circuitscape, showed several fine-scale, high-connectivity corridors in Central Apennines, while predicted connectivity was more 'diffused' in some areas of Northern Apennines (Fig. 2c). Importantly, areas with moderate connectivity appeared between the two sectors (Fig. 2c), suggesting the possibility for the lynx to disperse through the Apennines.

Habitat Functionality and reintroduction sites

High values of habitat functionality, indicating areas being both suitable and well connected, occurred in the Northern and Central Apennines, while the southern part of the mountain chain appears less 'functional' for the lynx (Fig. 3a).

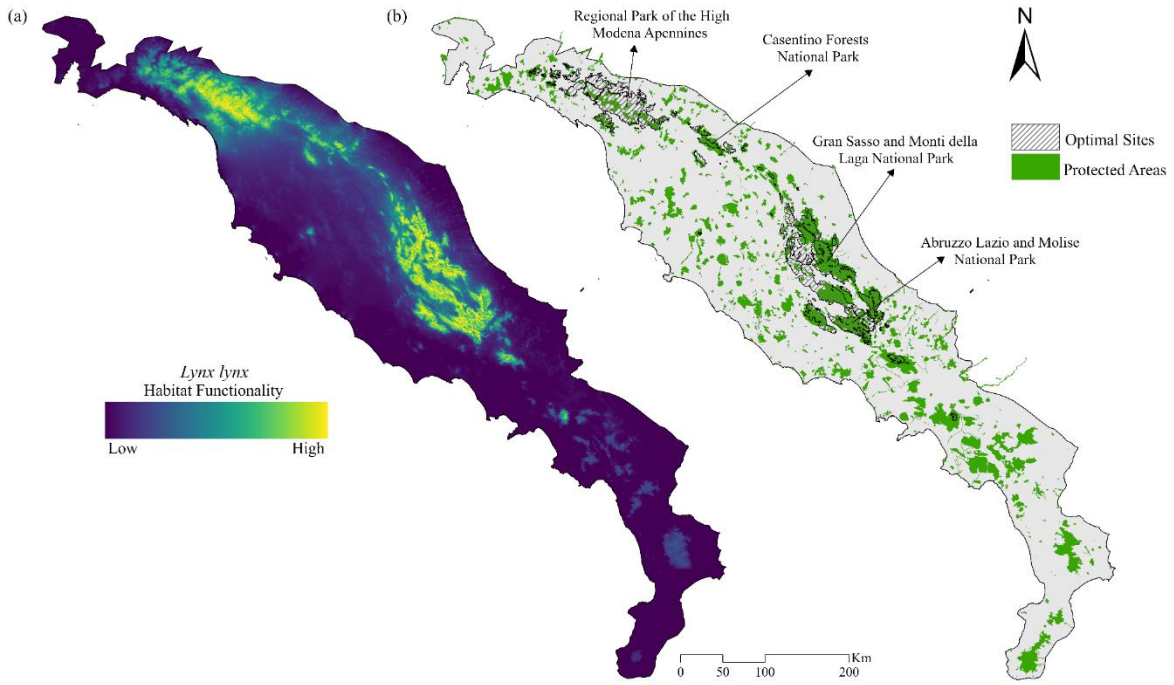


Fig. 3. (a) Habitat functionality for the lynx in the Apennines, estimated by integrating the ensemble SDM's predictions and the habitat connectivity layer; (b) the best reintroduction sites (hatched polygons) identified from the 'Locate' tool in fifteen different scenarios, overlapped with PAs (green polygons).

The 450 potential suitable release sites for lynx reintroduction in the Apennines identified through the 'Locate' tool were mainly distributed in Northern and Central Apennines, with some important stepping-stone areas between these two areas, while only a few sites were in Southern Apennines (Fig. 3b). Despite some differences between the tested scenarios, some areas were selected more frequently by the algorithm (Supplementary Fig. S6). Furthermore, the best identified sites partially overlap with PAs, particularly those of Central Apennines (67%), followed by those of Northern Apennines (33%).

Population Viability Analyses and reintroduction scenarios

The best reintroduction scenario, leading to an estimated population size of ~250 individuals after 100 years, involved the reintroduction of ~20 individuals in both Northern and Central Apennines, with several sites showing high occurrence probability in both areas (Figs. 4a, b). A faster colonization process was predicted in Northern Apennines, while in Central Apennines some patches were predicted to be colonized only after more than 90 years (Fig. 4c).

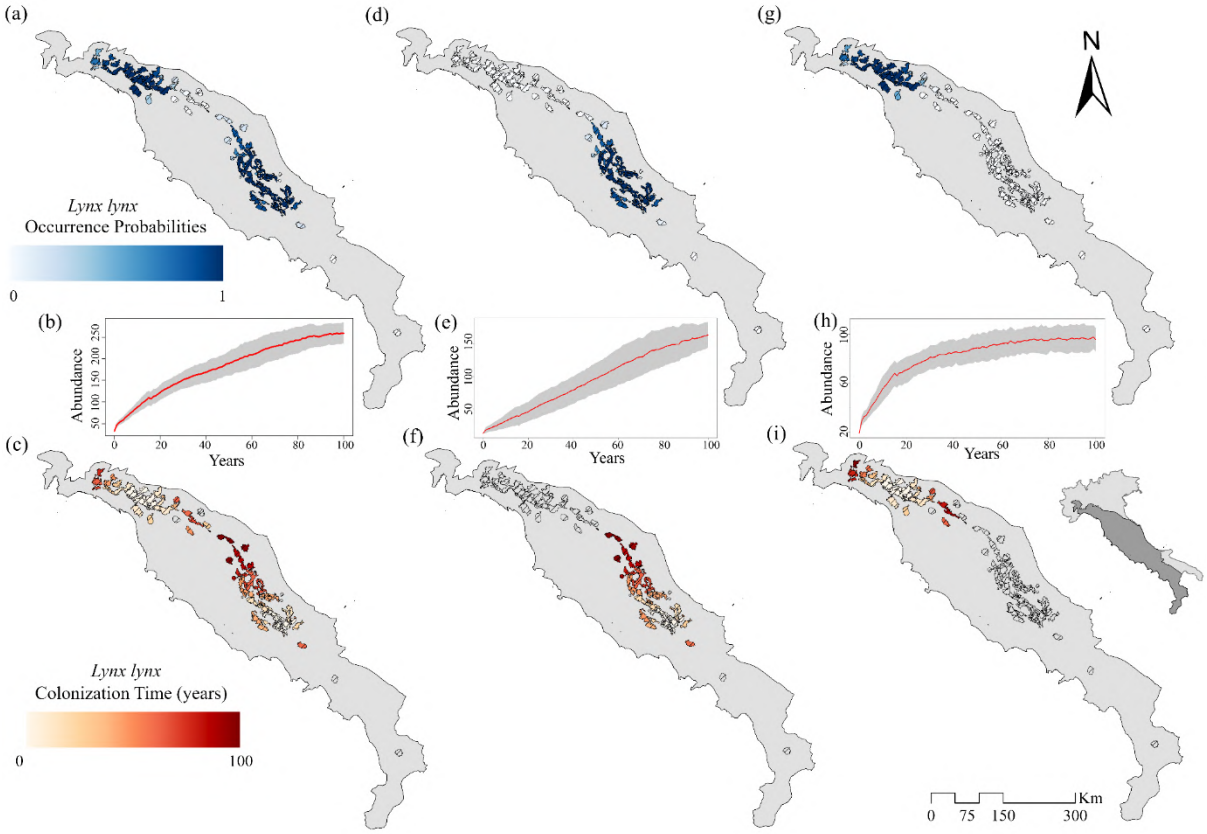


Fig. 4. Colonization stats and Population Viability Analysis (PVA) for different reintroduction scenarios. Specifically, occurrence probability, PVA chart (i.e., predicted abundance over time), and colonization time are shown for a reintroduction starting in both Northern and Central Apennines (panels a, b, and c); Central Apennines only (panels d, e, and f); Northern Apennines only (panels g, h, and i).

The single-site reintroduction scenario (in both case involving the reintroduction of ~15 individuals) focusing on Central Apennines seemed better than the one centered in Northern Apennines, due to high occurrence probability in most patches and higher predicted population size (Figs. 4d, e, g, and h). Moreover, simulating reintroduction only in Northern Apennines produced the smallest population after 100 years, with an asymptote in population growth and, concurrently, fewer patches occupied (Figs. 4g, h, and i). Considering simulations with increasing mortality (Supplementary Figs. S7-S8-S9), as expected smaller populations resulted in every reintroduction scenario, with lower occurrence probability (average percent reduction ± SD = 23% ± 7) and longer colonization time (average percent increase ± SD= 20% ± 9).

Movement probabilities

Dispersal heatmaps, highlighting those parts of the landscape matrix that are predicted to be frequently used for dispersal, showed higher values of movement probability outside the patches selected for the reintroduction, as expected, both in Northern and Central Apennines, under different simulation conditions (Figs. 5a, b, and c). However, interesting differences emerged between the two areas, with movements in Northern Apennines primarily clustered close to the reintroduction patches, while in Central Apennines individuals were predicted to disperse farther, especially northwards (Figs. 5a, b, and c).

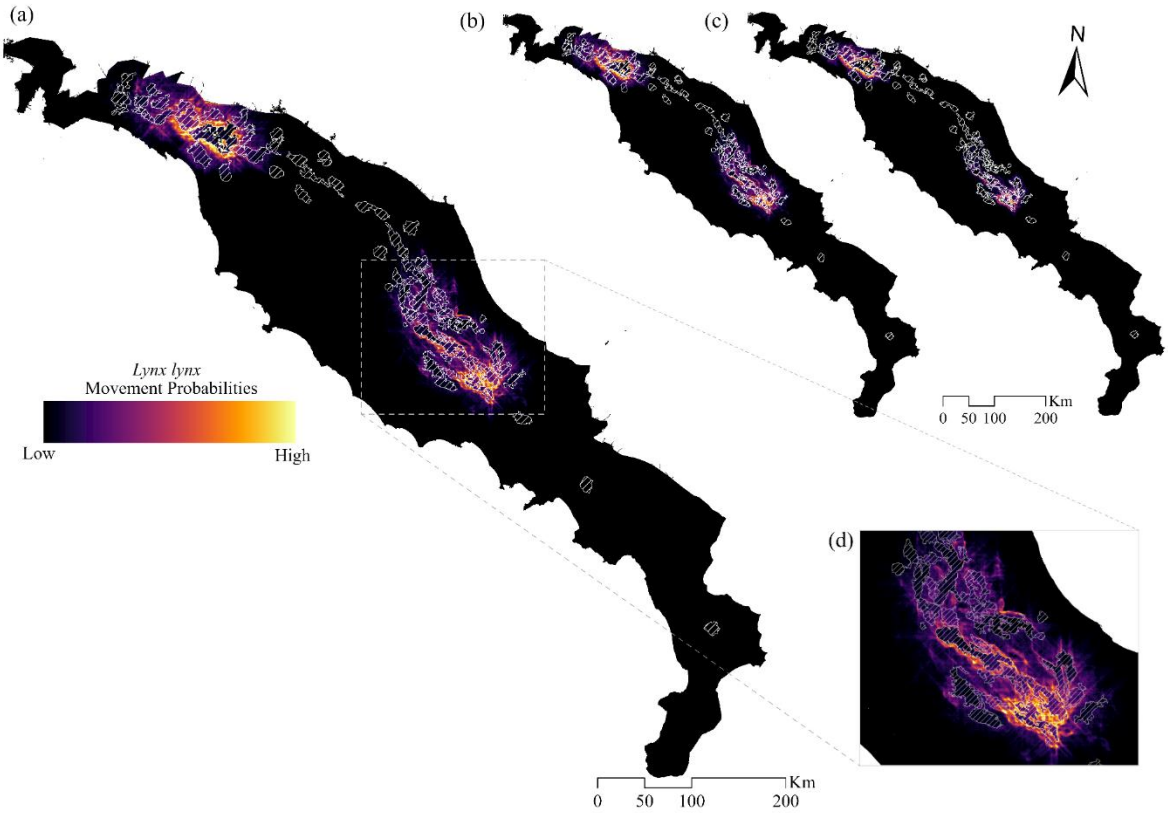


Fig. 5. Dispersal heatmaps representing the predicted movement probabilities across the landscape matrix considering: (a) ‘red-noise' environmental stochasticity, with a zoom on Central Apennines (d); (b) ‘white-noise' environmental stochasticity; (c) 'red-noise' environmental stochasticity and increased mortality. Hatched areas are the optimal reintroduction sites identified in the habitat functionality layer.

Considering different scenarios of environmental stochasticity did not significantly change the results, except when simulating increased mortality (Fig. 5c). In this latter scenario, movement probabilities were higher around the reintroduction patches, and some corridors disappeared in Central Apennines, like those connecting the patches around the “Majella National Park” to the “Gran Sasso and Monti della Laga National Park” (Fig. 5c). Focusing on Central Apennines, multiple corridors can connect most of the suitable patches, especially between “Abruzzo Lazio and Molise National Park” and “Sirente Velino Regional Park” (Fig. 5d).

Discussion

A new framework to identify sites for reintroduction purposes

In this study, using the lynx reintroduction to the Apennines as a case study, we developed a new framework for identifying the best release sites for reintroduction purposes and assessing the feasibility of such conservation effort. By combining spatially-explicit predictions derived from SDMs and connectivity analyses with individual-based modeling (IBMs), we demonstrated how such an integrated modeling approach could help in defining reintroduction scenarios and testing their probability of success.

Our approach assesses several important prerequisites for planning reintroductions. It measures niche overlap between environmental conditions in source and target areas, ensures the identification of the best release sites, and evaluates the success and threats of various reintroduction scenarios. Currently, most reintroduction studies involved the use of SDMs alone, to define the most suitable areas (e.g., Bellis et al., 2021; Finn et al., 2024). However, for many species, connectivity is as important as suitability for the long-term persistence of a population but is often ignored or considered separately (e.g., Iannella et al., 2024). Moreover, the improved accessibility of IBMs is a significant step forward, as it allows researchers and conservationists to evaluate the various reintroduction scenarios considering the specific target species ecology.

We encourage the use of this framework, at least partially, when planning reintroductions, as crucial information for decision-making can be obtained. The use of these modeling tools, which robustly establish the demographic, landscape, and genetic factors most sensitive to potential reintroduction success, can help prioritize future data collection to iteratively reduce model uncertainties. Furthermore, we underline the importance of considering the target species' ecology and requirements when determining the best release sites for reintroduction. For a species like the lynx, connectivity between suitable patches is crucial, as demonstrated by several studies (Kramer-Schadt et al., 2004; Zimmermann & Breitenmoser, 2007). The integration of habitat suitability and habitat connectivity is a key step in determining the potential suitability of a site. However, few studies have proposed frameworks to integrate these two parameters (Van Morter et al., 2023). Here, we propose a new approach to achieve this, developed for ArcGIS software but easily implementable in other environments.

Double-site vs. Single-site reintroduction scenarios in the Northern and Central Apennines

Connectivity analyses between the Alps and the Apennines revealed low connectivity, making natural recolonization unlikely and reintroduction the only viable option for the lynx's return to the Apennines. Selecting optimal release sites and assessing potential movements of translocated individuals are critical for successful reintroduction (Devineau et al., 2010). In our study, the double-site reintroduction scenario outperformed the single-site ones, and was the only one where most of the patches in the Central and Northern Apennines were colonized at the end of the simulation. However, this approach is more challenging due to the increased distance between sites and the greater resources needed for reintroduction and monitoring. If a single-site reintroduction is chosen, the central Apennines are the best option, producing a more robust population capable of expanding northward. The presence of large, well-connected PAs further supports this strategy. Although a viable lynx population is proposed to range between 50–100 individuals (Zimmermann & Breitenmoser, 2007), a population of 200–250 individuals in well-connected habitats would better avoid inbreeding and protect against unexpected population declines, such as from disease (Breitenmoser, 1998). Our simulations, however, suggest that lynx from the Central Apennines would not naturally colonize the Northern

Apennines within 100 years, risking long-term isolation, as seen in other reintroduced lynx populations in Europe (Mueller et al., 2022). To mitigate this, creating a stepping-stone network to facilitate lynx movement between the Northern and Central Apennines or managing the population through occasional translocations would be necessary.

Currently, no formal proposals exist for lynx reintroduction to the Apennines. However, our results support feasibility planning in the Central and Northern Apennines, reaffirming these areas' suitability as identified by previous larger-scale studies (Oeser et al., 2023; Serva et al., 2023) and providing further guidance on optimal release sites and potential connectivity. Before reintroduction, key steps must include assessing public support among local communities, identifying knowledge gaps, and understanding conditions for accepting the lynx's return. Experiences from previous projects show that public attitudes toward large carnivores are shaped by value orientations, awareness, and perceived costs and benefits. Effective communication strategies and stakeholder engagement are therefore essential (MacDonald, 2009). Political support and leadership are also crucial to reintroduction success (MacDonald, 2009). Addressing these issues can reduce negative sentiments and incentives for illegal killings, thus supporting long-term lynx conservation (Bath et al., 2008). Previous studies indicate generally favorable public acceptance of lynx, especially compared to other large carnivores in Europe (Whiley & Tzanopoulos, 2024). Nevertheless, after several centuries of absence of the lynx in the Apennines there is considerable work needed to increase public awareness and basic knowledge about the species.

Challenges and Benefits of the lynx in the Apennines

Maintaining or restoring ecologically-effective densities of large carnivores is crucial for preserving ecosystem structure and function (Ripple et al., 2014). Reintroducing the lynx in the Apennines, for instance, could help regulate ungulate and mesocarnivore populations, support endangered scavengers, and potentially trigger trophic cascades by affecting wild ungulate (Ripple et al., 2014). Such reintroductions thus not only serve species conservation goals but also aid in restoring ecosystem functions (Bakker & Svenning, 2018). Additionally, the return of Europe's largest felid could boost ecotourism, since iconic species like large felids are highly attractive to wildlife enthusiasts (Lindsey et al., 2007).

However, reintroducing large carnivores poses challenges, particularly related to spatial requirements and resource availability, including prey (Wolf & Ripple, 2018). Human-wildlife conflicts, especially in areas where these predators have been absent, may also arise, leading to retaliatory killings, that significantly affect lynx populations (Heurich et al., 2018). Although lynx generally pose less risk to livestock compared to wolves and bears, concerns about their impact on wild ungulates and competition with hunters often drive low acceptance and poaching (Zimmermann & Haller, 2010). Since our simulations indicated that population development would be sensitive to additional mortality, ensuring adequate support for lynx conservation among the local hunting communities and preventing excessive illegal killing should be one of the essential activities supporting the potential translocation of lynx to the Apennines.

Other potential barriers to successful reintroductions include genetic isolation, small release numbers, hunting difficulties, inadequate feasibility studies, and insufficient knowledge of the species' ecological needs (MacDonald, 2009). This study addresses these concerns by assessing connectivity, determining optimal release numbers, and identifying suitable reintroduction sites. While prey availability is likely sufficient given the abundance of roe deer, further analysis of other ungulate populations in potential reintroduction areas would be beneficial.

To mitigate human-wildlife conflicts, selecting PAs as reintroduction sites is recommended. The size of PAs, along with low human disturbance and high prey density, are key factors for large carnivore persistence (Wolf & Ripple, 2018). In our study, most optimal reintroduction sites overlapped with PAs, even though the model was not specifically informed of their presence. This overlap may enhance lynx survival, particularly during the vulnerable initial reintroduction phase, as previous studies have shown (Vandel et al., 2006; Linnell et al., 2009; Heurich et al., 2018).

Conclusion

In conclusion, this study provides a foundation for the potential reintroduction of the lynx in the Apennines, where it has been extinct for centuries. By evaluating habitat suitability, connectivity, and reintroduction scenarios, we identify optimal sites for translocation. Our analysis suggests that a double-site reintroduction in the Northern and Central Apennines or a single-site in the Central Apennines would be most effective. The Carpathian population is confirmed as a suitable source for reintroduced individuals. However, public acceptance and political support are essential for the success of reintroducing a large carnivore like the lynx in Europe's human-dominated landscapes.

Supporting Information

Table S1. Sources used to collect Eurasian lynx occurrences.

Title	**First Author**	**Year**
An ecological network for large carnivores as a key tool for protecting landscape connectivity in the Carpathians	Vlková	2024
Distribution and minimum population size of Eurasian lynx (*Lynx lynx*) in Croatia in the period 2018–2020	Gomerčić	2021
Genetic constraints of population expansion of the Carpathian lynx at the western edge of its native distribution range in Central Europe.	Krojerová-Prokešová	2019
Status and Conservation of the Eurasian Lynx	von Arx	2004
Eurasian lynx (*Lynx lynx*) in the Austrian Alps in period 2005–2009	Fuxjager	2012
Status and distribution of Eurasian lynx (*Lynx lynx*) in Slovenia from 2005 to 2009	Kos	2012
Troglostrongylus brevior in an Eurasian lynx (*Lynx lynx*) from Bosnia and Herzegovina	Alic	2015
Genetic data confirm critical status of the reintroduced Dinaric population of Eurasian lynx	Sindičić	2013
New insights into the distribution of cardio-pulmonary nematodes in road-killed wild felids from Romania	Deak	2022
Environmental correlates of Eurasian lynx occurrence in Poland–Large scale census and GIS mapping	Niedziałkowska	2006
Long-distance Eurasian lynx dispersal – a prospect for connecting native and reintroduced populations in Central Europe	Gajdárová	2021
Distribution and Conservation Status of the Balkan Lynx (*Lynx lynx balcanicus* Bures, 1941)	Melovski	2013
Incorporating natural and human factors in habitat modelling and spatial prioritisation for the *Lynx lynx martinoi*	Laze	2016
Evidences for the Lynx recovery in Bulgaria: the Lynx discovered in Western Rhodopes.	Spassov	2015
First Hard Evidence of Lynx (*Lynx lynx L.*) Presence in Bulgaria	Zlatanova	2009
Modeling Eurasian lynx (*Lynx lynx*) distribution and estimation of patch and population size in the Alps	Becker	2013
Action Plan for Eurasian *Lynx lynx lynx* Conservation and Management (Figura 19)	Ozoliņš	2017
Citizen Scientists Showed a Four-Fold Increase of Lynx Numbers in Lithuania	Balciauskas	2020

Status of Game populations in Estonia and proposal for hunting in 2021	Veeroja	2021
Datasets and projects		
GBIF (year: 1970-2022; Basis of records: human observation, machine observation) (GBIF Occurrence Download. doi: 10.15468/dl.t6ejs7)		
LifeLynx Technical Reports (https://www.lifelynx.eu/reports/)		
KORA Technical Reports (https://www.kora.ch/it)		
3Lynx Project (Interreg Central Europe) Technical Reports https://programme2014-20.interreg-central.eu/Content.Node/3Lynx.html		

Table S2. Details about all the predictors used

DEM	From Amatulli et al., (2018)
TRI	From Amatulli et al., (2018)
TC	From GEE (Hansen et al., 2013; Gorelick et al., 2017)
HFI	From Mu et al., (2021)
Snow Cover	From MODIS in GEE (Gorelick et al., 2017)
BIO1	From WorldClim (ver. 2.1) (Fick & Hijmans, 2017)
BIO15	From WorldClim (ver. 2.1) (Fick & Hijmans, 2017)
FII	From Grantham et al., (2020)
Night Light	From GEE (Gorelick et al., 2017)
Human Impact	Created by merging, in ArcGIS (ESRI Inc, 2023), three layers representing Euclidean distance from urban areas (located through the Corine Land Cover map of the Copernicus repository), highways, and major roads (GRIP dataset, Meijer et al. (2018)), respectively (Iannella et al., 2024).
NDVI	From GEE (Gorelick et al., 2017)

Figure S3. (a) Results of the VIF and (b) correlation plot

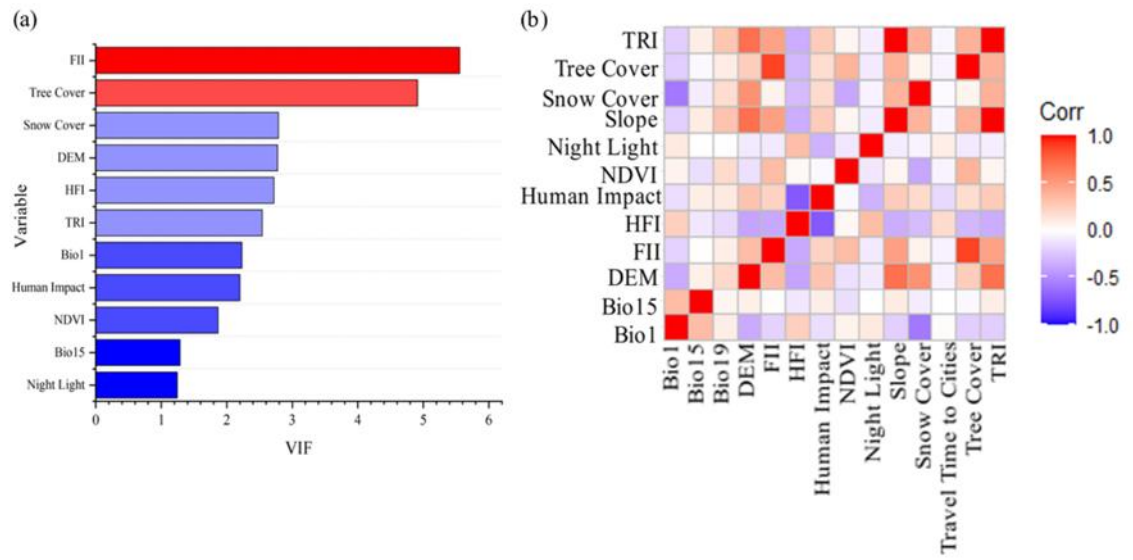


Table S4. Modeling final parameters returned after the 'OptimizeModel' function

ANN	Size: 14, Decay: 0.1, Rang: 0.7, Maxit: 300
MaxEnt	Fc: lp, Reg: 2.2, Iter: 2400
BRT	Distribution: Bernoulli, N. trees: 1100, Int. depth: 2, Shrinkage: 0.01, Bag fraction: 0.6
RF	Mtry: 8, N. trees: 1750, Node size: 1

Table S5. Parameters used for the 'Locate' analysis to find the potential reintroduction sites

Scenario	Total Area (km^2)	Minimum Area (km^2) [(a)]	Maximum Area (km^2) [(a)]	Number of sites	Forma/Suitability %	Method
No Distance	2800	45	120	30	30	Highest Average
No Distance	3200	45	120	30	30	Highest Average
No Distance	3600	45	120	30	30	Highest Average
No Distance	4000	45	120	30	30	Highest Average
No Distance	4400	45	120	30	30	Highest Average
With Distance	2800	45	120	30	30	Highest Average
With Distance	3200	45	120	30	30	Highest Average
With Distance	3600	45	120	30	30	Highest Average
With Distance	4000	45	120	30	30	Highest Average
With Distance	4400	45	120	30	30	Highest Average
No Distance No PAs	2800	45	120	30	30	Highest Average
No Distance No PAs	3200	45	120	30	30	Highest Average
No Distance No PAs	3600	45	120	30	30	Highest Average

No Distance No PAs	4000	45	120	30	30	Highest Average
No Distance No PAs	4400	45	120	30	30	Highest Average

(a) Breitenmoser-Würsten et al. 2001.

Table S6. Parameters used in RangeShiftR where a stage-structure model was implemented, with a Stochastic Movement Simulator

Demography	
Number of life stages (a)	3
Juvenile (kitten) survival probability [a, b, c, d, m]	53%
Sub-adult survival probability [a, b, c, d, m]	63%
Adult survival probability [a, b, c, d, m]	80%
Maximum age (years) [f]	17
Maximum fecundity at low density [f]	5
Mean fecundity at equilibrium density / year [a, c, g]	2
Number of reproductive seasons / year [h, i]	1
Probability of being male in founding population and at birth [c, d]	50%
Probability of reproducing annually [a, j]	100%
Number of years after reproduction before subsequent reproduction [n]	0
Carrying capacity in optimal habitat cells [c]	0.000465 ind/ha*
Emigration Parameters	
Juvenile female maximum emigration probability [i, l]	0.4
Juvenile male maximum emigration probability [i, l]	0.9
Sub-adult maximum emigration probability (male & female) [a]	0
Adult maximum emigration probability (male & female) [a]	0
Alpha (slope of density-dependent function)	10
Beta (relative inflection point of density-dependent function)	1
Stochastic movement simulator settings[o]	
Perceptual range	500m
Perceptual range method	2
Directional persistence	5.0
Memory size (steps)	5
Goal type	2
Goal bias	2
Settlement parameters	
Female	Find a suitable patch + density dependence
Male	Find a suitable patch + density dependence + mating requirements
Maximum settlement probability (male & female)	1.0
AlphaS (slope of density-dependent function)	−10
BetaS (relative inflection point of density-dependent function)	1
Maximum number of steps [p]	2500
Minimum number of steps per year [p]	80
Maximum number of steps per year [p]	300

(a) Breitenmoser-Würsten et al. (2007), (b) Andren et al. (1997), (c) Breitenmoser-Würsten et al. (2001), (d) Jędrzejewsjki et al. (1996) (e) Vandel et al. (2006), (f) von von Arx et al. (2004), (g) Gaillard et al. (2014), (h) Schmidt et al. (1997), (i) Zimmermann et al. (2005), (j) White et al. (2015), (k) Hetherington and Gorman (2007), (l) Samelius et al. (2012), (m) Vandel et al. (2006), (n) Schmidt (1998), (o) SMS parameters, (p) according to a resolution map of 250m.

*according to lynx densities in the Alps; Optimal habitat cells were defined as those with values from 8 to 10, based on a reclassification into ten classes of the continuous layer according to a distribution of natural breaks; then this value was scaled linearly (from 8 to 4); for cells with value <4 the dependence of the strength of habitat specific density on fecundity (1/b) was set to 0, since these areas are generally highly impacted by human activity.

	Cell Value	1/b value
Carrying capacity in optimal habitat cells [(a)]	10,9,8	0.000465 ind/ha
Carrying capacity in optimal habitat cells	7	0.00023 ind/ha
Carrying capacity in optimal habitat cells	6	0.00012 ind/ha
Carrying capacity in optimal habitat cells	5	0.00006 ind/ha
Carrying capacity in optimal habitat cells	4	0.00003 ind/ha
Carrying capacity in optimal habitat cells	1,2,3	0 ind/ha

(a) Breitenmoser-Würsten et al. (2001).

Figure S7. Resulting AUC from the four different algorithms used in SDMtune

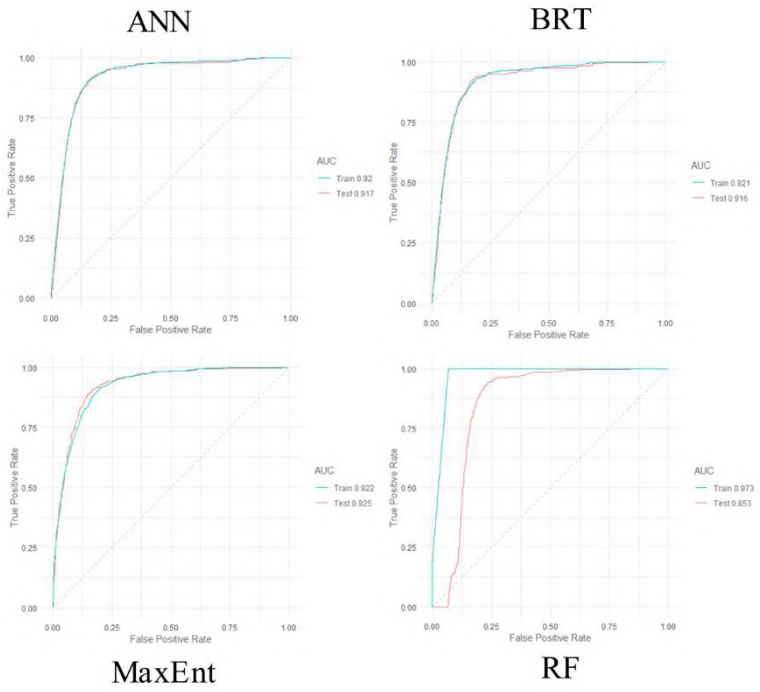


Figure S8. Response univariate curves from the ANN algorithm

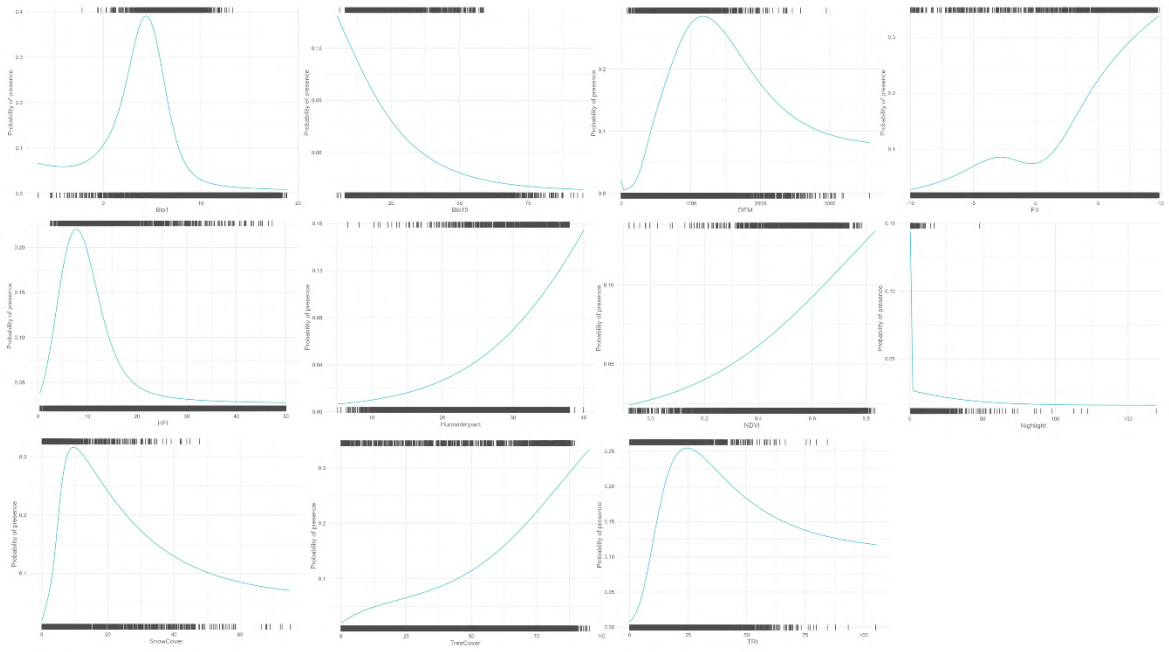


Figure S9. Variable importance means across the different algorithms

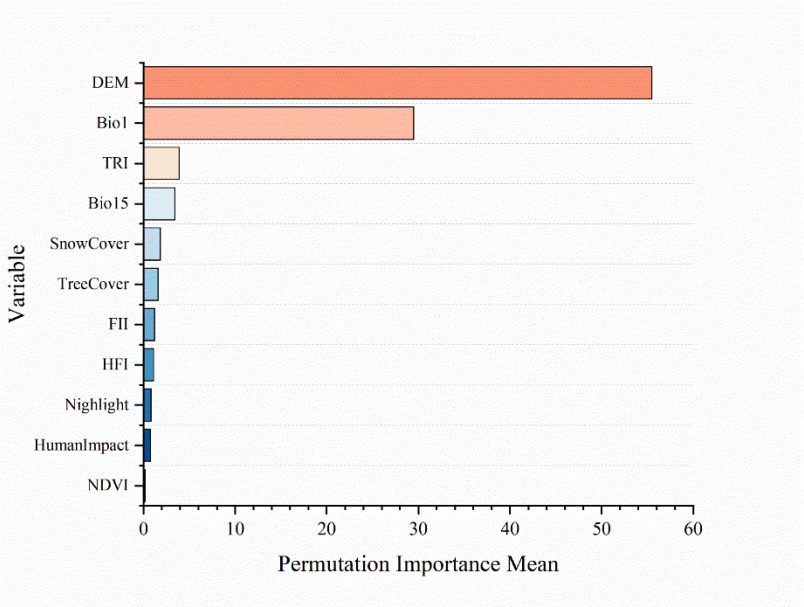


Figure S10. The calibrated SDM and the lynx occurrences used.

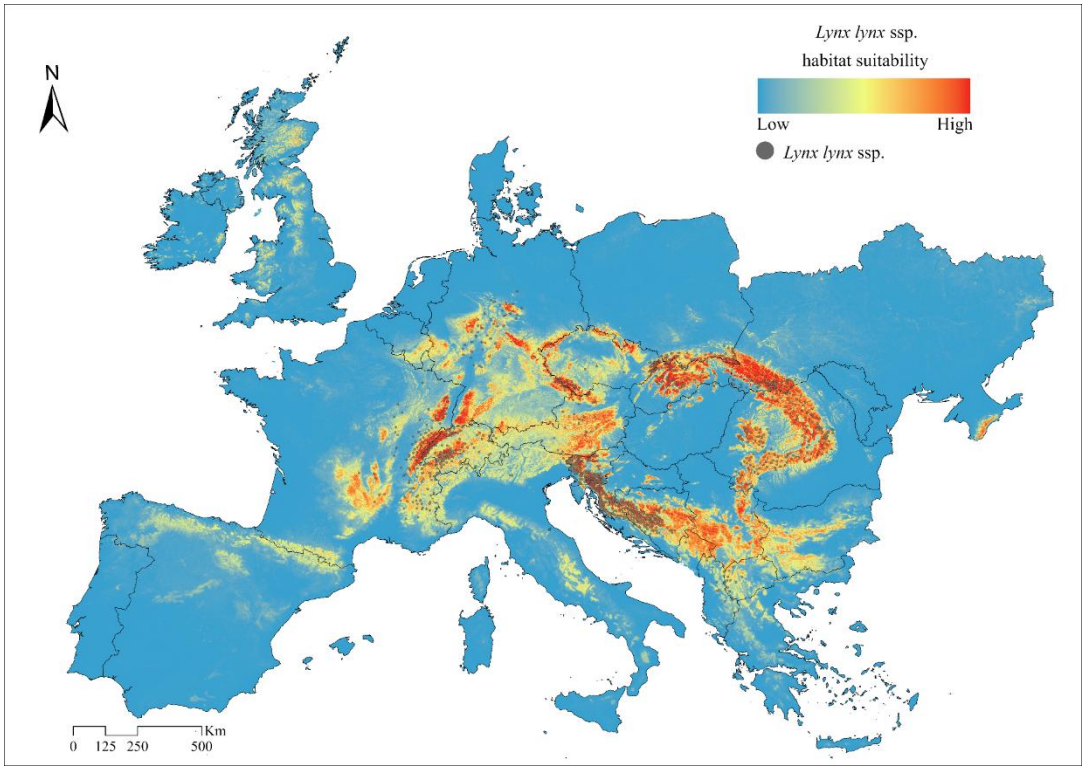


Figure S11. Model validation results comparing lynx telemetry data and null models (random distribution), showing a significative difference ($p<0.01$) in habitat suitability.

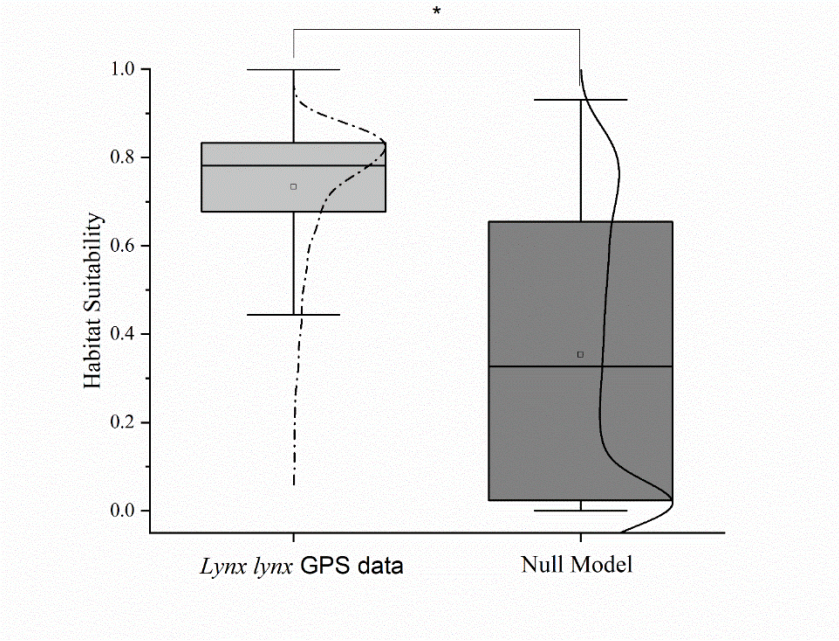


Figure S12. (a) PCA and niche overlap considering some of the most important variables: (b) DEM, (c) Bio15, (d) HFI, (e) TRI, and (f) Bio1.

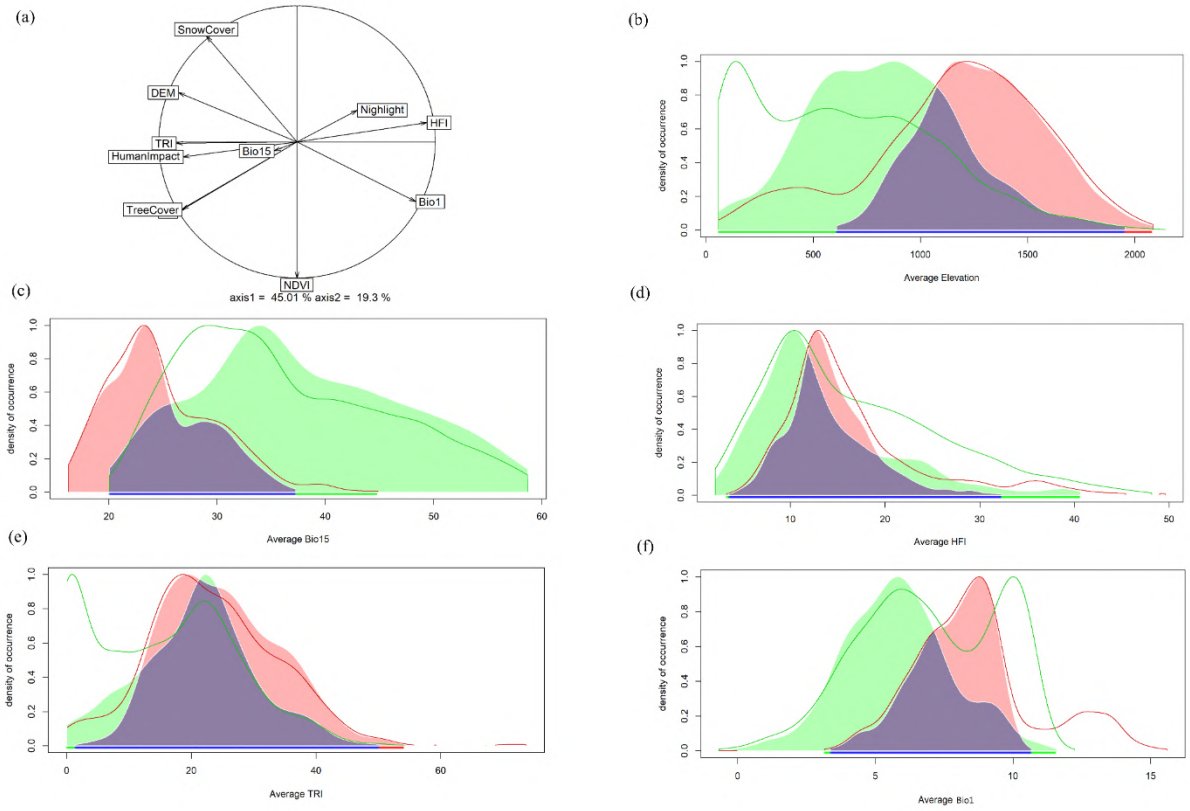


Figure S13. All the 450 identified sites in green. Most green sites are those always selected in the different scenarios.

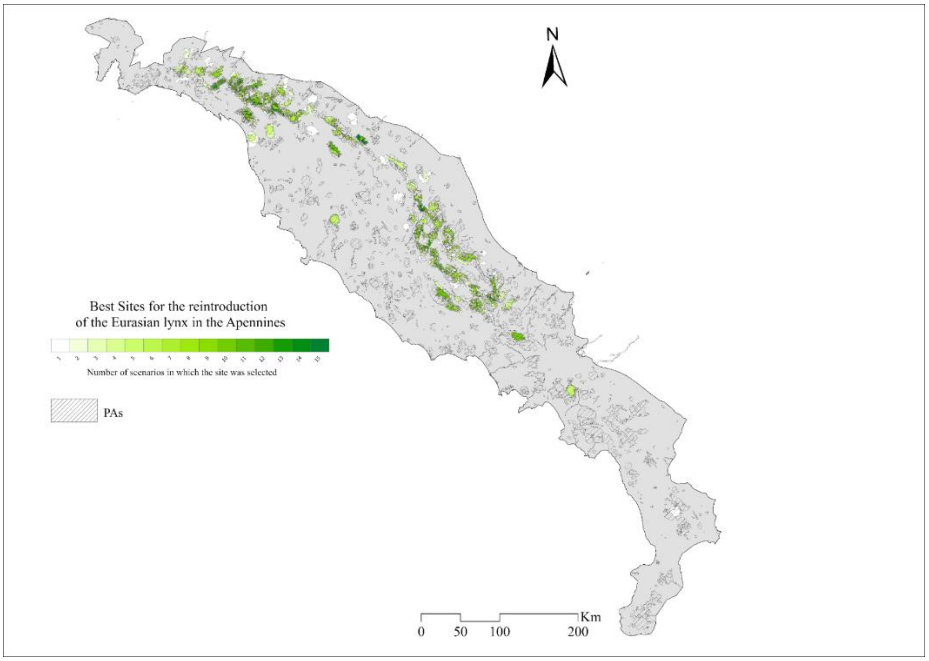


Figure S14. Reintroduction scenarios with a white-noise environmental stochasticity

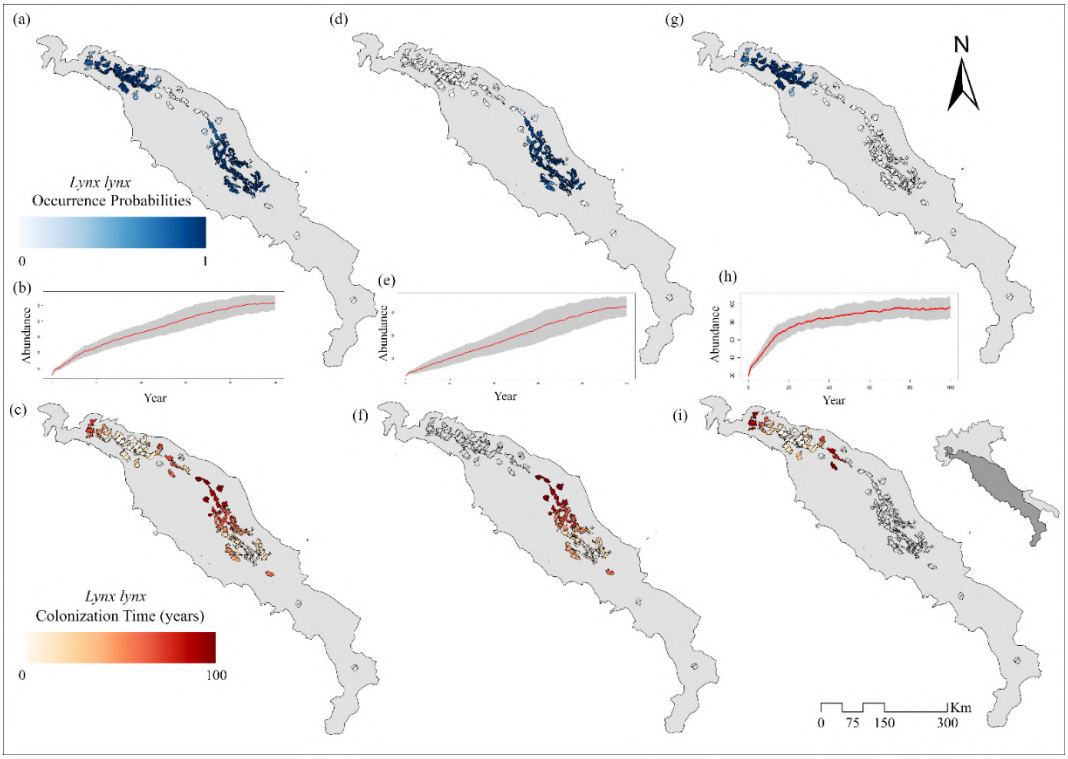


Figure S15. Reintroduction scenarios with a red-noise environmental stochasticity and increased mortality

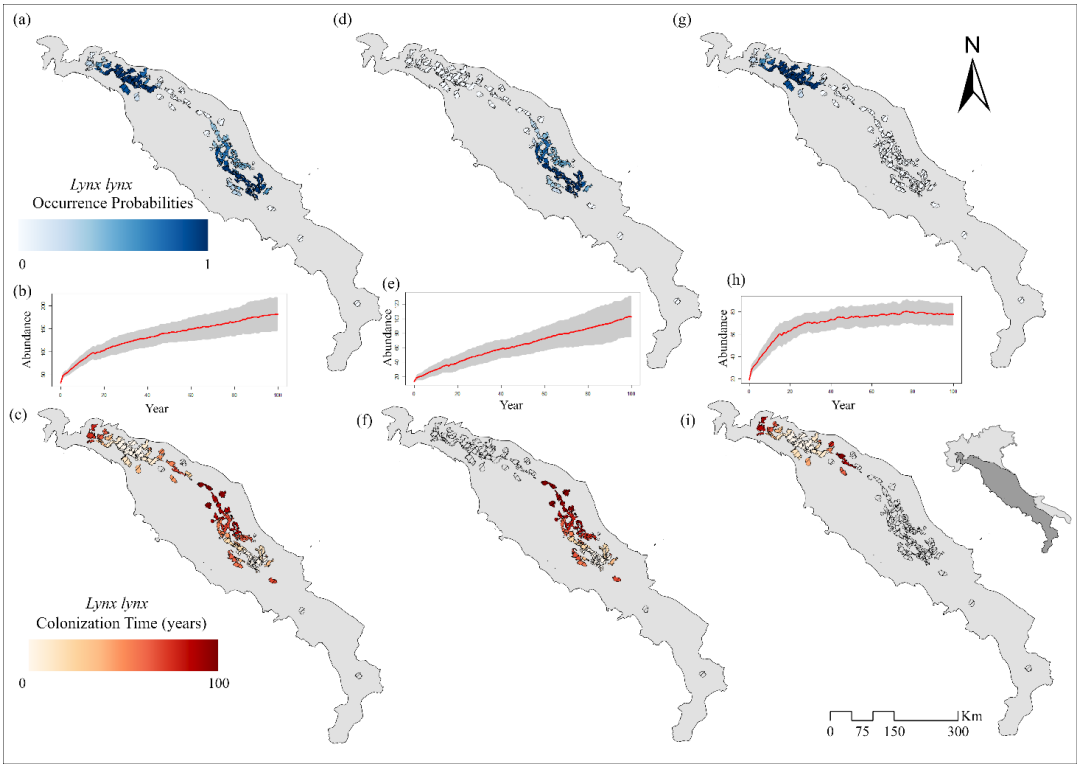


Figure S16. Reintroduction scenarios with a white-noise environmental stochasticity and increased mortality

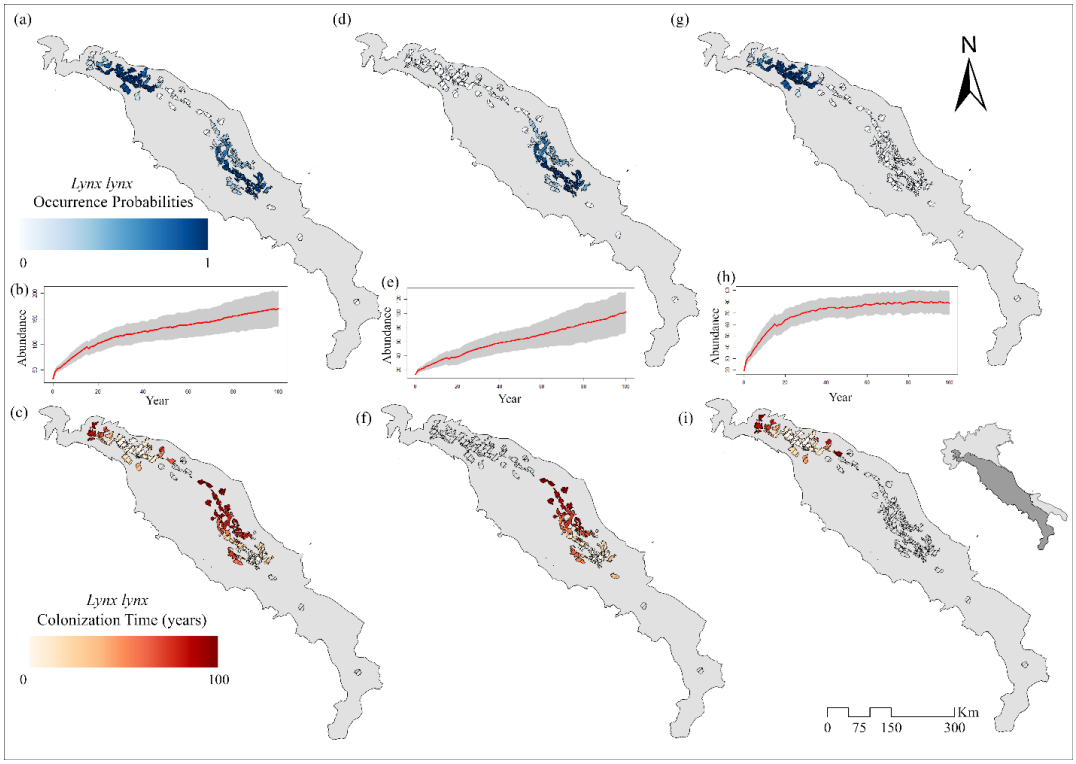
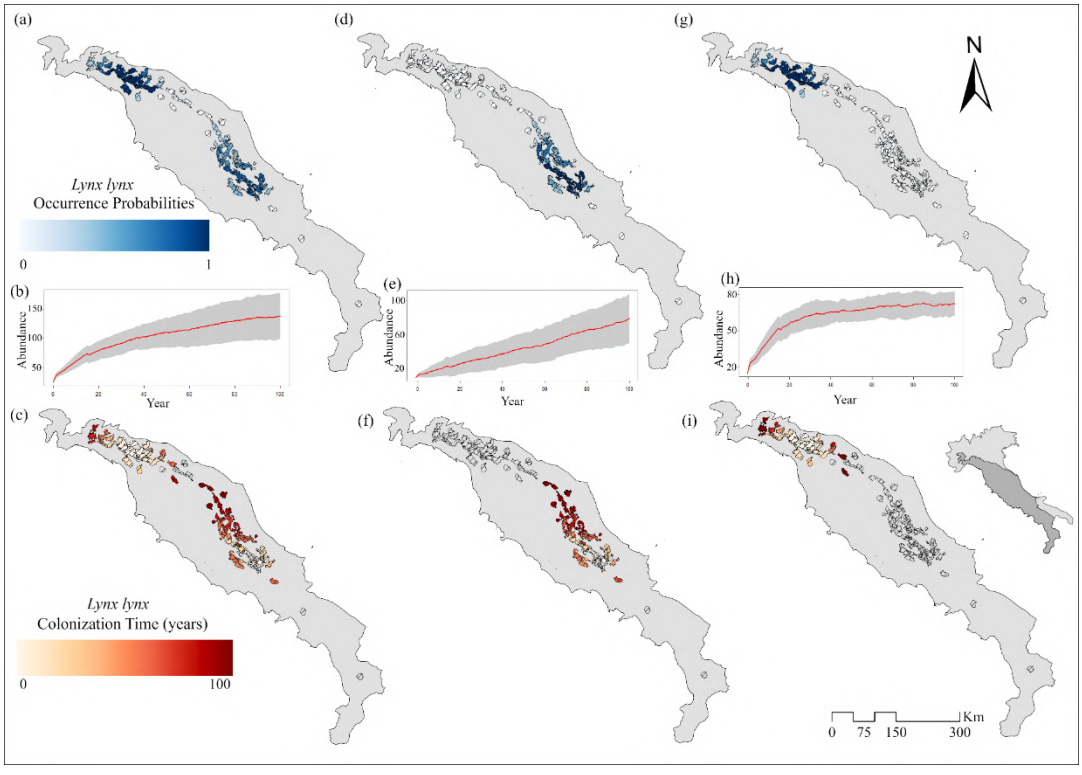


Figure S17. Reintroduction scenarios with using the same parameters as in Ovenden et al. (2019), with a red-noise environmental stochasticity



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Case Study II: Identifying crucial areas for preserving landscape connectivity in Europe

Introduction

Destruction and degradation of natural ecosystems are the primary causes of decline in global biodiversity [1,2]. Habitat loss is typically associated with landscape fragmentation, i.e., the division into smaller and more isolated fragments separated by a matrix of human-transformed land use. Humans modify ecosystems by converting land for agricultural, residential, or commercial use, building roads, railways, transmission lines, or by altering natural habitats through exploitation [3,4]. Currently 58.4% of terrestrial Earth is under moderate or intense human pressure [5]. The loss of extent of natural areas, the increase in isolation of habitat patches, and greater exposure to human activities along fragment edges initiate long-term changes in the structure and function of the ecosystems [6,7].

Ecologists agree that habitat loss is detrimental to biodiversity, but the extent to which habitat fragmentation itself is to blame is under debate [8–11]. Previous studies have consistently demonstrated strong responses of organisms and ecosystem processes to fragmentation caused by reduced fragment area, increased isolation, and the creation of habitat edges [12,13]. Decreased fragment area lowers animal residency within fragments, while increased isolation hinders movement among fragments, thereby reducing the likelihood of fragment recolonization following local extinctions [13]. Reduced fragment area and increased isolation generally lead to declines in the abundance of birds, mammals, insects, and plants [12,13]. Moreover, all aspects of fragmentation—reduced fragment area, increased isolation, and increased edge effects—consistently degrade a wide range of core ecosystem functions.

Considering the pervasive threats of habitat loss and fragmentation, conservationists recommended stop destroying habitat [14,15], and to ensure that natural habitat fragments remain connected [16,17], in order to support species movements and associated ecological processes. These solutions are challenging, especially in highly-modified areas, such as Europe [5], where preserving natural lands is even more difficult, considering the exponential growth of human population predicted in the next future.

To that scope, the establishment of protected areas (PAs) aims to preserve and protect biodiversity, and in Europe, among PAs, there are also Natura 2000 sites, designated under the Habitats Directive (92/43/EEC) and the Birds Directive (2009/147/EC). However, despite many positive outcomes at global [18] and European scale [19], in other cases this tool has proven insufficient to slow biodiversity loss [20–22]. Indeed, often PAs are constrained in size, ecological representation, and governance [23], with ≥90% occurring within a matrix of human-dominated, increasingly fragmented land [24]. As a result, PAs and the animal populations they harbor can become isolated, interrupting the ecological and evolutionary processes that maintain populations abundance, ecosystems functioning and diversity [13,25].

Thus, to enhance the conservation efficiency of PAs and promote biodiversity conservation, an expansion of the current network of PAs has been proposed during the 15th Convention on Biological Diversity (CBD, Montreal 2022) (ref. 1, Target 3), to achieve the protection of 30% of terrestrial land and marine areas in every ecoregion. To reach this target, the conservation

of the few remaining large natural habitat areas is insufficient, especially in highly-urbanized countries, so that the protection and restoration of many small habitat patches is required [26].

When prioritizing where to put or expand new PAs, it is important to consider the geographic and ecological coverage, total surface, and connectivity of native habitat areas [26]. Connectivity among PAs is essential because it ensures access to sufficient and complementary resources for wildlife when remnant habitat patches are too small for a single patch to sustain a population [26] and can therefore act as stepping-stones [27]. Connectivity is also fundamental when patches are larger, as movements between them decrease population extinction risk by maintaining gene flow and facilitating re-colonization [28] and may allow species to shift their ranges in response to climate change [26].

Considering the need to protect multiple species [29], even with different prerequisites, we need to define common key areas for their movement. There are different approaches for identifying priority locations for maintaining or restoring connectivity, with least-cost paths, least-cost corridors, resistant kernels, and methods applying circuit theory being among the most common [30–34]. All these approaches require a resistance layer reflecting resistance to movement. Some recent approaches aim to develop resistance surfaces that are "species-agnostic" in that they integrate assumptions of how individuals of multiple species are predicted to move in response to landscape context [35,36], to identify potential movement patterns of myriad species [37,38].

Usually, using maps of human footprint (i.e., representative of human modification to the environments) often serves as the basis of resistance under the assumption that maintaining connectivity through the most "natural" lands will provide the best opportunities for successful movement for the greatest number of species [39–44]. Furthermore, identifying connectivity priorities for "human-tolerant" [35] species compared to "human-sensitive" [35] species can be done using different transformations of human footprint data when creating maps of landscape resistance to movement [40,45].

Despite recent conservation policies that have recognized the crucial role of ecological connectivity, with related efforts to restore and protect areas important for connectivity, there is still a gap today on which areas are important for connectivity in Europe. In fact, while some studies have assessed landscape connectivity with multispecies approaches at global level [36,46] and several studies have been published in other continents [35,39,40,43], there are currently no studies focused on Europe, where only a few single species' level studies have been published [47], and others that have assessed climate connectivity [48].

Here, we aim to model landscape connectivity for multiple species at the European scale, considering different scenarios, where different traits, such as the size of the species and the dispersal ability, and the sensitivity to human disturbance are included. Furthermore, to test the reliability of our connectivity models, we validated them with independent GPS-movement data, a crucial but rarely applied step [49]. From the resulting maps, we identified important areas for connectivity throughout Europe, and then we assessed their level of protection, as well as the connectivity within the current network of PAs, to inform conservationists about current protection gaps and where to establish new PAs considering land's connectivity. We hypothesize that the highest connectivity is concentrated in areas with lower human impact [44], such as Scandinavia and the major European mountain systems, even if we expect that some corridors also persist in highly modified regions of Central and Southern Europe. Additionally,

we expect that protected areas host higher connectivity than unprotected ones. Finally, we anticipate that connectivity patterns under different scenarios will be significantly influenced by the size, dispersal ability, and sensitivity to human disturbance of the target species [35].

Material and methods

Study areas and target species

The study area is formerly Europe, including western part of Russia and countries outside of the European Union.

We selected 41 mammal species protected under the Habitat Directive (92/43/EEC) and 3 more species not protected, and we considered the size and the dispersal ability of each species using the COMBINE dataset[48]. Then, we computed a cluster analysis in the R environment[49], to obtain three final classes of sizes (small, medium and large size mammals) and four different dispersal thresholds (small, medium, long, and very-long dispersers).

Landscape resistance

We used the most recent map of human footprint index (HFI) at 1-km resolution (with Lambert azimuthal equal area projection) [52] global composite of variables that represent human impacts to natural ecosystem structure and processes such as roads and transmission lines, modified land cover (e.g., urban areas, agriculture, mines), and density of human population [52].

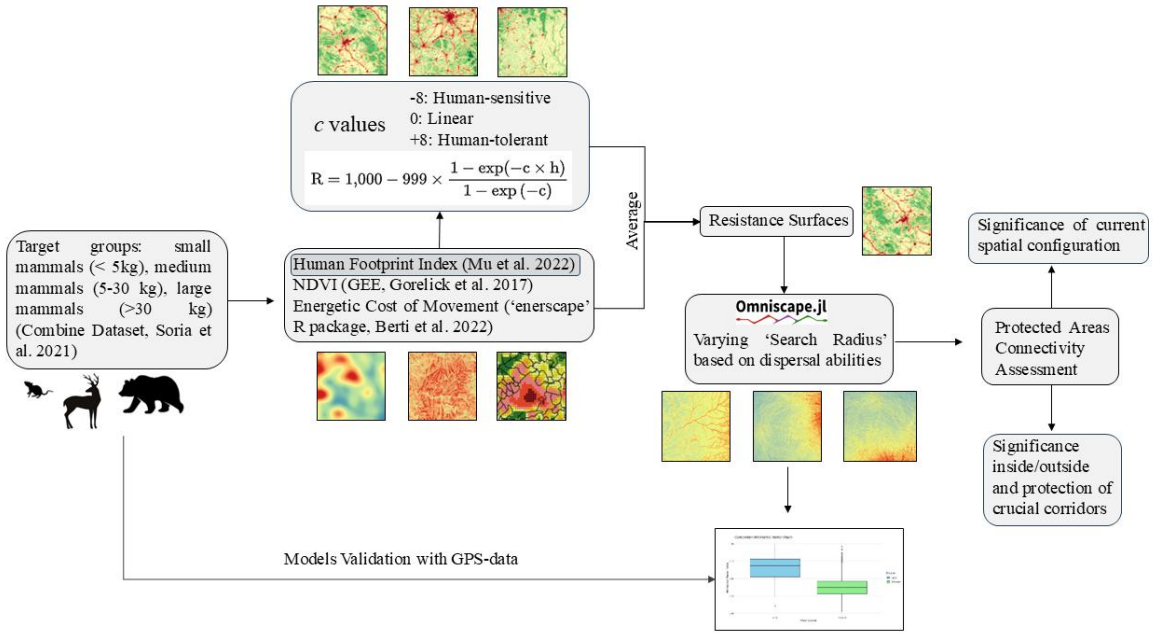


Figure 1. Schematic workflow reassuming the main processes performed: in the formula, *h* refers to human footprint, while *c* is the constant factor that determines the shape of the curves.

We assumed that movement of wildlife species is least disrupted on lands with lower human modifications. However, the degree of resistance to movement, along gradients of human modification are typically unknown. For some species (e.g., human-tolerant species like the

golden jackal, *Canis aureus*), low and moderate levels of human modification may have little effect on movement [53]. In these cases, only moderate to high levels of human modification may impede movement. For other species or processes (e.g., human-sensitive species like the brown bear, *Ursus arctos*), low levels of human modification may have a relatively large effect on movement. And, in other cases, movement may be resisted in a way that is proportional to the degree of human modification. These alternative ways that human modification may influence resistance can be represented spatially through alternative mathematical transformations of the human footprint layer. Here, we used three transformations [45] that represent landscape resistance as a function of habitat suitability for species-specific connectivity models. In our cases, we used the map of human modification as the basis of the species-agnostic resistance layer. We normalized the HFI layer into 0-1, reclassifying 0 with 0.001 (since 0 is considered as a non-passable barrier). Then, we used the function [45]:

$$R = 1{,}000 - 999 \times \frac{1 - exp(-c \times h)}{1 - exp(-c)}$$

To create three maps of resistance where h is the human modification index and c is equal to -8, 0.25, or 8 [35] representing resistance for human-sensitive species or processes, resistance that varies linearly with human modification, and resistance for human-tolerant species or processes, respectively (Fig. 1).

Furthermore, we used two other variables known to influence mammal's movements, namely the normalized difference vegetation index (NDVI) [36,54], and the Energetic Cost of Movement (ECM) [36,44,55].

The use of the NDVI reflects the assumption that in areas with high productivity mammals (both cursorial and arboreal) tend to move less, as they can gather sufficient resources to meet their requirements over a smaller area [54], compared with mammals living in areas with low productivity [44,56,57]. The concept of ECM has been developed to better understand how animals move in relation to physical features of the landscape and energetic costs of movement [58]. An energy landscape quantifies the energy costs of movement in a spatially explicit habitat and can be derived by understanding how metabolic and biomechanical processes are affected by physical factors of the environment [55]. To define the ECM, we used the 'enerscape' R package [55], which uses body mass information and the slope as a topographic characteristic, to create a landscape that reflects the energetic cost of movement. This map highlights regions that have high landscape connectivity based on movement efficiency, considering the energetic cost related to topography.

Thus, overall, we assumed that movement of wildlife species are least disrupted on lands with lower human modifications, and lower energetic cost of movement, and that species move more in low productivity areas, as demonstrated by the above presented studies.

After normalizing to 0-100 scale (i.e., the same scale of the resistance derived from the HFI layer), and resampling each variable to 250m, we integrated them together using a weighted mean, assigning higher weight (50%) to the HFI, and lower weight to ECM (25%) and NDVI (25%), given the greater support for HFI as the primary driver modifying species movement [35,36,39,43,44].

However, as a sensitivity analysis, we repeated the procedure in some specific areas, but using an arithmetic mean to create the resistance layers. We selected specifically some target areas where the greater weight of the human footprint index could have biased the results, detecting high connectivity values in areas rarely used by the species (e.g., mountains peaks). After repeating the analyses, we calculated the Pearson correlation index between the two normalized connectivity layers, and the Root Mean Square Error (RMSE).

Omniscape overview and parametrization

A crucial component when computing connectivity is the position of the nodes (e.g., the core areas from and to assess connectivity), and several studies proved how the position of the nodes can influence the resulting connectivity estimates [59]. Considering the model sensitivity to the number and location of the nodes, when their position is not well-known, new 'coreless' methods were developed, such as the 'wall-to-wall' or 'omnidirectional' current flows using circuit theory [33,60,61]. Omniscape is a recently developed circuit-theory technique that computes omnidirectional connectivity [62], producing three different outputs: a cumulative connectivity map (i.e., the total current flowing through the landscape), a flow potential map (the predicted flow without barriers), and a normalized connectivity map (calculated as cumulative connectivity divided by flow potential). The latter connectivity representation helps identify areas where current is impeded or channelized.

We used Omniscape v0.5.8 to run connectivity models in Julia [62]. Omnidirectional connectivity is assessed within moving windows where the center pixels constitute targets, while pixels within the moving window serve as sources of connectivity, which flow through the map of landscape resistance. Like other circuit theory models, movement of electrical current serves as a model metaphor for random-walking organisms moving through the landscape [32].

Omniscape parametrization requires defining source strength, blocking, and moving window size. Source strength of pixels constitutes the amount of current injected into a pixel and can represent locations of core habitat or known populations. Because our models are species- and population-agnostic, we did not use predetermined locations to represent variability in the sources of dispersing organisms. For our models, we used the inverse of the resistance surface as a source strength layer [35,60,62,63]. The 'block size' option allows to reduce computational time by coarsening the source strength layer. We evaluated processing time and sensitivity of spatial results by varying block sizes and moving windows, and then we chose to use a block size that is 10% of the size of the radius of the moving window. This choice reduced processing time with minimal conspicuous spatial artifacts associated with larger blocking sizes. We choose to vary moving window size according to the medium dispersal abilities of the species groups selected: small, medium and large mammals, based on the dispersal reported in the dataset COMBINE [50], and in other cases on what is reported in literature (Bowman et al., 2002). We choose: 5 km and 30 km, for small and medium mammals respectively. For large mammals, considering the different dispersal abilities, we choose two moving window sizes: 90 and 200 km. (e.g., [64–67]).

After completing the 12 Omniscape model scenarios (i.e., representing alternative scenarios using three resistance surfaces × four moving window sizes), we created composite scenarios, integrating all the scenarios together. Thus, we created the four single dispersal scenarios (by averaging the three resistance scenarios), and the three human-footprint scenarios. Then, we

normalized each average scenario to a 0-1 scale. We repeated the same procedure for the cumulative current flow maps, and in this case, after checking the distribution of the values using the 'hist' function in R, we transformed each map using the square root transformation, also creating other layers with values scaled to a 0-1 scale.

Model validation with independent GPS-movement data

We performed a model validation based on independent GPS-movement data. We compiled GPS-data across all Europe, selecting some of the species included in the model, for which telemetry data are available (Appendix S1). We resampled GPS-data to a frequency of 1 fix/48h, selecting only individuals collared for ~9 months, in order to consider differences in the seasonality. For our analyses, we selected a minimum of ~10 individuals for each population of target species, with exceptions made for some rare species (e.g., *Felis silvestris, Ursus arctos*). We conducted the validation phase at the individual level for each population of each target species. For each individual we created a minimum convex polygon enclosing all the GPS fixes, buffering it with ~10 km, and then assessing for this area of interest, if the movements of the individual *i* of the species *y* will fall in areas with higher connectivity values when compared with a null model (e.g., the same number of random points). To avoid problems of autocorrelation, when needed, we thinned the dataset to match the same resolution of the models (250 m), i.e., one occurrence/cell for each individual. We extracted connectivity values on the GPS-data occurrences and with the random-points, and then, we assessed any significant differences with a t-test. All the processes were implemented in R using the 'terra', 'sf', and 'tidyverse' R packages [68–70].

Furthermore, we fitted some integrated step selection functions (iSSFs) on different case studies (*x* species * *y* site), using the 'amt' R package [71]. While SSFs are estimated by comparing observed steps connecting successive animal locations to random steps, iSSFs include movement facets, allowing for simultaneous inference of habitat selection and movement processes. Thus, starting from the GPS fixes, we created the steps taken by each individual, then creating 10 random steps for each observed step, and extracting the connectivity values. Then, we transformed to a log scale the step length and we computed the cosen of the turning angle. Finally, we used the function 'fit_clogit' to fit the iSSF. The aim was to assess if long-distance movements follow paths of higher connectivity values compared to random movements.

Role of protected areas in determining connectivity patterns

To assess if the current spatial configuration of PAs plays a role in shaping connectivity patterns within the study extent, we set a randomization experiment [72,73]. First, we searched the World Database on Protected Areas (https://www. protectedplanet.net, accessed in June 2024) to retrieve the GIS layers of the protected areas falling within the study extent and belonging to IUCN categories I and II (i.e., nature reserves and national parks, respectively). As for focusing on the most important and representative protected areas, we extracted only areas with an area > 1 km^2. For each group of species, we first calculated the difference between the mean values of connectivity inside and outside of national protected areas, i.e., the observed ones. Then, we assessed the statistical significance of these observed differences by randomly generating 999 alternative configurations of the same number of original protected areas, changing their geographic position but not their extent. For each of these randomly generated configurations, we calculated the difference between the mean values of connectivity inside

and outside of simulated protected areas, thus obtaining a random distribution of differences. If, for a given species group, the observed difference fell above/below the density of 95 % of the simulated values, we then considered that difference as being lower/ higher than expected by chance.

Results

Normalized connectivity

The spatial patterns of normalized connectivity varied depending on the size of the moving window and the landscape resistance maps used (Appendix S3). Generally, smaller moving windows produced more fragmented spatial patterns of high normalized connectivity , while larger window sizes yielded more concentrated flows (Appendix S3). The composite maps combining the four-moving windows and the three resistance layers (Appendix S4-S5) showed several differences, with overall greater moving windows and lower human sensitivity producing clearer connectivity patterns. The composite map of normalized connectivity shows a consensus scenario among all the models (Fig. 2). High normalized connectivity occurs in Norway, southern Italy, and across the main European mountain systems, such as the Alps and the Carpathians (Figs. 2b and c). On the contrary, the lowest normalized connectivity in the composite map occurs in areas where relatively high development is adjacent to relatively natural lands (e.g., at the interface of the Padano plain and the Alps), not in the lands with the absolute highest resistance, such as in the most urbanized areas (Fig. 2).

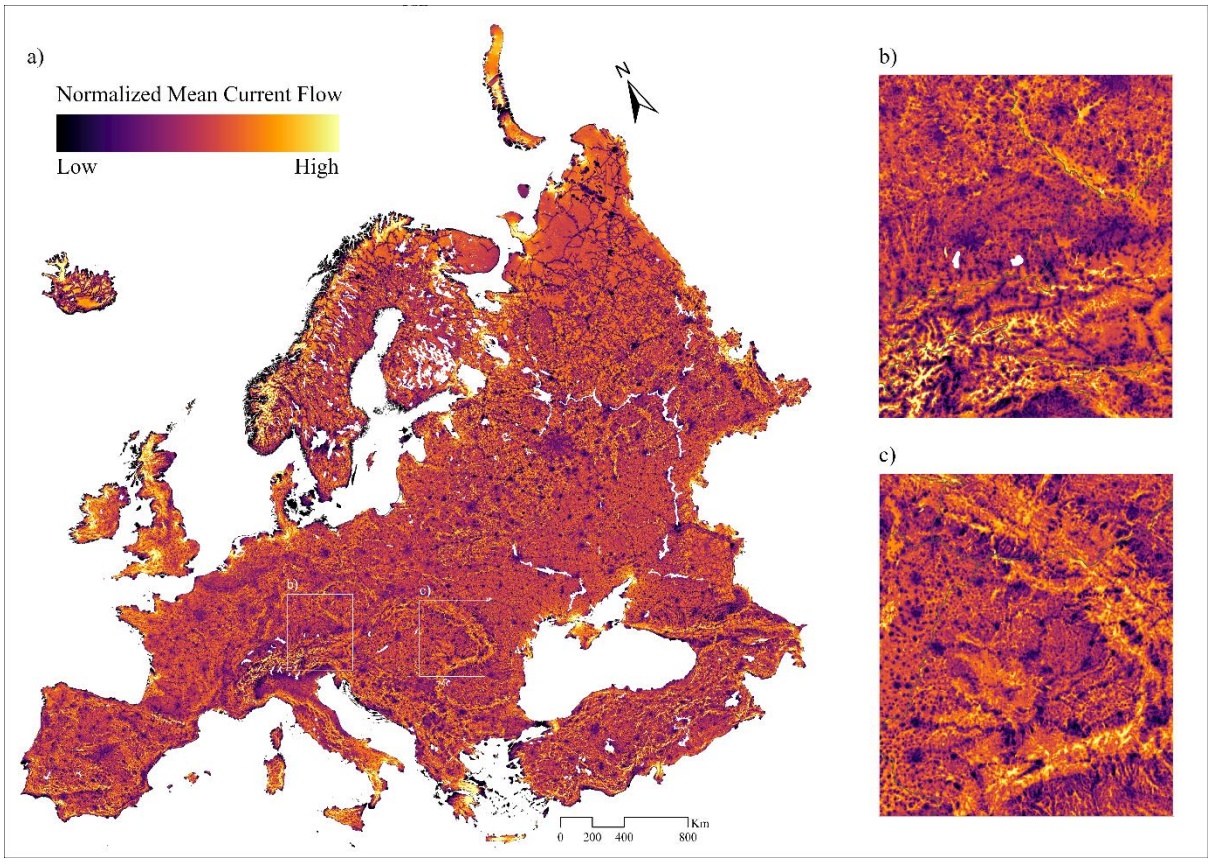


Figure 2. (a) Composite normalized connectivity map that combine all the 12 scenarios (4 dispersal thresholds x 3 resistance surfaces) obtained from Omniscape, and (b) a focus in the Alps, and (c) in the Carpathians.

When considering the composite cumulative connectivity map, higher values occur in northern Europe, especially in Scandinavia, and in the main mountain systems, such as the Alps and the Carpathians (Figs. 3a, b, and c). Still, moderate connectivity values are observed from the Dinaric Mountains to the Balkans, and in the Iberian Peninsula.

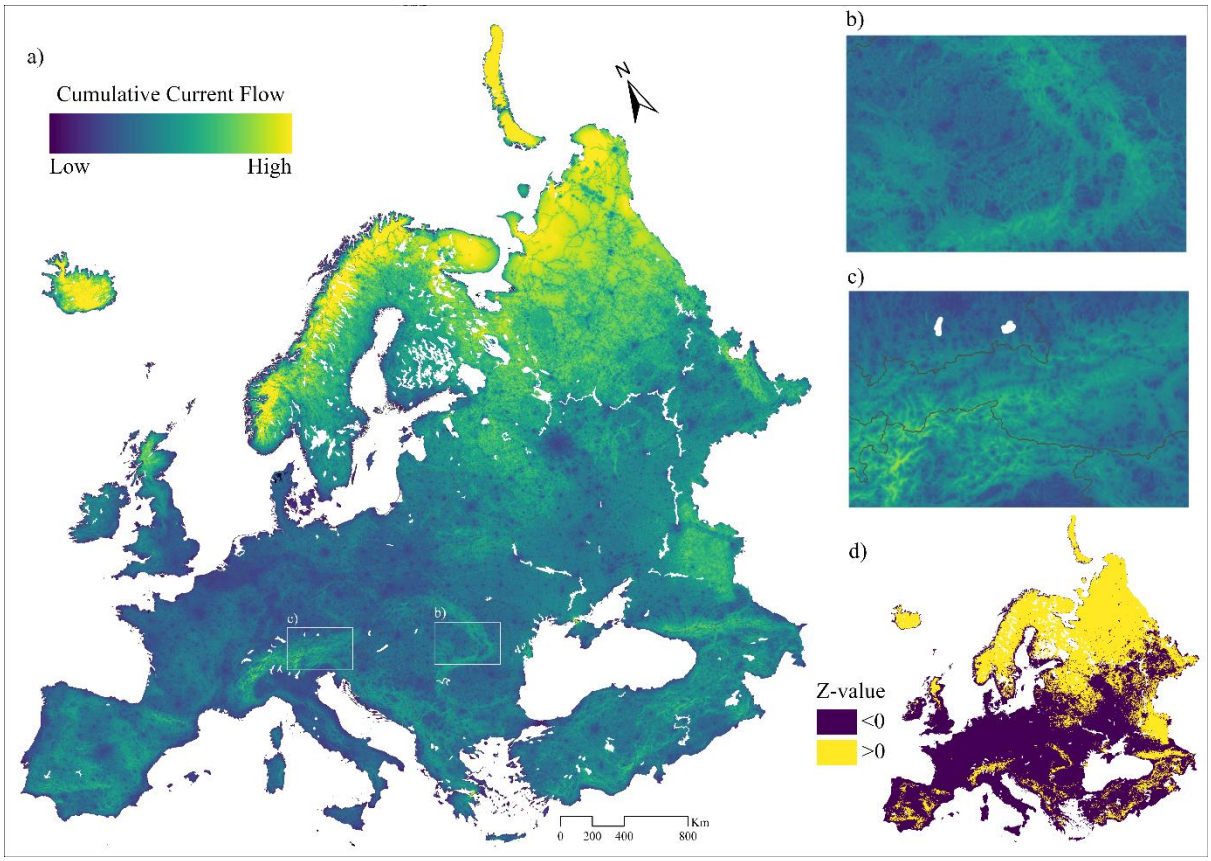


Figure 3. (a) Composite map of the 12 cumulative connectivity scenarios obtained from Omniscape, with a focus on (b) the Carpathians and (c) Eastern Alps, and (d) standardized version of the composite cumulative current map, showing areas where connectivity is above and below the mean.

The standardized cumulative connectivity map confirms this pattern (Fig. 3d). Low connectivity values occur elsewhere, especially in Central Europe, Italy and the UK (Fig. 3d).

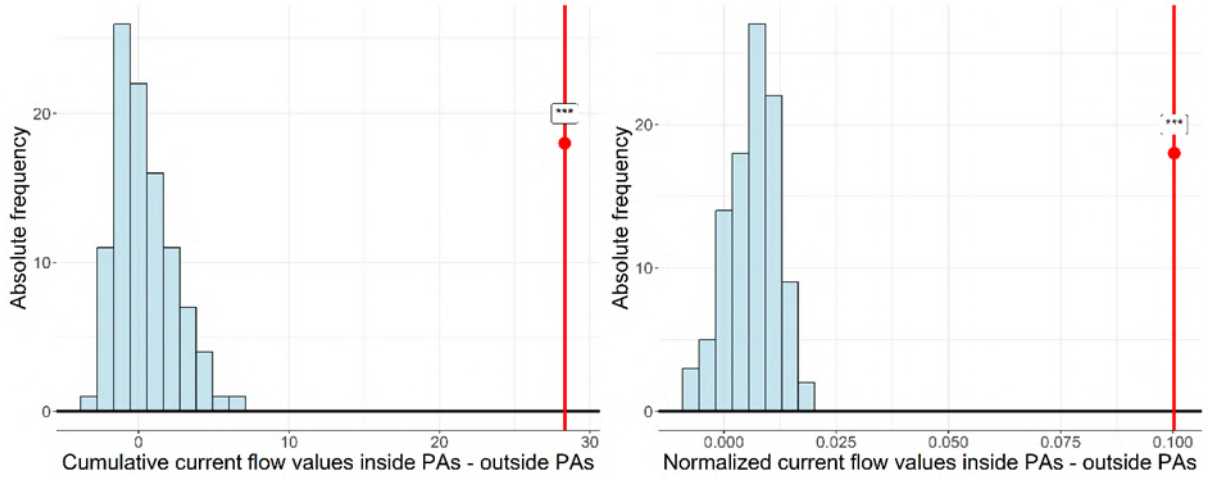


Figure 4. Azure bars represent differences of connectivity values inside and outside randomly simulated PAs, while red lines indicate observed differences. Left and right panels depicts randomized and observed differences as generated by cumulative and normalized connectivity values, respectively, showing statistically significant differences (p-value <0.001).

Overall, randomized landscape analysis showed that both cumulative and normalized connectivity values inside PAs are significantly higher than values occurring outside (p-value < 0.001; Fig. 4).

Considering the composite normalized connectivity within PAs for each country (Appendix S6), higher values occur in Slovenia, Lithuania, Albania and Bosnia and Herzegovina, while lower values are observed within the PAs of Hungary and Austria (Fig. 5a). In general, in EU countries Natura 2000 sites have higher normalized connectivity values than National and International designed PAs (Fig. 5a).

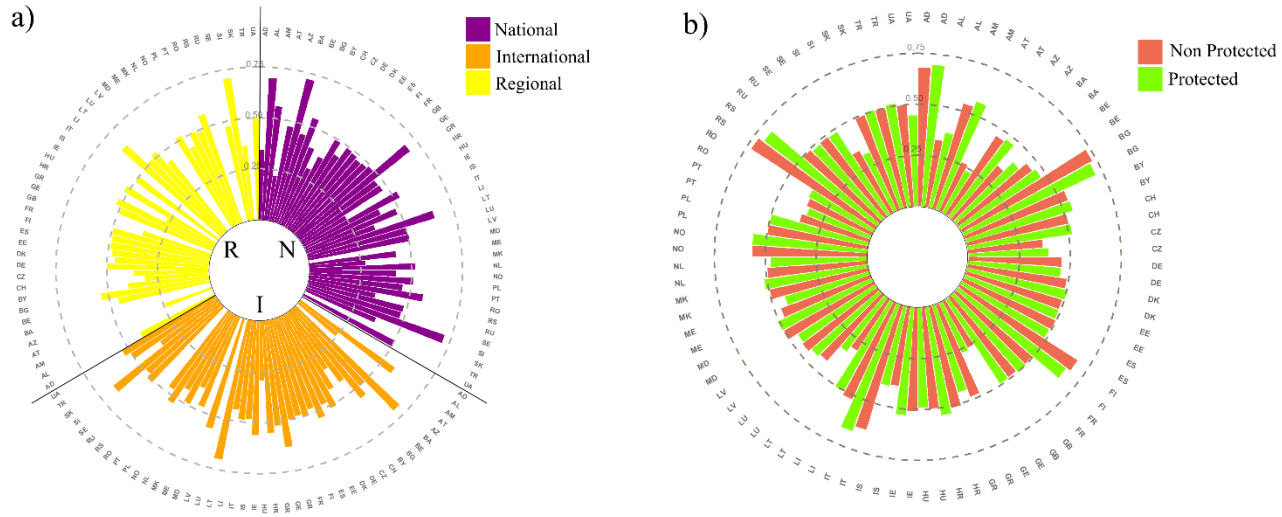


Figure 5. (a) Normalized connectivity values for the PAs in every country, considering Regional, National and International designations, (b) mean normalized connectivity values for each country within and outside PAs.

When assessing the difference in normalized connectivity within PAs and outside PAs for each country, in general, PAs host greater values, even if some exceptions exist (e.g., Austria) (Fig. 5b).

The reclassified map of the composite normalized connectivity map shows areas where the connectivity is impeded and channeled ('crucial normalized corridors') (Fig. 6a). From this map, crucial corridors (areas where the connectivity is channeled) are highlighted, spanning from Norway in Northern Europe, and in the Apennines in Southern Europe (Fig. 6a). Mountainous areas show a clear pattern, with channeled connectivity in the highest and wilder parts, and impeded flow in the valleys (e.g., in the Alps) (Fig. 6a).

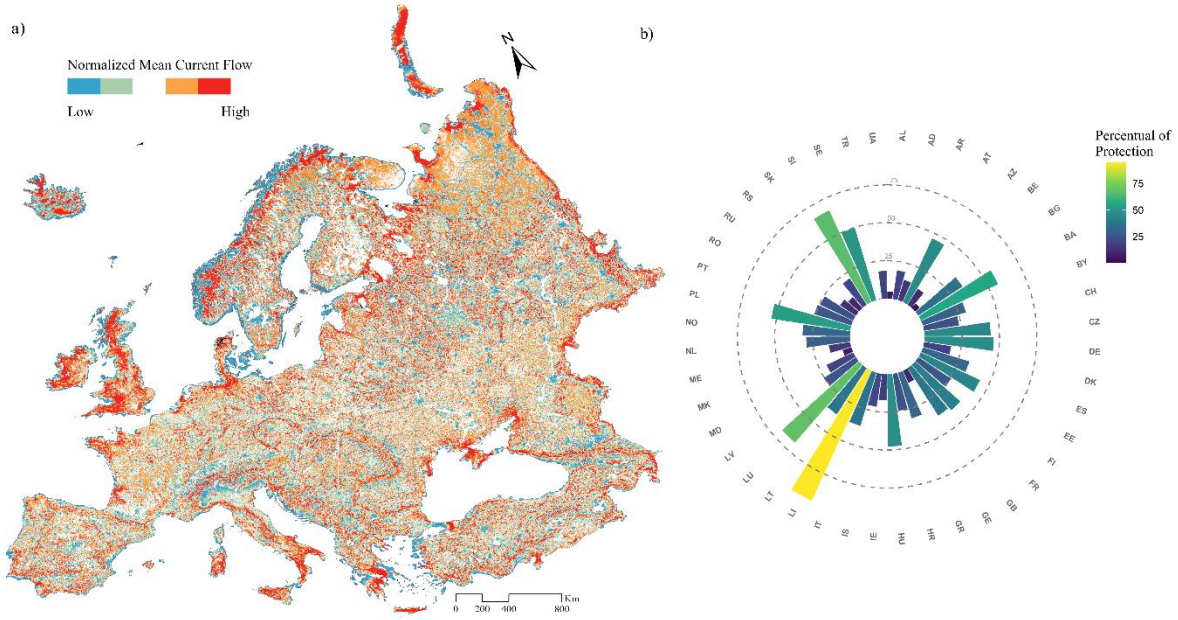


Figure 6. (a) Reclassified mean normalized connectivity values, showing areas with impeded flow (blue) and channeled flow (red), and (b) percent of the channeled corridors within PAs for each country.

The assessment of the level of protection of these crucial normalized corridors (Appendix S7), shows that only some countries have a high level of protection of these corridors, such as Slovenia, Bulgaria and Liechtenstein (Fig. 6b). Setting the target of protection to 30%, according to Target 3 of the CBD (i.e., legally protect 30% of land prioritizing ecological corridors), less than half of the countries considered exceed this threshold (Fig. 6b).

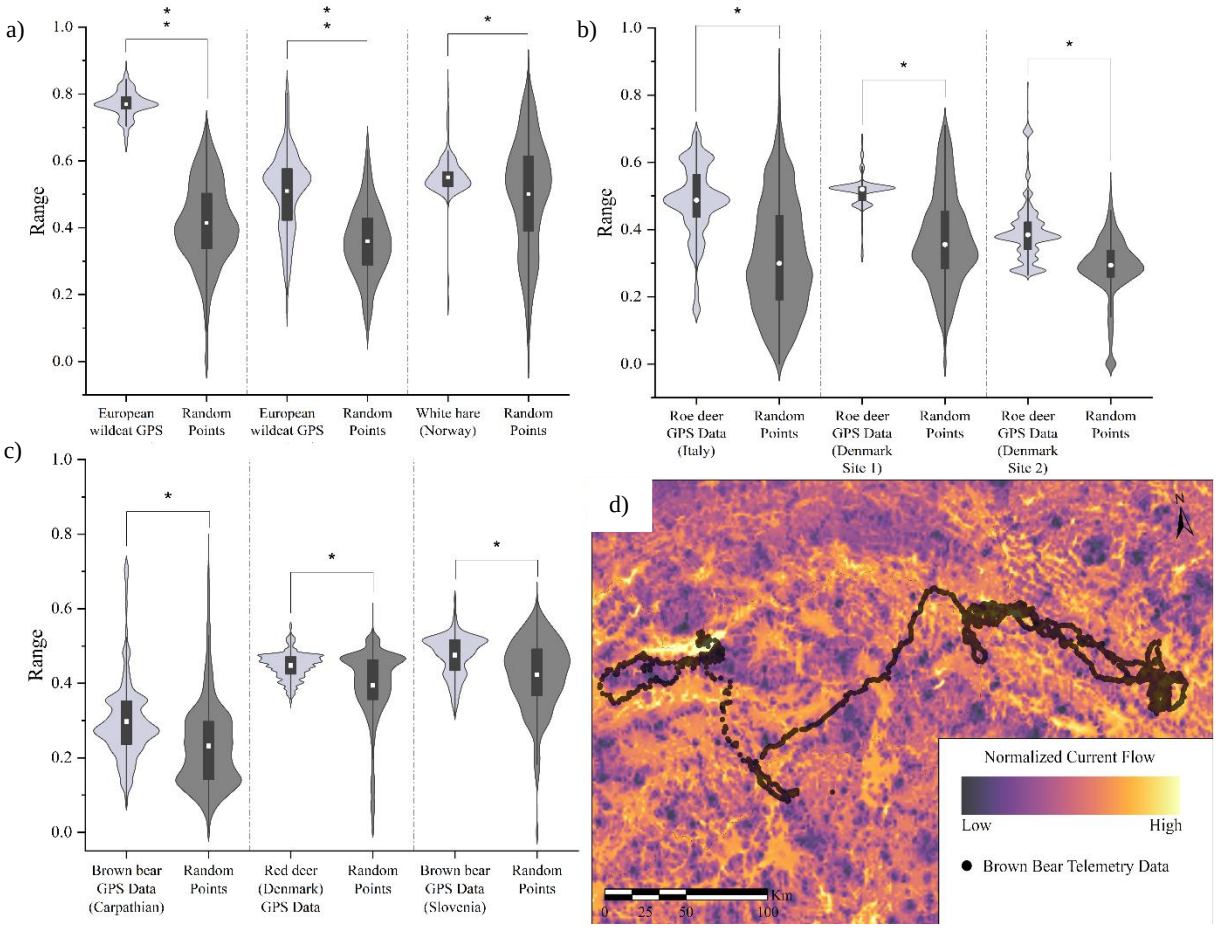


Figure 7. Validation phase using telemetry data for (a) small, (b) medium, and (c) large species (range in the y axis refers to connectivity values), and (d) the movement of a long-distance dispersing bear in the Carpathians [66].

The validation phase showed in most cases that telemetry data of the target species falls generally in areas with a significantly higher normalized current flow compared to null models (Figs. 7a, b and c; Appendix S8-13). In most cases, when inspected, the movement of the target species fell in areas where higher connectivity values were observed (Fig. 7d).

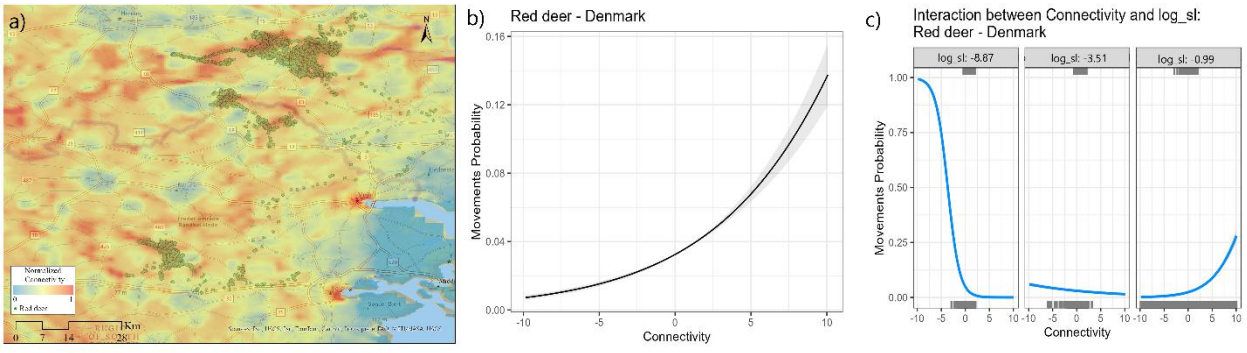


Figure 8. Results of the model validation using an iSSF function: (a) red deer GPS fixes in the study area (Denmark), (b) overall effects of connectivity on the movements probability, and (c) interaction between connectivity and movement patterns, with longer steps positively associated with connectivity increases.

Generally, the iSSF showed that movements of the target species are positively influenced by high connectivity values (Fig. 8; Appendix S15-19). In particular, in most cases the step length was greater in areas with higher connectivity values compared with areas with lower connectivity (Fig. 8; Appendix S15-19). However, some exceptions occurred in some specific areas, such as the Alps (Appendix S15-19).

Discussion

Deforestation and land conversion for agriculture and urbanization have reshaped temperate regions since the mid-18th century and continue today. Currently, 20% of the world's forests lie within 100 meters of an edge, often bordering human-modified landscapes, and over 70% are within 1 kilometer [13]. Cropland covers 1.53 billion hectares and is expected to expand by 18% by mid-century [74,75], while urban areas are projected to triple, reaching 0.18 billion hectares by 2030 [76]. The ability of remaining forests and other natural habitats to sustain biodiversity and ecosystem services will depend on the total amount and quality of habitat in fragments, the degree of connectivity among these fragments, and their resilience to other anthropogenic pressures, such as climate change and invasive species.

Our results from validated ecological corridors identify critical areas for multi-scale, species-agnostic connectivity planning in Europe. These areas could support the expansion of the current network of PAs in alignment with Target 3 of the Convention on Biological Diversity (CBD), which aims to conserve 30% of land, with the overarching goal of maintaining ecological connectivity between habitat patches, particularly those that are less impacted by human activity. Additionally, our composite maps highlight regions with consistently high current flow across models. Differences among the models offer alternative hypotheses regarding how organism movement varies in response to human impacts and species-specific movement abilities, providing insights for targeted conservation strategies.

While several studies have explored species-agnostic connectivity approaches in North America [35,77,78], no comparable studies currently exist in Europe. To date, only a few species-specific studies have been conducted at the European scale [47], and most multispecies connectivity research in Europe has focused on national or smaller scales [29,79]. Interestingly, our results reveal a pattern of ecological corridors that partially overlap with those identified for climate connectivity in Europe [48], particularly in regions such as the Apennines, the Alps, and the Balkan Peninsula. Our study highlights the critical role of natural and permeable anthropogenic landscapes in facilitating mammal movement and evaluates the performance of PAs in safeguarding critical connectivity zones. However, we do not explicitly assess PAs as potential sources or destinations of movement. As such, our continental-scale connectivity maps are most valuable for understanding the intensity and distribution of connectivity patterns independently of the existing PA network. To maximize their utility, these maps should be integrated with locally derived connectivity studies to effectively prioritize conservation actions at finer spatial scales.

Interestingly, the cumulative current map showed that Scandinavian countries generally host greater connectivity values. These findings are in line with another study [46] where climate connectivity among PAs was assessed through least-cost path, showing that Finland, Sweden

and Norway PAs perform well in covering climate connectivity (low climate connectivity failure).

In line with area-based conservation principles, it is essential to (i) protect and restore native habitats in all threatened ecoregions, (ii) conserve both large and small patches of native habitats, and (iii) prioritize habitats that enhance and support connectivity [26,80]. Our findings provide critical insights, particularly regarding the latter, by identifying areas that are important for connectivity and could inform the expansion of protected areas (PAs). These connectivity-important areas vary considerably in size, being smaller in Central Europe, where human alterations are more pronounced, and larger in Northern Europe. In Central and Southern Europe, PAs are generally small and densely distributed, making dispersal distance a key determinant of the connectivity provided by the network. This variation in PA arrangement reflects differences in landscape scale and socio-economic heterogeneity (e.g., expansive natural areas versus densely populated regions), which have distinct ecological implications [81] and require tailored conservation strategies.

Previous studies have demonstrated that the mean size of protected areas (PAs) is the strongest predictor of the amount of reachable habitat within a PA network, followed by the number of PAs [82]. However, establishing large PAs can be challenging in human-dominated landscapes, such as much of Europe [5]. In such contexts, an alternative strategy could involve creating smaller PAs that function as "stepping-stones" [27], facilitating species movement between larger habitat patches.

Protecting as much habitat as possible, regardless of the size, is pivotal [26]. The choice between large or small PAs must be contextualized, balancing conservation objectives with socioeconomic costs [83]. Our randomization experiment shows that the current PA network in Europe has significantly higher connectivity values than other possible configurations and, in general, we found higher connectivity values within PAs than outside, although there is some variation between countries.

Our models offer alternative hypotheses for how different organisms navigate landscapes with varying degrees of human modification, providing diverse predictions of movement patterns. These studies suggest that while some species can traverse suboptimal habitats, they tend to avoid areas of very poor habitat quality. Our species-agnostic models are grounded in the assumption that organisms avoid highly modified landscapes [44,84], incur higher movement costs in steep areas [55], and are less likely to cover long distances through regions of high productivity [54]. Unlike approaches that rely solely on human modification variables (e.g., [35]), our models incorporate additional factors, including areas with low human impact but high movement costs (e.g., mountain peaks) and varying productivity levels (e.g., forests versus deserts). These inclusions make our models potentially more realistic for reflecting diverse ecological contexts. Further research into the interplay between species movement, human modification, and climate could yield valuable insights for refining future connectivity studies. However, we acknowledge that our connectivity models are primarily informed by mammal movements and may not fully represent connectivity for other taxa or mammal species that are less sensitive to human impacts. Using circuit-theory techniques, areas with low normalized current flow may be difficult to distinguish from areas with impeded flow [35]. When using output maps to guide conservation priorities, areas with low to moderate current flow might be deemed less critical for connectivity. While the lowest current flow values often indicate unimportant areas, regions

with moderately low values could include some of the least fragmented lands in the study area. Conservation objectives in large, contiguous areas of low resistance (e.g., diffuse flow) differ significantly from those in regions of high resistance and high current flow (channelized" flow), which are considered more unambiguous indicators of connectivity [35]. Given this, we focused primarily on areas with the highest current flow values when assessing the protection status of critical corridors.

A potential limitation of our study concerns the connectivity patterns in certain areas, such as the Alps. Since the human footprint was the primary variable influencing the resistance layers, our models predicted high connectivity in steep, high-elevation areas that most species typically avoid, as confirmed by our analysis (Appendix S2-S16). This effect persisted even after accounting for the energetic cost of movement and remained present when using an unweighted mean to combine human footprint, energetic cost, and NDVI (Appendix S2). Consequently, our models may have limitations in providing conservation-relevant insights for these regions, and alternative approaches—such as species-specific models incorporating habitat suitability or quality layers—should be considered. Nonetheless, all the validation analyses indicated that, overall, our models effectively predict species movement across the landscape.

In conclusion, we present the first multispecies-agnostic assessment of functional connectivity at the European scale, validated using independent telemetry data. Our analysis evaluated connectivity within protected areas (PAs) for each country and identified existing protection gaps. These findings are particularly relevant for supporting the "30x30" Target, which aims to expand the current PA network in each ecoregion. This goal can be achieved by conserving the remaining large habitat areas and protecting and restoring smaller habitat patches in regions most affected by human activities, where meeting area-based targets will require a combination of protection and restoration efforts. Additionally, our connectivity models (e.g., Fig. 6) can contribute to achieving Target 3 of the Convention on Biological Diversity (CBD), which seeks to restore 30% of all degraded ecosystems to improve ecological integrity and connectivity. While our results provide critical insights into achieving these targets from a connectivity perspective, it is essential to consider additional factors, including habitat quality, ecological integrity, ecosystem services, resilience to climate change, associated costs, and land-use scenarios [85].

Appendix

Appendix S1. Species and relative traits considered for connectivity modeling.

Species	Adult mass (g)	Dispersal ability (km)	Habitat Directive	Maximum dispersal (km)	Validation Phase
Marmota marmota latirostris	NA	NA	Yes	NA	No
Sus scrofa	135.000,00	16	No	307 km	Yes
Martes martes	1.299,00	1.225	Yes	NA	No
Genetta genetta	1.866,00	1.494	Yes	NA	No
Galemys pyrenaicus	60,735	1.647	Yes	NA	No
Herpestes ichneumon	2.950,01	1.922	Yes	NA	No
Lepus timidus	3.027,00	1.949	Yes	NA	Yes
Lepus europaeus	3.673,00	2.168	No	17 km	Yes
Nyctereutes procyonoides	4.232,00	2.344	Yes	NA	No
Canis aureus	11.000,00	3.963	Yes	223	No
Gulo gulo	12.792,00	4.307	Yes	NA	No
Vormela peregusna	542,50	4.817	Yes	NA	No
Castor fiber	19.000,00	5.353	Yes	70–80 km	No
Hystrix cristata	19.166,00	5.379	Yes	NA	No
Capreolus capreolus	21.524,00	5.754	Yes	32.2 km	Yes
Mustela putorius	809,00	5.859	Yes	NA	No
Cervus nippon	52.999.00	9.411	Yes	NA	No
Capra pyrenaica	60.898,77	10.159	Yes	NA	No
Dama dama	63.612,00	10.405	Yes	NA	No
Vulpes lagopus	3.600,00	12.176	Yes	NA	No
Rangifer tarandus	101.250,00	13.436	Yes	NA	No
Felis silvestris	5.036,54	14.354	Yes	NA	Yes
Cervus elaphus	160.166,00	17.291	Yes	NA	Yes
Lynx pardinus	10.225,00	20.307	Yes	NA	No
Ursus arctos	240.500,00	21.623	Yes	467 km	Yes
Alces alces	359.750,00	26.984	Yes	300-800 km	No
Lynx lynx	21.150,00	28.994	Yes	450 km	No
Canis lupus	29.190,00	33.953	Yes	1092 km	No
Bison bonasus	624577.07	36.549	Yes	NA	No
Sicista betulina	8,92	0.079	Yes	NA	No
Sicista subtilis	11,75	0.092	Yes	NA	No
Muscardinus avellanarius	27,315	0.146	Yes	NA	No
Microtus oeconomus	33,1	0.163	Yes	NA	No
Chionomys nivalis	42,01	0.185	Yes	NA	No

Myomimus roachi	44,00	0.19	Yes	NA	No
Microtus cabrerae	52,5	0.21	Yes	NA	No
Dinaromys bogdanovi	56,00	0.217	Yes	NA	No
Mesocricetus newtoni	105,00	0.307	Yes	NA	No
Glis glis	140,045	0.36	Yes	NA	No
Spermophilus citellus	228,5	0.471	Yes	NA	No
Cricetus cricetus	400,00	0.64	Yes	NA	No
Crocidura sicula	10,84	0.708	Yes	NA	No
Mustela lutreola	566,44	4.92	Yes	NA	No
Rupicapra pyrenaica ornata	31.633,00	7.1	Yes	NA	No
Ovis gmelini musimon	110.000,00	14.63	Yes	NA	No

Appendix S2. Weights assignment for the resistance layer and sensitivity analysis.

To create the resistance layer used for the connectivity assessments, we used a weighted mean, giving more weight to the Human Footprint Index (HFI) (50%), then to the Energetic Cost of Movement (ECM) (25%) and the NDVI (25%).

This choice is motivated by the high availability of studies that have demonstrated the predominant influence of human activities on species movements (e.g., Ayram et al., 2017; Barnett and Belote, 2021; Belote et al., 2016, 2020, 2022; Brennan et al., 2020, 2022; Cushman and Landguth, 2012; Dickson et al., 2017; Krosby et al., 2015; Tucker et al., 2018), while fewer studies have demonstrated the same for ECM (e.g., Brennan et al., 2022; Carter et al., 2024; Rahimi et al., 2024) and NDVI (e.g., Brennan et al., 2022; Broekman et al., 2024; Muratet et al, 2013; Pettorelli et al., 2011). Furthermore, having selected different species, it is likely that they can react in the same way to HFI, but not to NDVI or ECM. In fact, some species can still select very steep areas or at high altitudes, rather than valleys with high human impacts.

However, since our framework could produce biased results in some specific areas (e.g., the Alps), detecting high connectivity values in high and steep areas, since the valleys are generally high level of urbanization, we decided to run a second analysis, using a simple mean to create the resistance layer, and then repeating the connectivity assessments. Then, we computed the Pearson correlation Index between the two normalized connectivity layers (i.e., the original one obtained with the weighted mean, and the new one with a simple mean), and calculated the root mean square error (RMSE), to assess for high differences between the two scenarios.

We selected two study areas (i.e., the Alps and Scandinavia) where our original models showed in some cases divergences between areas of high connectivity and areas where species actually moved.

The results (Figures S1 and S2) showed that despite some differences, especially in the high altitudes, the connectivity models in the Alps are quite similar, as demonstrated also by the RMSE, which scored 0.089. Similarly, in Scandinavia, the models were similar, with a RMSE of ~0.05, and with the same pattern of connectivity in the narrow portions of land close to the coast, especially in Norway.

Figure S1. Results of the sensitivity analysis in the Alps: a) normalized connectivity obtained using a simple mean between HFI, ECM and NDVI, b) normalized connectivity obtained with the original weighted mean between HFI, ECM, and NDVI, and c) Pearson correlation Index and RMSE between the two models.

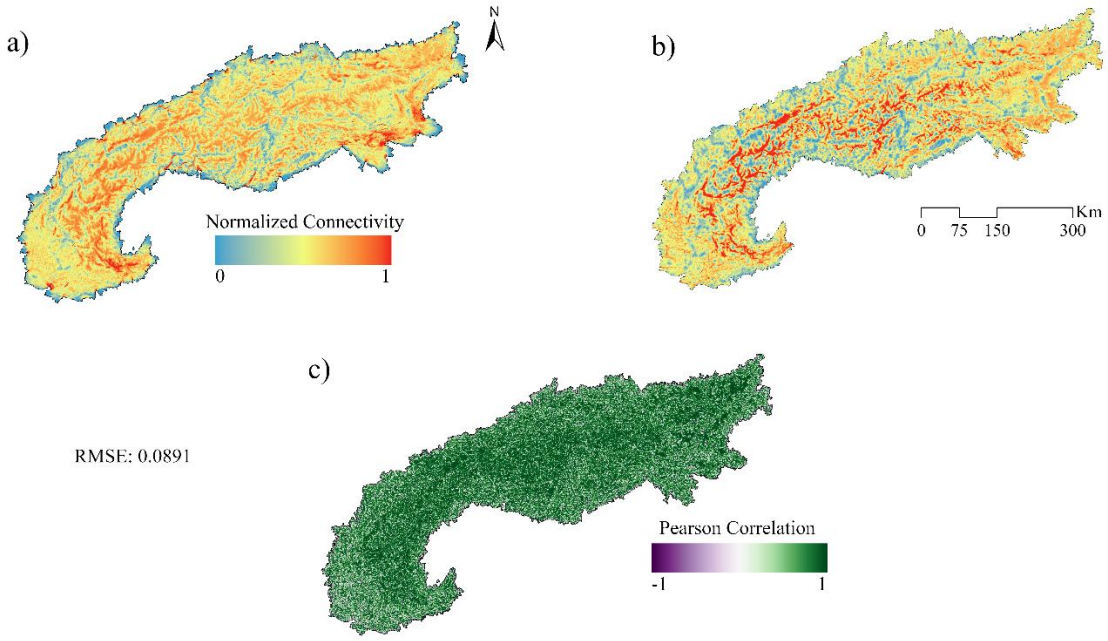
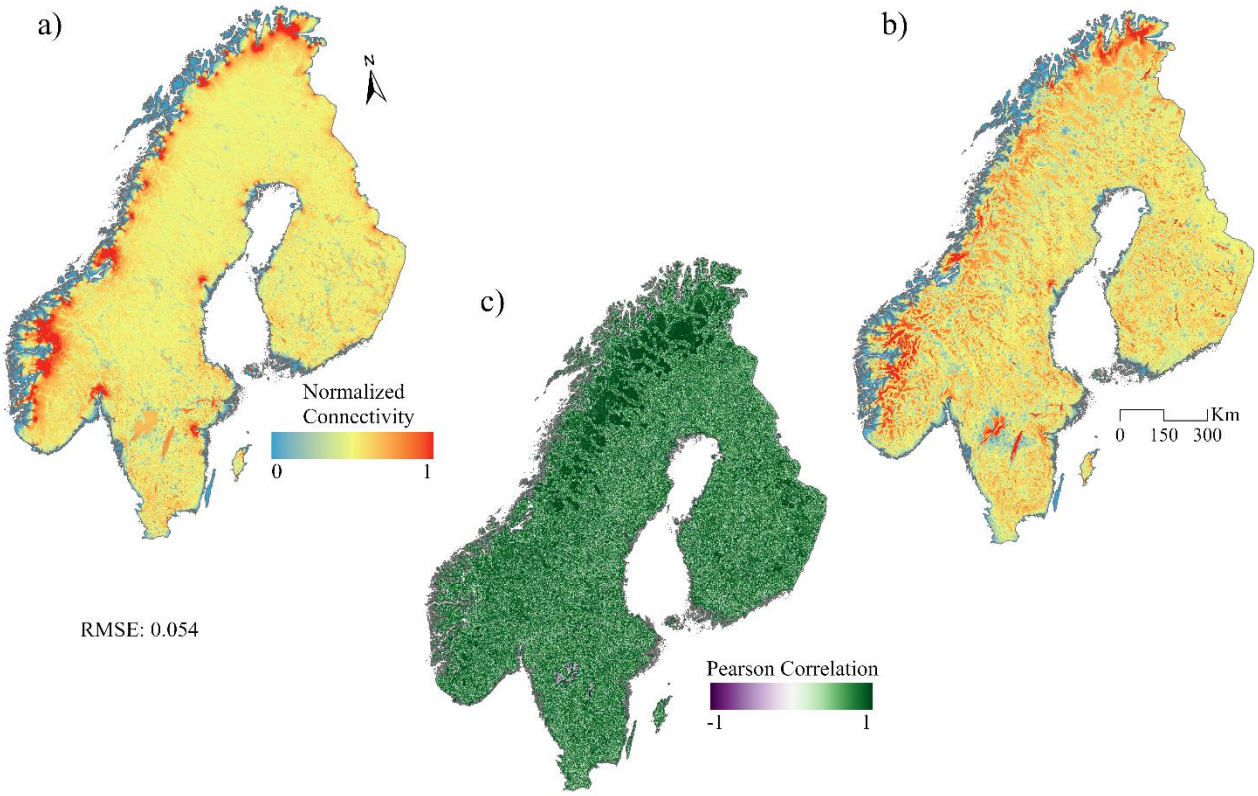
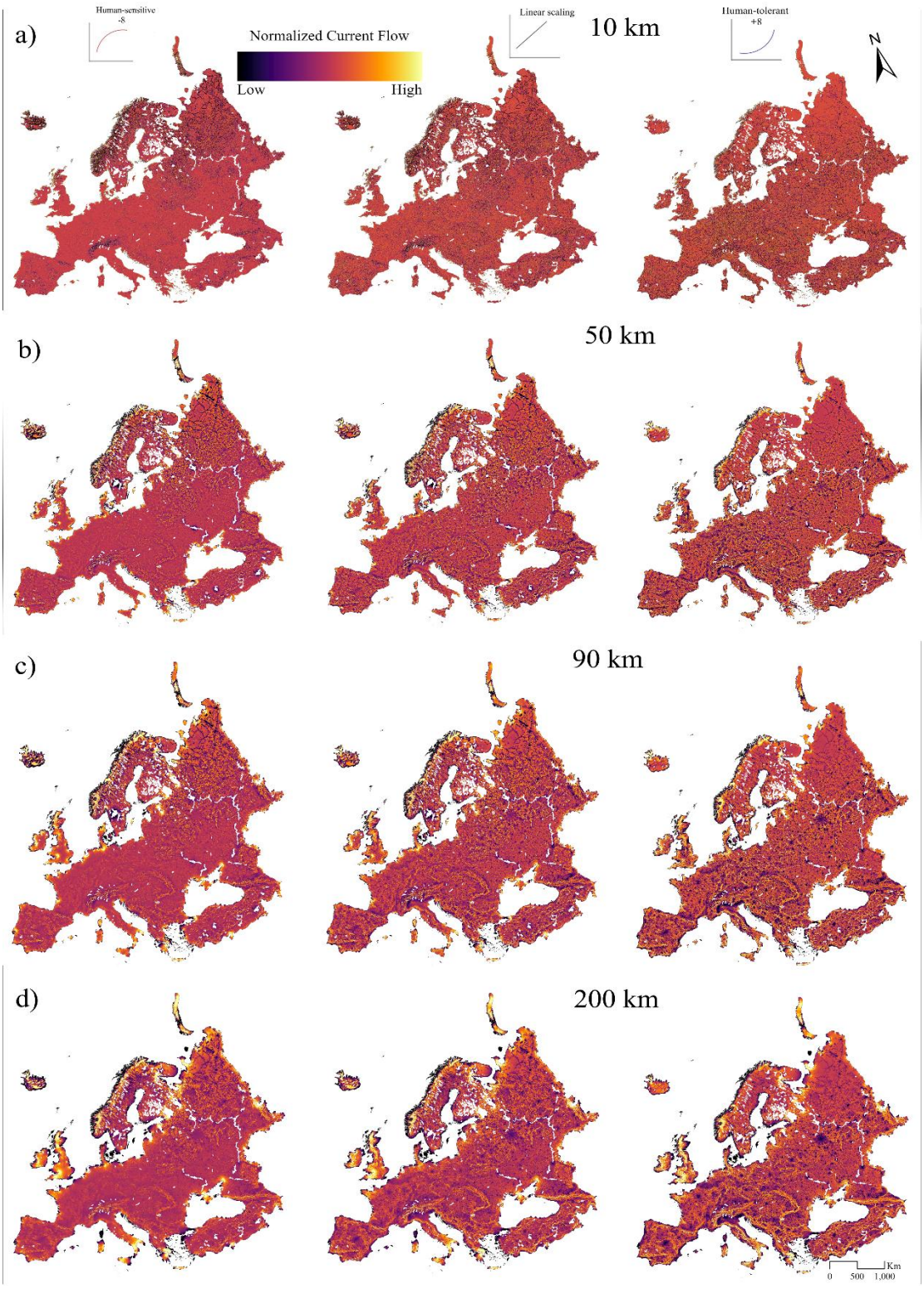


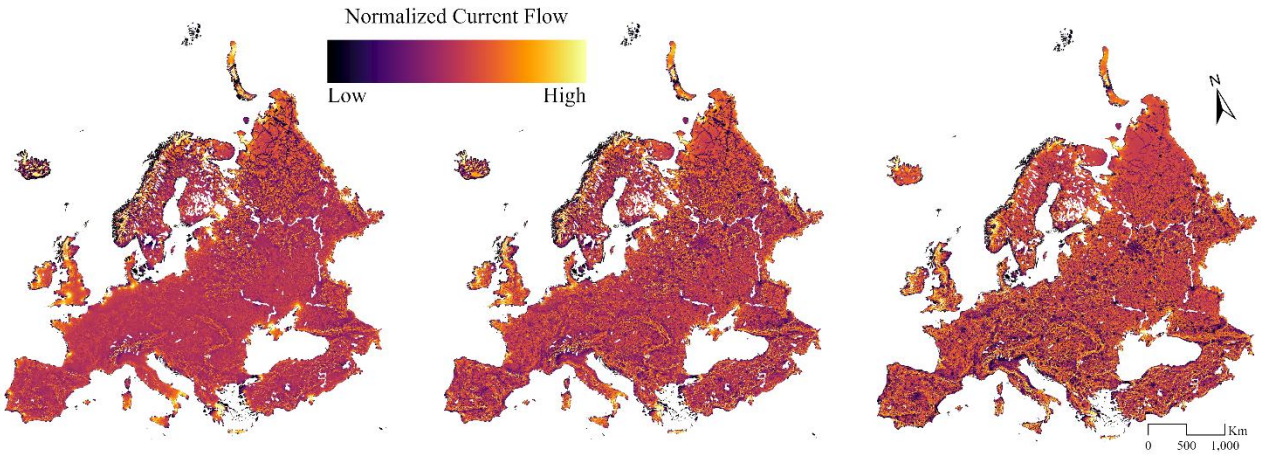
Figure S2. Results of the sensitivity analysis in Scandinavia: a) normalized connectivity obtained using a simple mean between HFI, ECM and NDVI, b) normalized connectivity obtained with the original weighted mean between HFI, ECM, and NDVI, and c) Pearson correlation Index and RMSE between the two models.



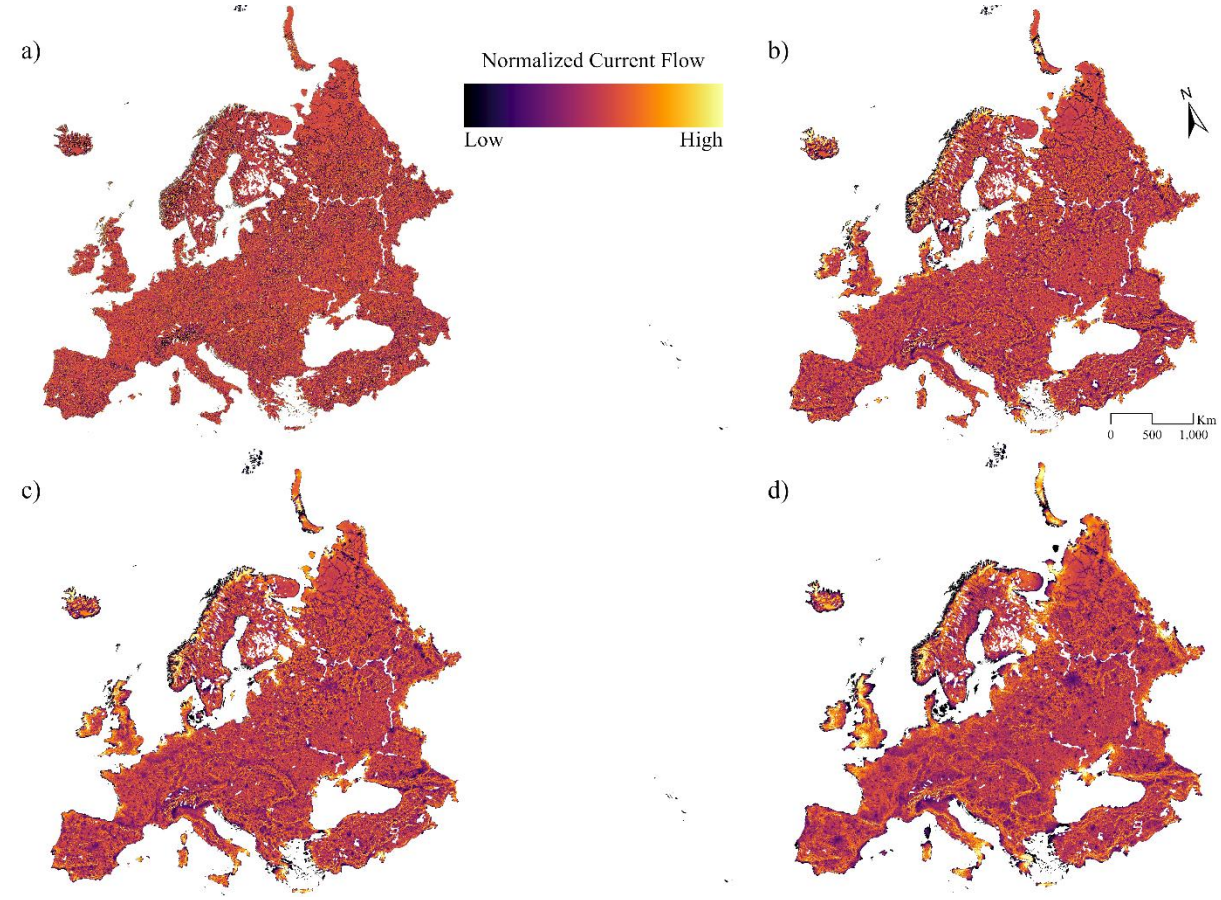
Appendix S3. All the scenarios of normalized current, combining the four moving-window within the three resistance maps.



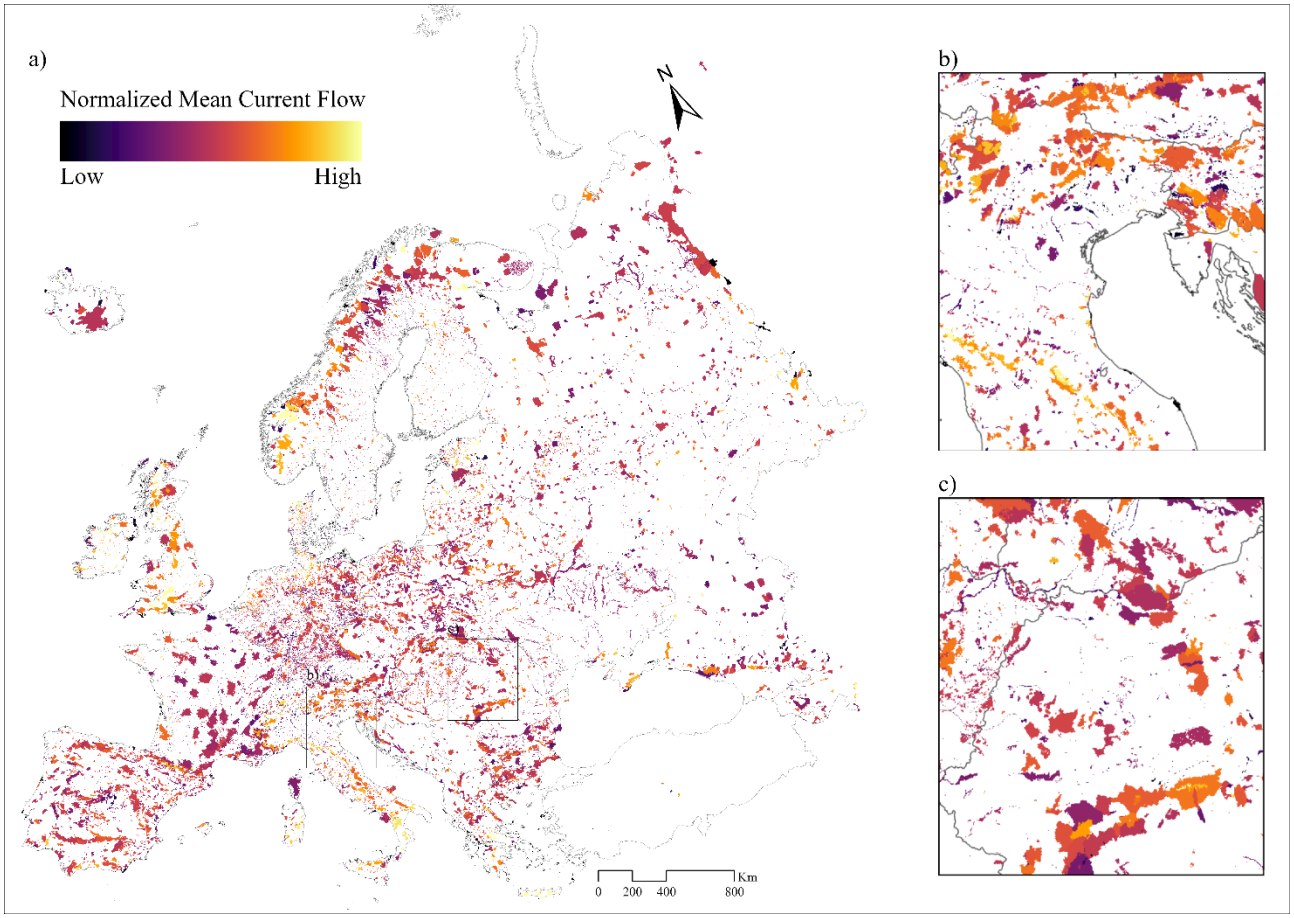
Appendix S4. Composite normalized current maps, combining the four moving-window within the three resistance maps: (left) human sensitive, (center) linear, (right) human-tolerant.



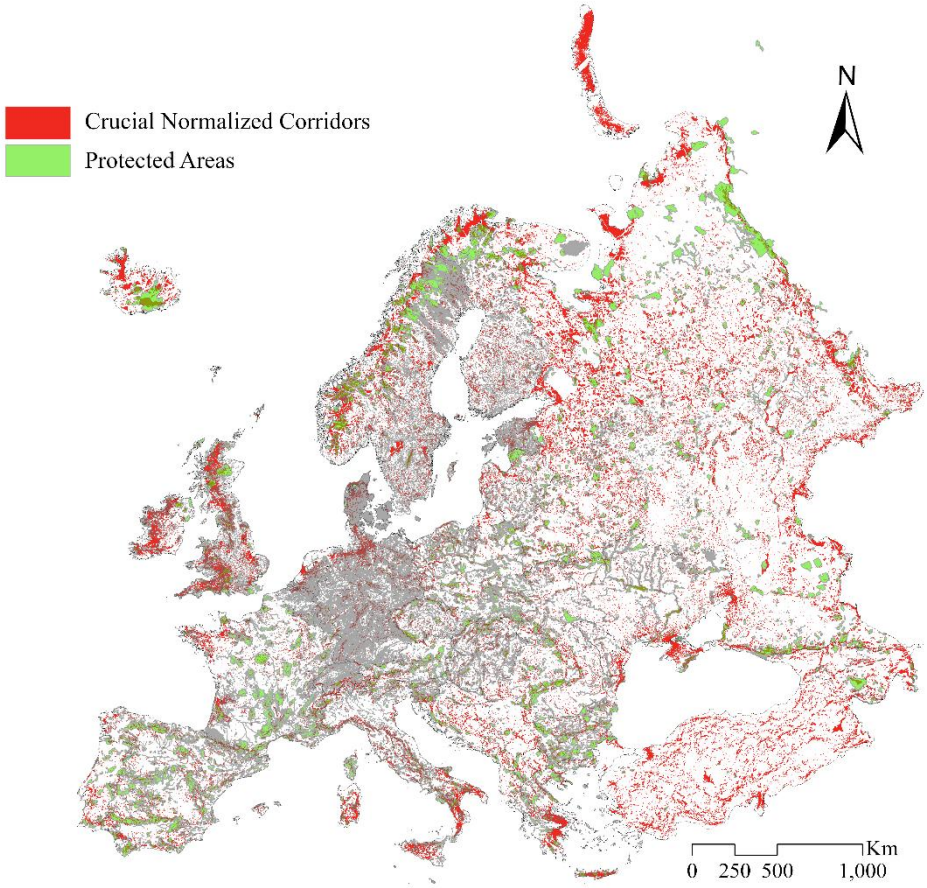
Appendix S5. Composite normalized current maps, combining the three resistance layers within the four moving windows: (a) 10 km, (b) 50km, (c) 90 km, and (d) 200 km.



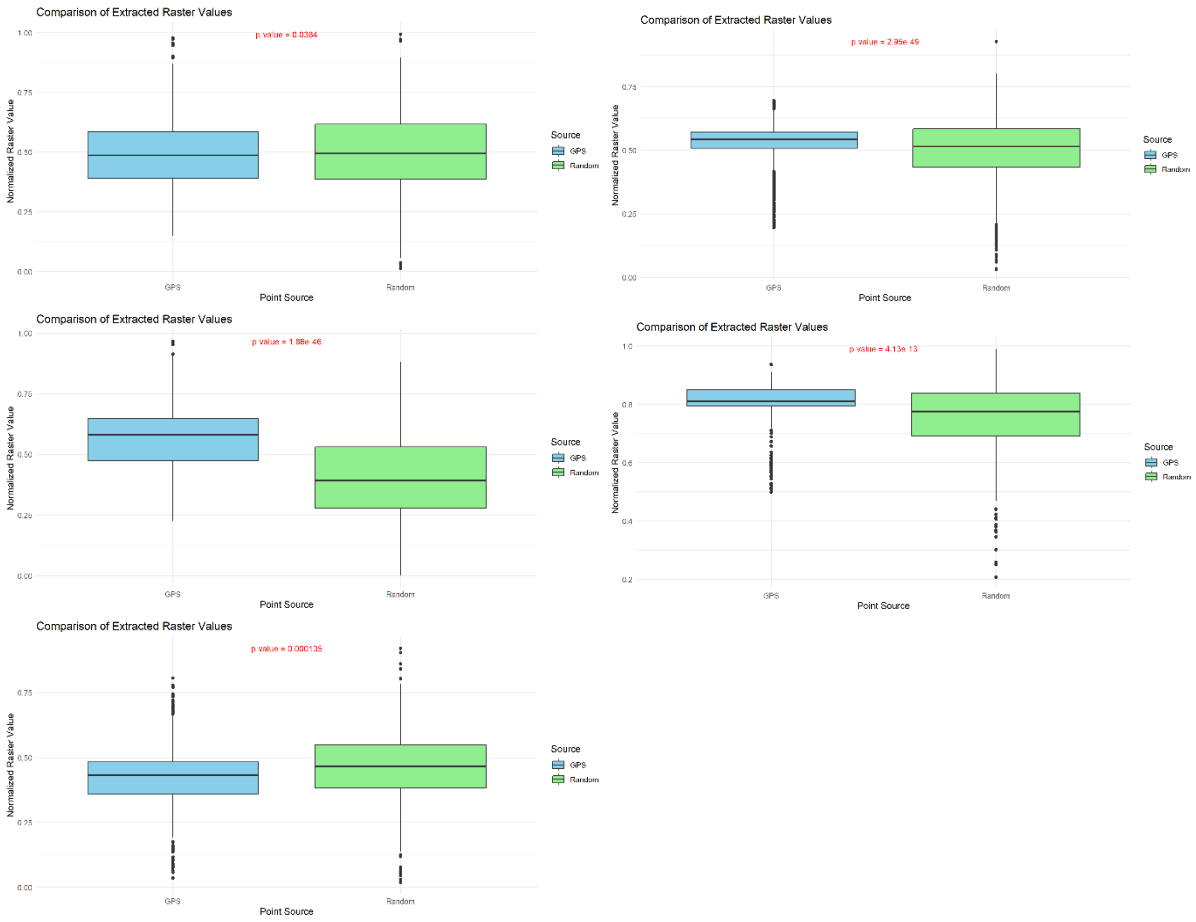
Appendix S6. The composite normalized current values within PAs in Europe.


a)
Normalized Mean Current Flow
Low
High
N
b)
c)
0 200 400 800
Km

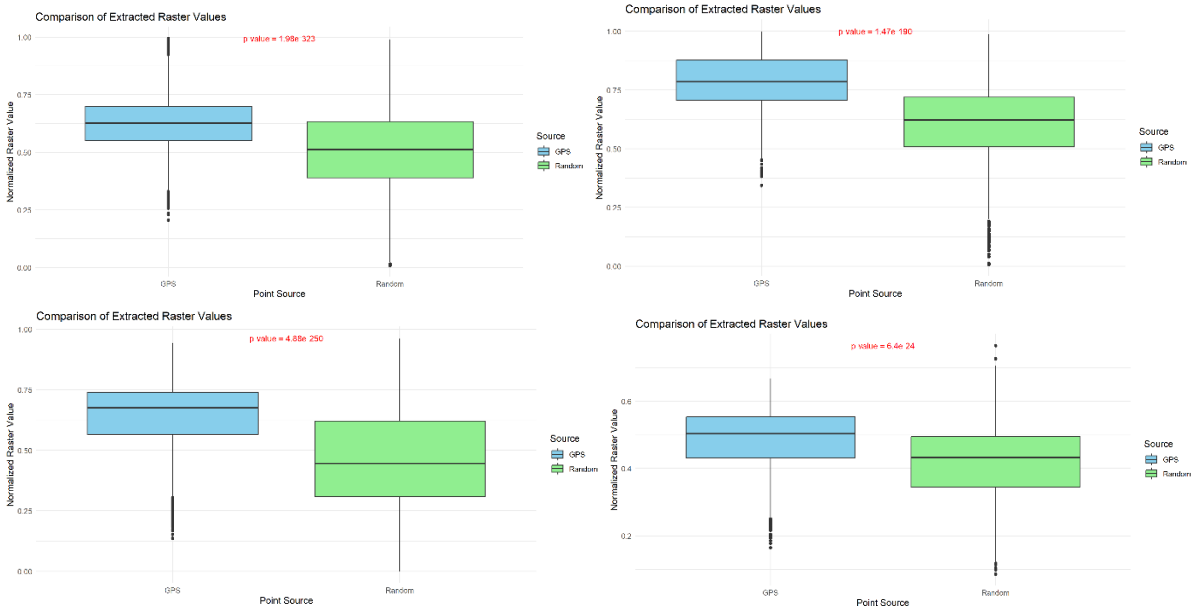
Appendix S7. Crucial normalized corridors (i.e., those values above 80th percentile from the composite normalized current map), and current network of PAs.

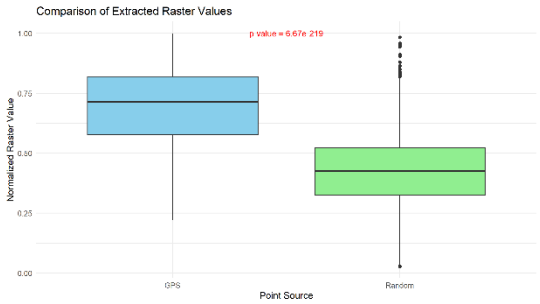


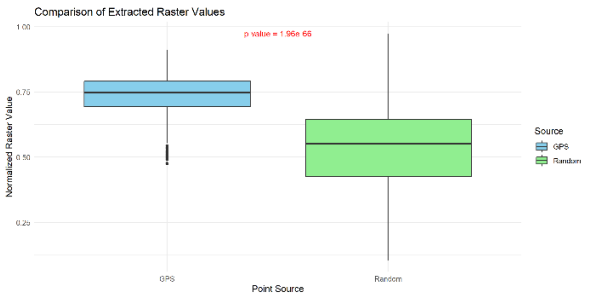
Appendix S8. Result of the models' validation using roe deer's telemetry data across Europe. Each plot represents a different study area

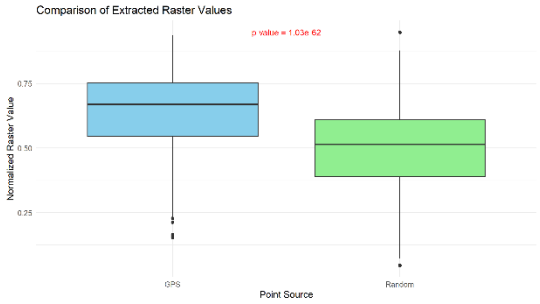


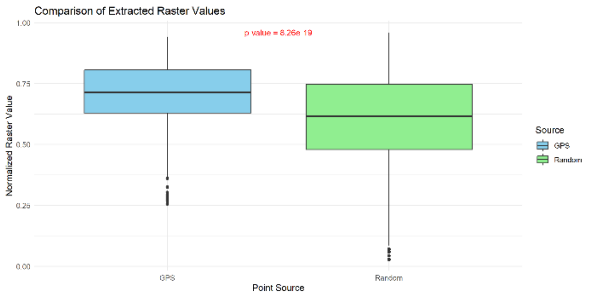
Appendix S9. Result of the models' validation using red deer's telemetry data across Europe. Each plot represents a different study area.

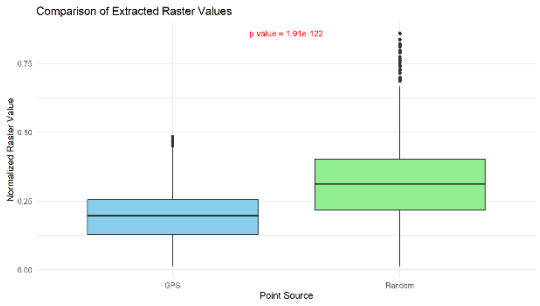


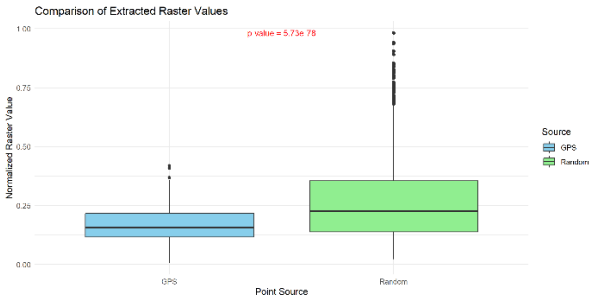

Comparison of Extracted Raster Values
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0.50
0.25
0.00
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Random
Point Source
Source
GPS
Random

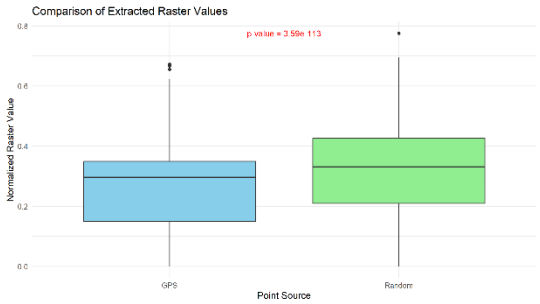

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Normalized Raster Value
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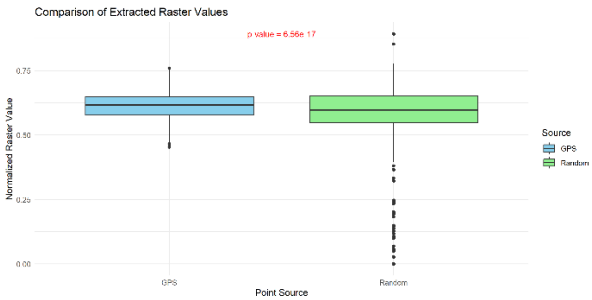

Comparison of Extracted Raster Values
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Normalized Raster Value
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0.25
GPS
Random
Point Source
Source
GPS
Random


Comparison of Extracted Raster Values
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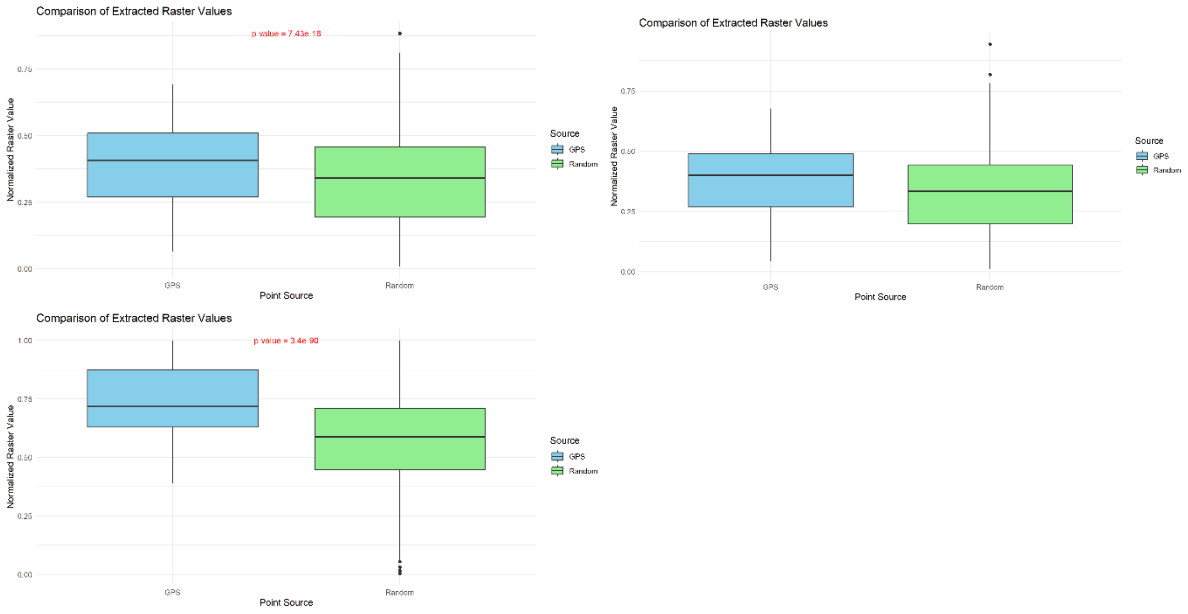

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Source
GPS
Random


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Random

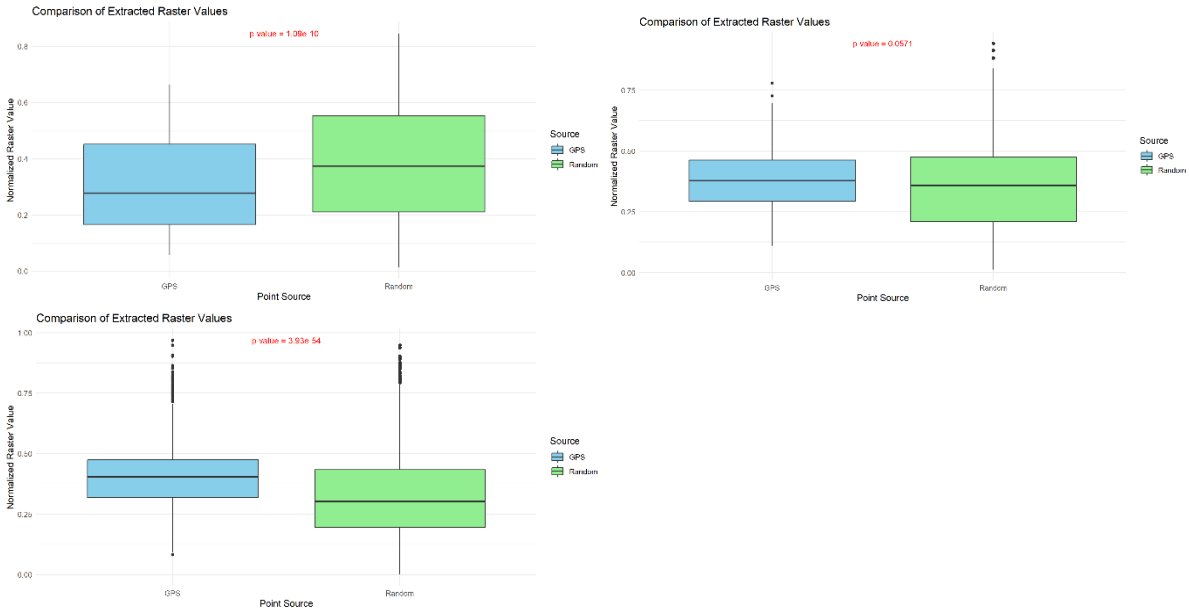

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Source
GPS
Random


Comparison of Extracted Raster Values
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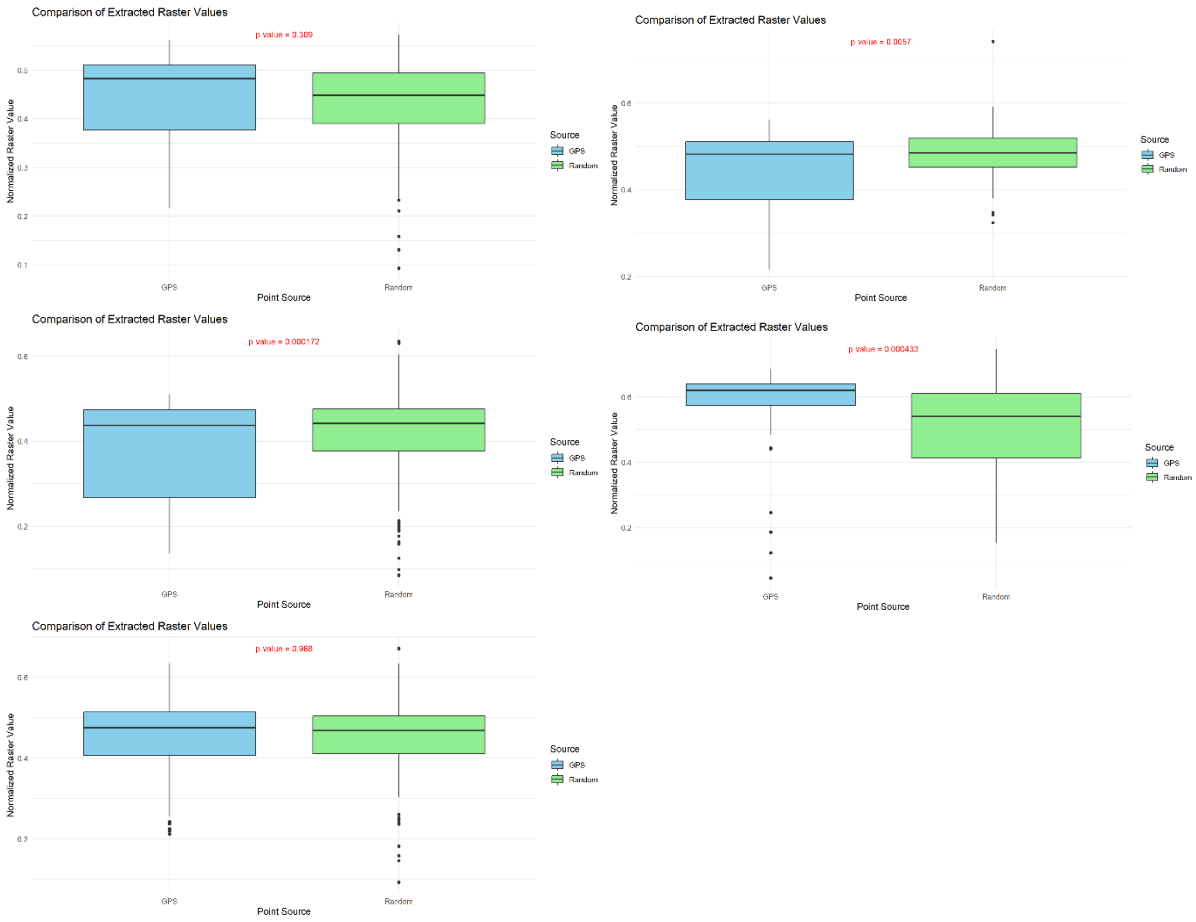
Appendix S10. Result of the models' validation using wild boar's telemetry data across Europe. Each plot represents a different study area



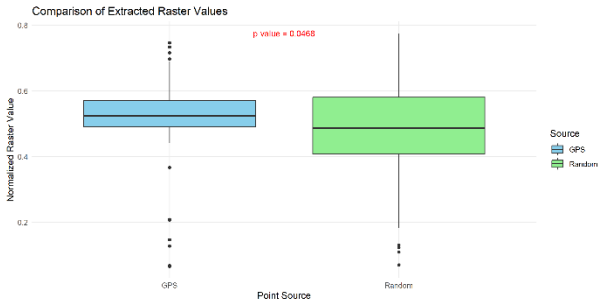
Appendix S11. Result of the models' validation using brown bear's telemetry data across Europe. Each plot represents a different individual.



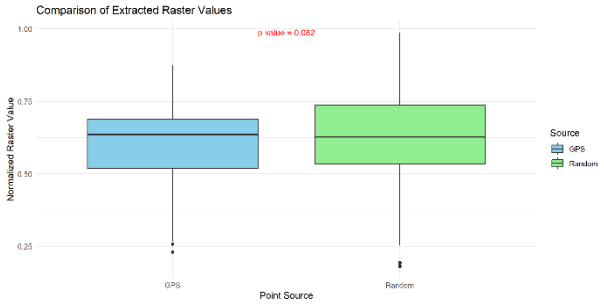
Appendix S12. Result of the models' validation using brown hare's telemetry data across Europe. Each plot represents a different individual.



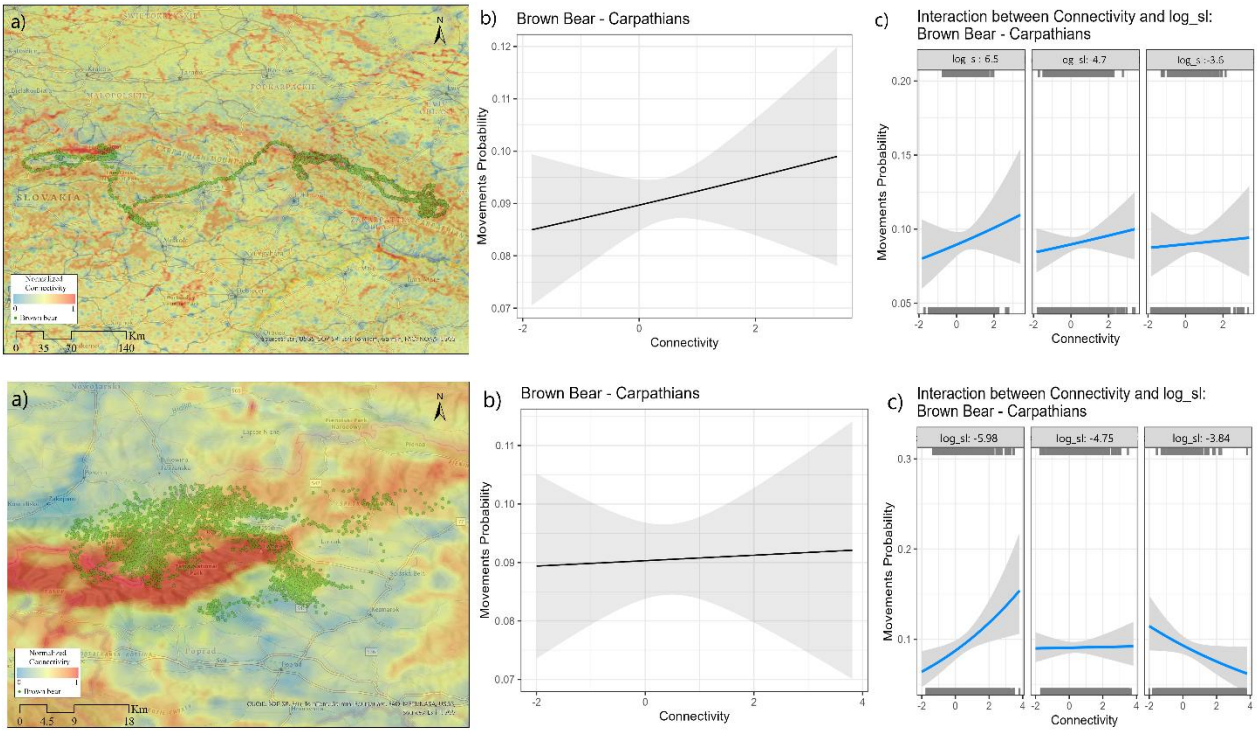
Appendix S13. Result of the models' validation using mountain hare's telemetry data across Europe.



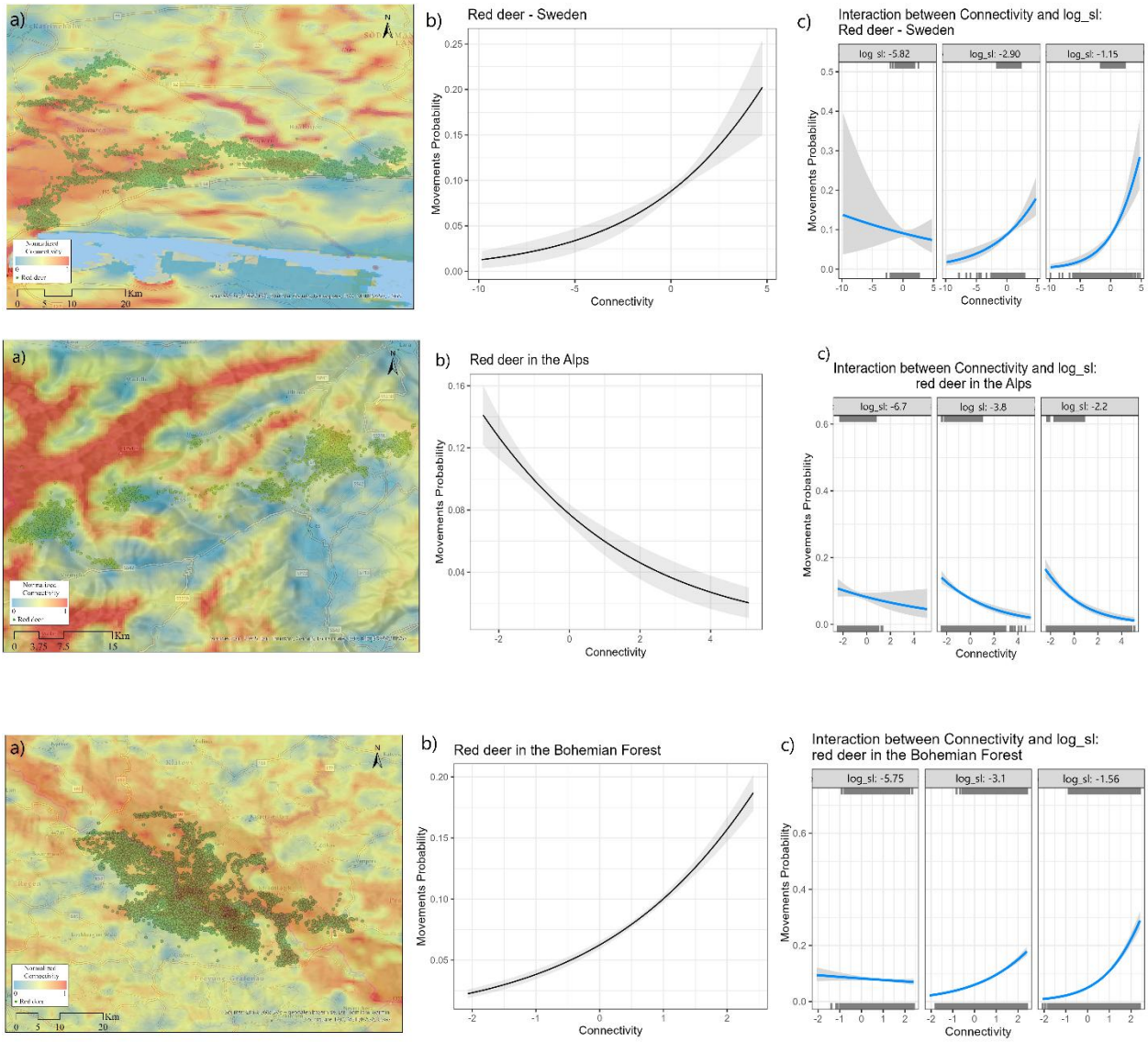
Appendix S14. Result of the models' validation using European wildcat's telemetry data across Europe.



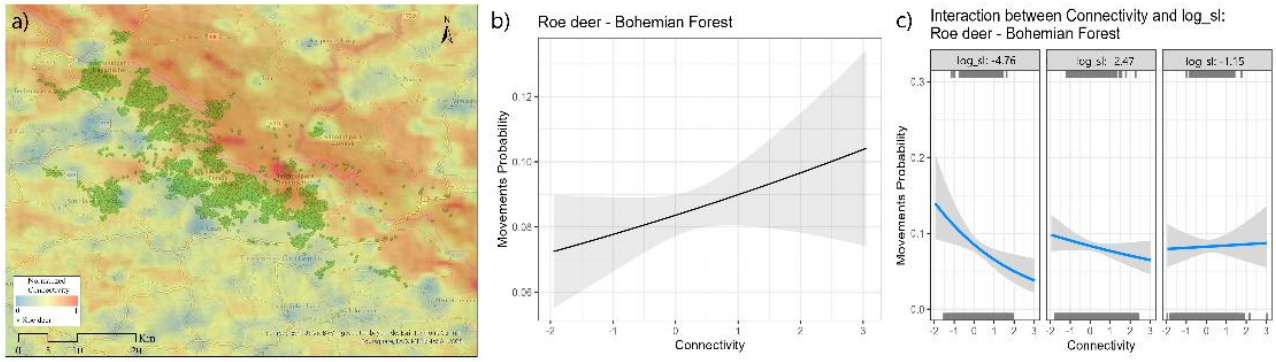
Appendix S15. Results of the model's validation using the integrated step selection function for the brown bear in the Carpathians: a) GPS fixes and normalized connectivity, b) overall effects of connectivity on the movements, and c) interactions between step length and connectivity.

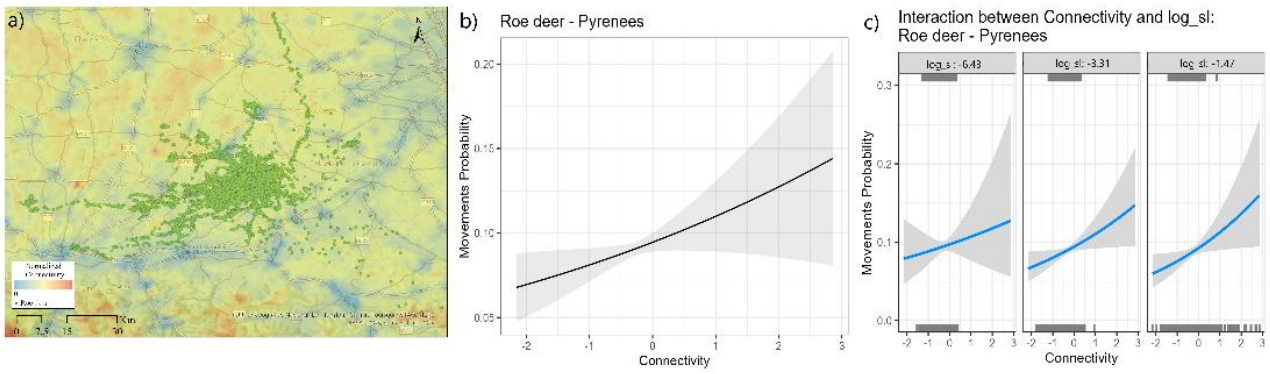


Appendix S16. Results of the model's validation using the integrated step selection function for the red deer: a) GPS fixes and normalized connectivity, b) overall effects of connectivity on the movements, and c) interactions between step length and connectivity.

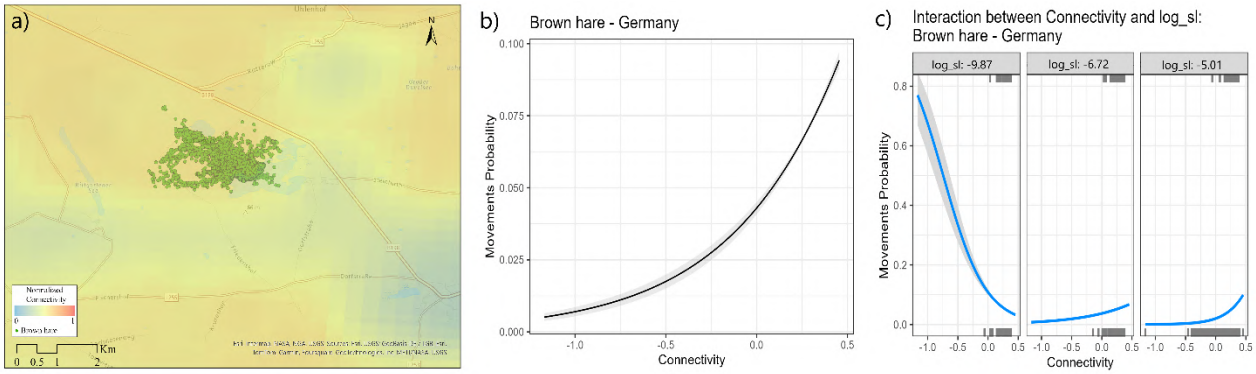


Appendix S17. Results of the model's validation using the integrated step selection function for the roe deer: a) GPS fixes and normalized connectivity, b) overall effects of connectivity on the movements, and c) interactions between step length and connectivity.

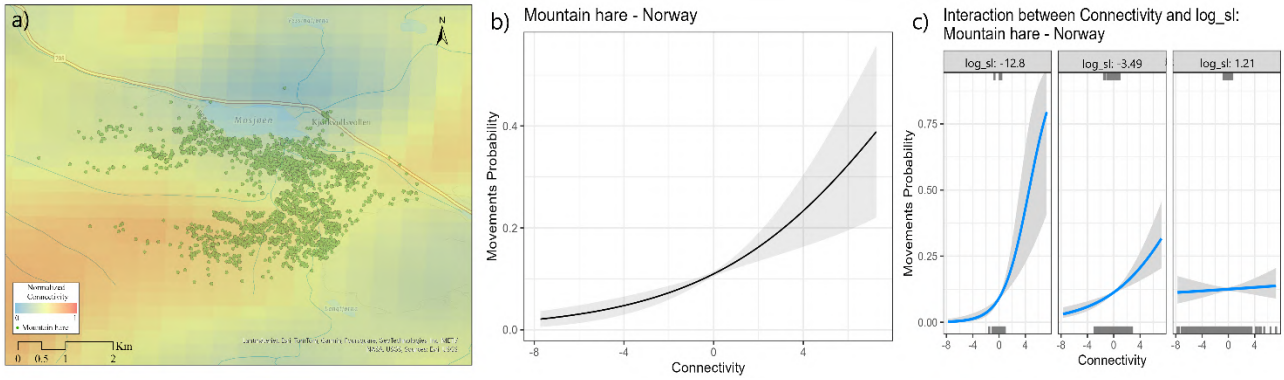




Appendix S18. Results of the model's validation using the integrated step selection function for the brown hare: a) GPS fixes and normalized connectivity, b) overall effects of connectivity on the movements, and c) interactions between step length and connectivity.



Appendix S19. Results of the model's validation using the integrated step selection function for the mountain hare: a) GPS fixes and normalized connectivity, b) overall effects of connectivity on the movements, and c) interactions between step length and connectivity.



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Conclusion

The results of this thesis contribute to a better understanding of spatial and temporal distribution trends of some target vertebrate species in Europe, improving the knowledge of expansion dynamics through species distribution models (SDMs) and connectivity modelling. Moreover, the results presented in this thesis could support future conservation efforts, supporting reintroduction scenarios by helping in identifying the best sites, and assessing reintroduction outcomes, and supporting the EU's Biodiversity Strategy for 2030 in expanding the current network of Protected Areas (PAs).

Europe represents a unique case, because of its high urbanization and human modification (Williams et al., 2020), and despite the widespread biodiversity crisis, in the last 50 years declines have been less dramatic (Living Planet Index, 2024). Furthermore, Europe has also witnessed the comeback of several wildlife species, especially mammals, such as ungulates, e.g., the European bison (*Bison bonasus*), the recovery of large carnivores (particularly the grey wolf (*Canis lupus*) and the Eurasian lynx (*Lynx lynx*), and the spread of other species, such as the golden jackal (*Canis aureus*) and the Eurasian beaver (*Castor fiber*), among the greater example of species expansion in Europe (Ledger et al., 2022).

There are several reasons for these conservation successes, especially the protective legislation, reintroduction efforts and the existence of conservation measures and management actions (Ledger et al., 2022; Living Planet Index, 2024). However, significant threats still exist in Europe, mainly related to species exploitation and habitat degradation (Ledger et al., 2022). For example, despite efforts to reintroduce and re-establish previously extincted lynx populations in Western and Central Europe, most of them are still threatened due to small population size, poaching, low genetic variability and isolation (Heurich et al., 2018; Mueller et al., 2022; von Arx et al., 2021).

The results reported are another demonstration of the wide utility of SDMs to answer biodiversity-related questions, such as species expansion and species interactions. Indeed, the Eurasian beaver represents one of the most important cases of recovery in Europe, with a population growth from 1,200 individuals to ca. 1,500,000 individuals (Wróbel, 2020). SDMs showed that this expansion process will likely continue in the future, as supported by recent studies (e.g., Calderón et al., 2022), and evidenced a possible contraction in Norway, as supported by Ledger et al., (2022). Concurrently, the golden jackal is expanding in Europe, pushing himself to areas that were never occupied (e.g., in Scandinavia) (Kojola et al., 2024). This expansion can lead to new interactions with other species, such as in the reported case of kleptoparasitism toward the Eurasian lynx in the Dinaric mountains, where the lynx population is endangered (Krofel et al., 2022). Habitat modelling showed that the spatial overlap between these two predators would increase in the future, mainly because of the expansion of the golden jackal, while the lynx will face some range contractions, especially in Southern and Central Europe. To improve the status of some lynx populations, especially to increase genetic variability, it has been proposed to create a functional viable metapopulation across West and Central Europe (Mueller et al., 2022). Connectivity modelling reported a key message, showing several unprotected ecological corridors in Europe. This underlined the critical gaps in the current network of PAs, especially when covering areas important for connectivity, as shown also by multispecies connectivity models. Thus, connectivity modelling and its outputs represent an essential tool to support biodiversity conservation in Europe, especially considering the EU's Biodiversity Strategy for 2030. Freshwater ecosystems are another environment where connectivity restoration is urgently needed, especially in Europe, where an

average density of 0.74 barriers per kilometer has been reported (Belletti et al., 2020). Unlike functional connectivity, where connectivity metrics are defined based on target species, structural connectivity considers the physical characteristics that support or impede a connected natural landscape. Approaches to prioritize barriers can provide crucial information about where to act with practical management actions to remove barriers or to understand their effects on the target species. For example, for the Eurasian beaver, several dams can act as barriers, especially in the Iberian Peninsula. Interestingly, comparisons between functional and structural connectivity can highlight similar patterns in connectivity and fragmentation, despite the differences within the algorithms used.

Finally, starting from SDMs and connectivity analyses to individual-based models (IBMs), different frameworks applicable in real-world scenarios were implemented. For example, reintroduction projects can be supported by ecological modelling in identifying the potential sites where to focus, and then IBMs can assess the outcomes of different reintroduction scenarios, to test which lead to the best performances, such as assessing population viability, occurrence probabilities and colonization time. Furthermore, considering the EU Biodiversity Strategy for 2030 and the goal to extend the current network of PAs to legally protect at least 30% of land, identifying where to establish new PAs is crucial. Even in this case, ecological modelling can help by informing the portions of land that should be protected using biodiversity-informed frameworks that show these areas in a spatially explicit way. Applying this framework with multispecies groups representing conservation priorities, or different target groups, can provide solid information.

Overall, the results presented in this thesis reinforce the fact that ecological modelling can support the study of species range shifts under global change, also showing that these shifts will be widespread in the future across different taxa. It has been shown that despite the effects of global change, many species will be able to persist in Europe, and several methodologies can support the protection of these species. These results are crucial to understand and predict range expansions and contractions, and highlighting critical areas where conservation efforts should be prioritized to aim at the long-term conservation of European biodiversity.

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