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Baselines for Establishing meta-population connectivity of Eurasian lynx populations in the Alps, Dinarics and Balkan

Handbook on suitability and connectivity of the space for Eurasian lynx in the area
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1 Introduction

One of the most radical changes to the European landscape in recent centuries has been the creation of vast urban and agricultural areas and the subsequent expansion of infrastructure networks. After more than 5000 years of intensive human activity, only 2% of the original primeval forest remains (Luell et al. 2003). In Europe's human-dominated and highly fragmented landscape, the dispersal of large mammals such as the Eurasian lynx is hindered by natural (e.g. big rivers, deep valleys) and anthropogenic barriers such as extensive urban and agricultural areas and the subsequent expansion of transportation infrastructure networks (Breitenmoser et al. 2000, Potočnik et al. 2023). In addition, dispersing sub-adult lynx show a strong tendency to establish home ranges in areas adjacent to their conspecifics (Zimmermann et al. 2005). Thus, the combination of anthropogenic and ecological factors makes it unlikely that lynx will spontaneously colonise new patches in the Alps, Dinaric Mountains and the Balkans. A priority goal for lynx conservation is therefore to connect the existing lynx populations in the Alps with the Jura and Dinaric Mountains (Molinari-Jobin et al. 2003), possibly also with the populations in the Vosges, the Bohemian, Bavarian Austrian Forest and the Balkan populations, and in the long term possibly even with the remnant populations in the Carpathians (European Commission 2013). Natural dispersal alone would probably not be sufficient to establish this interconnectivity, making translocations and reintroductions necessary (e.g. Zimmermann and Breitenmoser 2007, Molinari-Jobin et al. 2010).



2 The Eurasian lynx

The Eurasian lynx (*Lynx lynx*) is a middle-sized, spotted felid and one of the four species belonging to the *Lynx* genus. It is considered to have one of the largest east-west distribution ranges in felids. It occurs along forested mountain ranges in South-eastern and Central Europe and from Northern and Eastern Europe through the Boreal forest belt of Russia, down into Central Asia and the Tibetan Plateau (Kaczensky et al. 2012, Nowell and Jackson 1996, Sunquist and Sunquist 2002). The global population trend of the Eurasian Lynx is estimated as stable with no severe fragmentation in the boreal range (Breitenmoser et al. 2015). Subspecies in the southwest of its range (Europe and Asia Minor) are generally small and widely separated. The European lynx population (excluding Russia and Belarus) has been estimated at 9,000-10,000 (Breitenmoser et al. 2015). Its native distribution stretches from Scandinavia and Fennoscandia in the north, the Carpathian Mountains in the east and the southwest Balkan Peninsula. The Balkan lynx population is thought to be stable with only 20-39 individuals remaining (Melovski et al. 2015). Densities are typically 0.69-2.39 resident adults per 100 km², although higher densities of up to 5/100 km² have been reported from Turkey, Eastern Europe and parts of Russia and lower densities of 0.24/100 km² from some reintroduced populations and from Scandinavia (Jedrzejewski et al. 1996, Sunde et al. 2000, Schmidt et al. 2011, Pesenti & Zimmermann 2013, Avgan et al. 2014, Gimenez et al. 2019, Dula et al. 2021, Mengüllüoğlu et al. 2018, Palmero et al. 2021).

Once widespread throughout Europe, the Eurasian lynx disappeared from Central and Southern Europe and many other parts of the continent during the 18th and 19th centuries, as a consequence of direct persecution, habitat loss through forest destruction, expansion of cultivated land, and the excessive reduction of wild ungulates (Breitenmoser 1998, Schadt et al. 2002, Zimmermann 2003, Potočnik et al. 2009). Except for the Carpathian Mountains, it also survived in a small area in the Balkans with a stronghold in North Macedonia, Albania and Kosovo. Since the end of the nineteenth century, forests have regenerated in many mountainous regions of Europe (Breitenmoser 1998, Zimmermann 2004), and the wild ungulate populations have recovered quickly (Apollonio et al. 2010). The improvement of the ecological conditions as well as protective legislation was favourable for the return of large carnivores as lynx populations reintroduced in Central Europe in the 1970s and 1980s, mostly sourcing animals from Slovakian Carpathians (Von Arx et al., 2004, Mueller et al 2020) still persist in the Jura Mountains, Northwestern Alps, Dinarics, Bohemian-Bavarian-Austrian forest and Vosges (Breitenmoser 1998, Chapron et al. 2014). The population sizes have fluctuated over the years, but distribution has not significantly expanded by natural colonisation. Following the first reintroductions, lynx were translocated to Harz (2000), Northeastern Switzerland in 2001 (Ryser et al 2004), to the Kalkalpen (Austria) in 2011-2013 and to Palatinate forest (2016 - 2019). Lynx' current distribution in Central and Southeastern Europe seems to be mainly limited to sites that were used for reintroductions and translocations where they were successful. The total has been estimated at only about 3,000 individuals, with little connectivity between subpopulations localised around mountain ranges (Chapron et al., 2014).

Dinaric lynx population

Lynx in Dinaric Mountains had become extinct at the beginning of the 20th century, was reintroduced to south-eastern Slovenia in 1973 (known as the Dinaric lynx population) with only six founders, some of them related, from Slovakian Carpathians (Čop & Frković, 1998; Kos et al., 2004). Although little experience and no guidelines were available for carnivore recovery programs (Breitenmoser et al. 2001), data on signs of presence like sightings, reproduction events, scats, prey kills or attacks on domestic animals were collected opportunistically, but only mortalities were recorded systematically since the reintroduction, both in Slovenia and Croatia (Čop and Frković 1998). The monitoring data made it possible to follow the forefront of the expansion of the growing population in subsequent years. Eight years after the reintroduction, young dispersing lynx or adult territorial lynx were recorded in all directions (but mainly along the Dinaric Mountains), at distances from 36 to 100 km from the release site (Čop and Frković 1988). The maximum distance of recorded area of presence of lynx in BiH from the release site was around 390 km, while from the northwest (NE Italy) was around 140 km. The proximate cause for the faster expansion towards southeast is not clear; however, it is obvious that fenced highway Ljubljana – Trieste/Koper represents strong barrier for dispersing lynx (Skrbinšek 2004, Kuralt et al. 2023, 2024). Given the apparent reduced necessity or ability of subadults, especially females, to cross the highway and reproduce in almost a half of century after the reintroduction, it is unlikely that lynx will be able to spontaneously establish new reproductive areas towards the SE Alps.

While the reintroduction initially appeared to be successful, the small founding population led to inbreeding, which resulted in signs of stagnation in the 1990s, which turned into drastic decline and local extinctions after 2000 (Kaczensky et al., 2012; Sindičić et al., 2013, Fležar et al. 2021). By the 2010s, signs of lynx presence became increasingly scarce, and extinction of the population became a tangible possibility. Genetic studies of the Dinaric lynx after 2010 showed that the population had the lowest genetic diversity and the highest inbreeding of all studied Eurasian lynx populations, although all reintroduced populations are inbred (Breitenmoser & Obexer-Ruff, 2003; Sindičić et al., 2013, Rueness, 2014, Krojerová-Prokešová, 2019, Mueller et al., 2022), with the exception of the reintroduced Harz lynx population in Germany (Mueller et al., 2020) where zoo animals were used as founders. In the Dinaric lynx, the average inbreeding coefficient exceeded 0.26 (Sindičić et al., 2013) and even $F = 0.316$ (Pazhenkova et al. 2023, 2024). This means that an average random



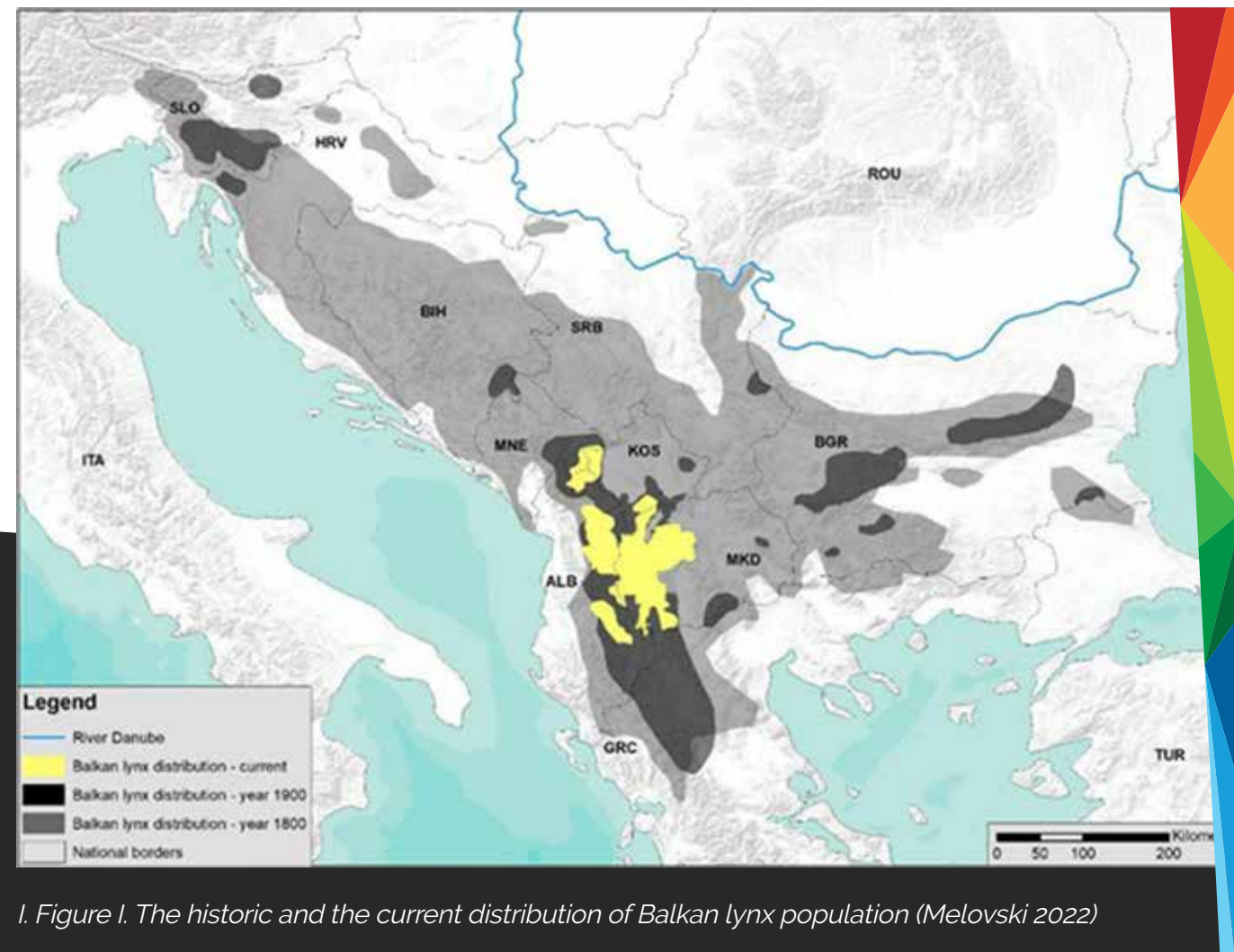
breeding event in the population would be equivalent to a direct brother-sister mating, which could result in considerable inbreeding depression, likely affecting the viability and fecundity of the Dinaric lynx. To prevent population extinction, reinforcement and restoration of lost population connectivity have been proposed (Breitenmoser et al., 2007; Zimmerman & Breitenmoser, 2007; Kramer-Schadt et al., 2011; Sindičić et al., 2013, Lucena-Perez, 2020, Port et al., 2020). In the Dinaric lynx population, three reinforcement projects started in 2013 (ULyCA, Urgent Lynx Conservation Action) in 2017 (LIFE Lynx Project, LIFE16 NAT/SI/000634) and in 2023 (ULyCA2 Project) to improve the genetic status and create a stepping-stone population in the SE Alps, within dispersal distance to the Dinaric population, to boost connectivity to neighbouring areas.

The population reinforcement, which included the translocation of 12 individuals to the Dinaric part of Slovenia and Croatia to enhance the genetic diversity of the population, was completed during 2019-2023 (Fležar et al., 2024). During the reinforcement process in the Dinaric Mountains, the mean lynx population density increased for 44.3% according to yearly monitoring surveys (from 0.88 ± 0.15 to 1.27 ± 0.15 independent lynx / 100 km² with the highest increase in the last survey (Fležar et al. 2024, Krofel et al. in preparation).

However, without gene flow, natural or assisted, the problem of inbreeding cannot be completely solved in the long term, as the effective population size would invariably remain low, with resulting high genetic drift causing inbreeding to keep accumulating. Lynx in the south-eastern Alps formally/administratively belong to the Alpine population (Kaczensky et al. 2013), although they demographically and genetically represent the same population since they have been colonised first by lynx from the reintroduction in Slovenia in 1973. Thus in order to improve the connection between the Dinaric and Alpine populations, between 2021 and 2023 10 animals were also translocated to the southeast Alps in Slovenia and Italy (Fležar et al., 2023a, Hočevár et al. 2024, Krofel et al. in preparation). With established reproductions in this area since 2021 (Fležar et al. 2024), SE Alpine lynx play an important role as the "stepping stone" that could with further spread enhance potential connections with the reintroduced populations in the northwestern Alps and Austria (Kalkalpen). If this will not lead to the movement between the Dinaric and Alpine population, then further conservation measures (assisted dispersal, translocations, improved permeability of Ljubljana - Trieste highway - green bridges) will be necessary.

Balkan lynx population

The Balkan lynx population was extirpated from most of the Balkan countries and confined to a small population in the South-west Balkans; Albania, North Macedonia and Kosovo (Melovski, 2022). It was described as a subspecies *balcanicus* in 1941 (Bureš, 1941), later solidified taking three different facets into account: morphology (Mirić, 1978), conservation (Melovski et al. 2015) and genetics – unique haplotypes (Gugolz et al. 2008, Cómert et al. 2018, Bazzicalupo et al. 2022). The population of the Balkan lynx has been intrinsically small for at least the past 150 generations (Bazzicalupo et al. 2022). Already experiencing few bottlenecks in the last 100 years, its genetic resistance is ever so weak in withstanding the rapid environmental change. The next steps of its recovery will most likely also involve a genetic rescue mission in order to strengthen its genetic variability. Given that the Balkan lynx is genetically and taxonomically unique question is which subspecies is a better candidate for such a measure. So, we need to know the phylogeny and the phylogeographic and current genetic makeup of the Balkan lynx and its closest neighbours; the Carpathian and the Caucasian lynx. Recent publications have covered these facets (Gugolz et al. 2008, Cómert et al. 2018, Bazzicalupo et al. 2022), however there is still lack of sufficient knowledge on which subspecies is better ecological fit for the given environment. However, based on the prey preference (roe deer being the main prey), local prey availability (lower lagomorph and higher ungulate availability) and habitat use (predominant use of the mixed and broadleaved forests) it has been suggested that the *L. l. carpathicus* is ecologically more similar to the *L. l. balcanicus* and therefore likely better suited for the environment of south-western Balkans (Melovski et al. 2022a). Potentially, Montenegro and Greece are also sharing this scattered and fragmented population. In



1. Figure 1. The historic and the current distribution of Balkan lynx population (Melovski 2022)

Albania, lynx occur on Munella Mt. and its surroundings in central-north Albania (Trajçe et al. 2014) and Shebenik-Jablanica NP on the eastern border with North Macedonia and Polis-Guri I Zi-Valamara in the south-west of the country. It occupies mixed deciduous and evergreen forests in the mountainous areas in the south-western Balkans. Deciduous forests consist of predominantly European beech and several oak species (*Quercus* spp.), mixed forests comprise more than 18% (mainly beech–fir mixed forests), nearly 10% are shrublands and around 1% are coniferous trees (Macedonian fir, *Abies borisii-regis* and European spruce, *Picea abies*) (Ivanov et al. 2018). The altitude at which Balkan lynxes occur ranges from 500 to 1,800 m, with rare exceptions when they venture into high mountain pastures above 1,800 m (up to 2,100 m) to cross territories or hunt chamois.

Reproduction was detected in Munella and Polis-Guri I Zi-Valamara (Melovski et al. 2015). Reports of lynx sightings in northern Albania (Albanian Alps) have not been confirmed by photos taken by locals. In North Macedonia lynx sightings have been reported in western part, mainly in the areas in and between Mavrovo, Galičica and Pelister National Parks, but also in Shar Planina National Park, Jablanica Mountains, Stogovo-Karaorman, Ilinska Plakenska Mountains and Jakupica Massif. In December 2010, lynx were discovered during a camera-trapping survey, revealing individuals in the central-northern part of North Macedonia (Jasen PA) (Melovski et al. 2013). The sightings were confirmed by camera trapping and telemetry studies in 2020 and 2021. In Kosovo, a camera trap photo confirmed the presence of two lynx in the Prokletije Mountains in March 2015, which were detected until 2022. In Montenegro, a baseline survey in 2013 found that two individuals had been killed in 2002 on the southern border with Albania and Kosovo (Prokletije Mountains). Their current presence is, however unlikely. In Greece, isolated, unconfirmed sightings are reported from the border regions of Greece with North Macedonia and Albania. The suspected presence of lynx in the Nestos river delta in eastern Greece, close to the Turkish border (Panayotopoulou and Godes 2004), has never been confirmed by reliable evidence, so their current presence in Greece is unlikely (Melovski et al. 2015).

The Balkan lynx population is estimated at 20-39 adult individuals (Melovski et al. 2015), and the density fluctuates between 0.8 to 2 individuals per 100 km² in the core area (Mavrovo NP in North Macedonia) using deterministic camera-trapping surveys conducted from 2008 until 2022 in seven occasions (Melovski pers comm, after CMS proposal, 2023). The population is considered stable, but no systematic abundance estimates have been done outside this core area.

General threats and Conservation status of the Eurasian lynx

The general threats to the lynx in Europe are low acceptance due to conflicts with hunters and livestock breeders, illegal killing, habitat loss and fragmentation mainly due to infrastructure development, poor management structures and incidental mortality (Kaczensky et al. 2012).

At the European level, a regional assessment has been made in the IUCN Red List of Threatened Species (von Arx 2018) and a number of European or regional strategies have been produced, e.g. the Action Plan for the Conservation of the Eurasian Lynx (*Lynx lynx*) in Europe (Breitenmoser et al. 2000), the Pan-Alpine Conservation Strategy for the Lynx (Molinari-Jobin et al. 2003), the Conservation Strategy and National Action Plans for the conservation of the Critically Endangered Balkan Lynx (Council of Europe 2011), the Key Actions for Large Carnivore Populations in Europe (Boitani et al. 2015) or the Lynx in the Alps: Recommendations for an internationally coordinated management (Schnidrig et al. 2016). The conservation measures for the Balkan lynx have been implemented as part of the Balkan Lynx Recovery Programme, a partnership project between non-governmental organisations from North Macedonia, Albania and Kosovo, which was launched in 2006 under the expert guidance (Breitenmoser et al. 2008). The programme is ongoing and represents an interdisciplinary approach to species conservation. However, none of these plans, which were mainly drawn up by experts, led to the desired improvement in formal transboundary cooperation or population-wide conservation and management coordination.

IUCN classifies the Eurasian Lynx as Least Concern on the global level given its wide range and stable populations in the north of Europe and its wide distribution in southern Siberian woodland stretching through Russia from the Ural Mountains to the Pacific, as well as Central Asia and the Tibetan plateau (Bao 2010, Bersenev et al. 2011, Kaczensky et al. 2012, Moqanaki et al. 2010, Matyushkin and Vaisfeld 2003). A recent assessment of the status of Eurasian Lynx in Europe shows that some isolated subpopulations remain Critically Endangered or Endangered (Kaczensky et al. 2012). Among the subspecies, *L. lynx lynx* and *L. lynx wrangeli* are likely to be considered Least Concern, whereas the status of the other subspecies is either unknown or should be considered within the threat categories. Only the Balkan lynx (*Lynx lynx balcanicus*) has been assessed at the subspecies level, so far and was listed as Critically Endangered in 2015. The population of the latter is estimated to be less than 50 mature individuals distributed mainly in North Macedonia, Albania and few individuals in Kosovo. There has not been recent evidence coming from Greece or Montenegro. However, no systematic monitoring is conducted in these two countries where dispersing individuals could have already appeared. Based on the population size estimates, the IUCN Red List assessment classifies the Balkan Lynx as Critically Endangered (CR: D) as the number of mature/adult individuals is estimated to be less than 50. The population is estimated to be 27-52 independent (adult and sub-adult) animals, corresponding to about 20-39 mature individuals. (Melovski et al. 2015). Currently, its distribution is restricted to three countries: North Macedonia, probably hosting around 70% of the population and Albania and Kosovo, with the rest of the individuals. The range is divided into two nuclei, indicating population fragmentation. The main threats involve poaching, prey depletion, habitat destruction and inbreeding (Bazzicalupo et al. 2022). Other subspecies of the Eurasian lynx are in a need for thorough conservation evaluation according to the IUCN

Red List criteria. Many populations of wide-spread subspecies could be hampered due to unsustainable development and fragmentation without realising it because of their seemingly intact distribution range.

The Eurasian Lynx is protected by the EU Habitats Directive: Annex II (designation of special areas of conservation for these species, which must be managed according to the ecological needs of the species) and Annex IV (strict protection – protected from killing, disturbance or destruction of their habitats).

The Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) lists the Eurasian Lynx under Appendix III (protected fauna species - special protection through 'appropriate and necessary legislative and administrative measures', of the listed wild fauna species). The Balkan lynx, as a subspecies, is listed under Appendix II (Strictly protected fauna species) in 2017 during the 37th meeting of the Standing Committee of the Convention.

The Eurasian Lynx is included on CITES Appendix II and protected under the Bern Convention (Appendix III). The Balkan Lynx is protected under Appendix II of the Bern Convention. The EU Habitat Directive protects the Eurasian Lynx in each state of the European Union under Annex II, (except the Estonian, Latvian and Finnish populations) and Annex IV (except the Estonian population).

At 14th meeting of the conference of the parties of the Convention on migratory Species in February 2024 the Eurasian lynx got accepted to be included in the Appendix 2 of the Bonn Convention and the Balkan lynx as a subspecies, included in the Appendix 1 of the convention. The proposal was supported by the EU, among a few other states. The concerted actions listed from this proposal are to be implemented in the next two years. They include conservation strategies and action plans for balcanicus and carpathicus subspecies and knowledge gathering through baseline survey data for isabellinus and dinikii. The lynx listing under the convention is expected to increase the global awareness of its conservation status and support different conservation programmes, strengthen the monitoring activities in the range countries, provide possibilities for identifying green infrastructure to ensure the invaluable migration of the species, transboundary cooperation between range countries for implementation of conservation measures and action plans, act in a prompt manner to recover native populations that are at threat, motivate research of populations where data is missing, as well as strengthening the institutional capacities of all relevant national and international stakeholders in regards to the monitoring and conservation activities (CMS 2023).



4 Habitat suitability

Top predators are generally not very sensitive to a particular habitat structure, vegetation or ecosystem type (Mladenoff et al. 1995). But among the European large carnivores, Eurasian lynx is certainly the one with the most specific demands regarding habitat and prey (Breitenmoser 1998). However, lynx can adapt to semi-natural landscape and their permanent disturbances (Breitenmoser-Würsten et al. 2001). The Eurasian lynx is present in large continuous lowland forest areas with more than 50% of forest cover. It is linked to forest areas with high amounts of forest fringe (Breitenmoser et al. 2000). The Eurasian lynx can also tolerate interruptions by open land habitat patches and land use types such as pastures or agriculture. Telemetry studies in 1990s in the Swiss Alps (Breitenmoser-Würsten et al. 2001) showed that re-introduced lynx originating from highly forested Carpathian Mountains, already adapted to open areas, when compared to the first telemetry studies in the early 1970s (Haller and Breitenmoser 1986). Intensive land use is tolerated as long as there is enough connected forest area for retreat (Breitenmoser 1998, Schadt et al. 2002). That was supported in a continental scale study with data of 434 lynx individuals (Oeser et al. 2023). They confirmed that lynx use refuge habitats more intensively with increasing landscape modification across spatial scales, selecting forests most strongly in otherwise open landscapes and rugged terrain in mountainous regions. Moreover, higher forest availability enabled lynx to place their home ranges in more human-modified landscapes. Human pressure and refuge habitat availability also shaped temporal patterns of lynx habitat use, with lynx increasing refuge habitat use and reducing their use of human-modified areas during periods of high exposure (daytime) or high vulnerability (postnatal period) to human pressure.

It is crucial to assess and mitigate the negative effect of habitat fragmentation on lynx populations and facilitate genetic exchange among isolated (sub)-populations or demes in Central and Southeastern Europe. Knowledge on the amount and distribution of suitable habitat available to a particular lynx population and to the obstacles it is exposed to is important for improvement of our understanding of lynx population connectivity within each population and across habitat patches at the metapopulation level. Apart from habitat suitability and connectivity studies, we provide also information on lynx home range size and movement activity, including dispersion, as a critical part of its ability to occupy sufficient interconnected areas to compensate for demographic variations and subsequently support genetic exchange between (sub)-populations, ensuring viability of the metapopulation.

Presence and availability of food/prey sources is an important parameter determining habitat suitability for animal species. Lynx diet varies greatly depending on prey availability and accessibility. Although other species within Lynx genus developed specializations for hunting lagomorphs, Eurasian lynx staple prey in Central Europe are roe deer (*Capreolus capreolus*) and Alpine chamois (*Rupicapra rupicapra*) as well as other ungulate species like red deer (*Cervus elaphus*) and European mouflon (*Ovis aries musimon*). In other parts of its distribution,

it can also prey on semi-domestic reindeer (*Rangifer tarandus*) and white-tailed deer (*Odocoileus virginianus*). In areas with low roe deer density Eurasian lynx diet can seasonally shift to other types of prey like rodents and birds (Krofel et al. 2011). In a research of lynx diet in Dinaric forests with low density of ungulates, rodents represented a considerable part of the diet (7.7%) especially at peaks of their population dynamics. This proves that Eurasian lynx is able to adapt to various food sources. Given present high population densities of ungulate species across Central Europe including Slovenia and Croatia (e.g. Apollonio et al. 2010) it is assumed that prey availability is mostly not a limiting factor for its habitat suitability in the Alps and Northern Dinarics but could be an issue for several parts of the Balkans (e.g. Macedonia, Serbia, Greece, Albania) (Apollonio et al. 2010).

Habitat fragmentation and connectivity

Habitat for any species is divided into "habitat patches", areas with favourable conditions for the species that are separated by "matrix", areas where individuals can move through but will not permanently reside, and "barriers", through which individuals are more or less difficult or even unable to pass (Andrén 1994, Luell et al. 2003, Bird Jackson and Fahrig 2013, Potočnik et al. 2019, 2023). This fragmentation can be caused by natural features like rivers, high mountain ridges or seas and divides species range into populations and subpopulations. However, human developments are changing the landscape, decreasing habitat, introducing new barriers and pushing fragmentation to the point where it is currently recognized as one of the main threats for many endangered species and a critical obstacle to species recovery (Andrén 1994, Fahrig 2001, 2003).

In addition, roads, railways and waterways impose movement barriers on many animals, barriers that can isolate populations and lead to long-term population decline. Habitat fragmentation, the splitting of natural habitats and ecosystems into smaller and more isolated patches, is recognised globally as one of the biggest threats to the conservation of biological diversity (Luell et al. 2003, Bird Jackson and Fahrig 2013, Fahrig 2003, 2007). Habitat fragmentation is mainly the result of different forms of land use change. The construction and use of transport infrastructure is one of the major agents causing this change as well as creating barriers between otherwise continuous habitat. On the other hand, barriers causing habitat fragmentation have a long-term effect that is not that easy to detect (Luell et al. 2003, Bird Jackson and Fahrig 2013).

Urban areas, agricultural landscapes and infrastructure networks divide natural habitats into small, isolated patches and create barriers between the remaining patches. This can affect species in two ways: firstly, habitat patches can be so reduced in size that they can no longer support viable populations of important species, and secondly, the remaining patches can be so isolated that individuals have little chance of moving between patches. The inability to move between patches renders species vulnerable to local and regional extinction. Although humans began fragmenting nature many centuries ago, the rapid increase in the density of transportation networks in the 1900s and the impact of improved accessibility have greatly accelerated these effects.

The barrier effect, especially of (fenced) roads and railroads, is probably their greatest negative ecological impact. The dispersal ability of individual organisms is one of the key factors for the survival of species. The ability to move across a landscape in search of food, shelter or mating is negatively affected by barriers that cause habitat isolation. The impact on individuals affects population dynamics and often threatens the survival of species.

Habitat loss and excessive fragmentation is a well-documented threat to wildlife (e.g. Andrén 1994, Hagan et al. 1996). As habitat is reduced, wildlife populations decrease in size and become more isolated. The extinction risks may be reduced by rescue effect due to

dispersal between local populations (Hanski et al. 1996). Connectivity between suitable habitat patches depends on the number of dispersers available in the population, the distance between the source and the target populations, and the dispersal ability of the species under consideration (Wiens 1997).

The Eurasian lynx, a charismatic large carnivore, is recovering in most of the European populations as a result of different management strategies applied on, often, well diverse scenarios of different intensities of human-pressure (Chapron et al. 2014). However, the viability of recovering populations and the well-being of the populations that have best withstood human pressure depend very much on appropriate decision-making in conservation strategies. Consequently, it is important to improve the understanding of the requirements of lynx in the current context of population recovery and likely expansion, including the specific spatial needs for the species.

The Central and South-Eastern European lynx populations are relatively isolated, and only limited movement occurs between some populations (Zimmermann and Breitenmoser 2007, Potočnik et al. 2009). In the fragmented mountainous regions of the Alps and Dinarics dispersal is constrained by barriers including high mountain peaks, anthropized valleys, canyons and glaciers, fenced highways, large rivers as well as settlements, agricultural, industrial and other urban areas. The ongoing refugee crisis in Europe has seen many countries rush to construct border security fencing to divert or control the flow of people (Linnel et al. 2016). The process of border fencing can represent an important additional threat to wildlife because it can cause additional fragmentation of habitat, reducing its connectivity and lower effective population size.

Further colonisation of Central, South-Eastern and Eastern Alps through natural or "human managed" expansion of lynx individuals from the Dinaric population in Slovenia, Italy and Croatia should be one of the priorities of lynx conservation in Central Europe. Connectivity between habitat patches is a critical issue for long-term survival of any wildlife population, as it directly affects not only its dynamics and chances of long-term survival, but also its possibilities for expansion. This makes improving of habitat connectivity between the Dinaric Mountains and the Alps, which will ensure the adequate number of dispersals and maintain gene flow, critical for establishing a viable lynx (meta)population in the Alps, but very challenging considering the needs and desires of humans. The impact of lynx translocations in the Dinaric and SE-Alps has been evaluated on the viability and connectivity of isolated lynx populations within a stepping-stone system (Sánchez Arribas et al. 2023, in preparation). Models have shown lynx translocations positively impacted the demography and connectivity on a local scale, but not at the regional level. Translocations in Dinaric lynx population improved the connectivity of the lynx sub-population in the SE Alps, increasing its viability.

Increased urbanisation of lynx inhabited areas and development of large transport infrastructure such as highways has accentuated this challenge in Slovenia and the neighbouring countries over the recent years. The cheapest and most effective way to preserve connectivity is to prevent development in small, critical areas that connect large habitat patches. An effective way to do this is to provide correct information for environmental impact assessment (EIA) that would include habitat connectivity for the Eurasian lynx in spatial planning, and conserve the most critical locations. This is becoming increasingly important as these locations are typically located on cheaper land between already developed areas, and are often the most desirable locations among investors for expansion of industrial and urban areas. While legislation and procedures concerning spatial planning are well developed, there is still a gap in expert knowledge when it comes to ensuring connectivity between habitat patches for large carnivores.



5 Isolation and Inbreeding

In conservation biology, inbreeding poses a significant threat to endangered species, particularly those in small, isolated groups, often resulting from the fragmentation or reduction of populations (Frankham et al., 2002). In large populations, rare deleterious alleles do not pose a major risk due to their rarity, but inbreeding increases the likelihood that these alleles will be expressed, reducing individual fitness and reproductive success (Charlesworth & Charlesworth, 1987). However, in inbred individuals, where both the maternal and paternal lineages meet in a recent ancestor, the opposite is true. In such individuals, there is a high probability that the phenotypic expression of such alleles will reduce individual fitness and reduce survival and reproductive success (Allendorf & Luikart 2009). This phenomenon, known as inbreeding depression, can contribute to the extinction of small populations. Traditionally, conservation efforts have focused on demographic factors such as population size and structure (Jamieson & Lacy, 2012). However, it is now clear that genetic considerations are critical to the long-term success of conservation.

Genetic rescue has emerged as a strategy to combat inbreeding depression by introducing genes from closely related populations to improve genetic diversity and population fitness (Tallmon et al., 2004; Bell et al., 2019). It aims to mitigate the risks of inbreeding depression by strengthening genetic health through gene flow. The correlation between genetic parameters such as heterozygosity and demographic outcomes has been widely documented, highlighting the central role of genetics in the health and persistence of populations (Agudo et al. 2012, Terrell et al. 2016, Velando et al. 2015). Genetic rescue has been shown to be particularly effective for small, isolated populations struggling with inbreeding. In summary, inbreeding is a serious threat to endangered species, exacerbated by factors like population fragmentation. Genetic rescue offers a promising solution by introducing genetic diversity from related populations, thus improving the fitness and long-term viability of endangered populations. This integrated approach underscores the importance of genetics in conservation biology and highlights the need to consider genetic factors alongside demographic ones for effective conservation strategies.

6 Lynx Movement

Movement is one of the most studied yet least understood concepts in ecology and evolutionary biology. It has been considered as a glue cementing subpopulations and allowing connections between usually isolated populations (Waser et al. 2001, Wiens 2001). Movements have consequences for individuals as well as for populations and communities, and their effects on inclusive fitness are ultimately the selecting forces for dispersal, migration, exploration, and other types of movement that affect the distribution, abundance, and dispersion of individuals (Clobert and Wolff 2001).

Understanding animal movement is fundamental to interpret spatial-temporal patterns of habitat selection, foraging behaviour, and the interactions between predator and prey (Bell 1990). Animal movements are influenced by intrinsic physiological factors (e.g., hunger and reproduction) and the sensory capabilities of organisms. Spatial structure also influences movement as long as there is a perceived difference in quality of the varying cover types as individuals search for resources such as food, mates, or den sites or use different cover types to avoid intraspecific and interspecific agonistic encounters (Zollner and Lima 1997).

Eurasian lynx movements are related to the needs of foraging, mating and rearing of young. Eurasian Lynx have two main types of movement during their lives: dispersal, which occurs when they are sub-adult to establish their own territories, and movement within their partly huge home ranges throughout their lives. The latter may show a seasonal pattern depending on the topography (mountains) and seasonal prey availability. Despite its relatively small size, this species uses large home ranges, therefore their moving paths are longer, too (Schmidt et al. 1997). The movement paths of an individual arise from sequential decisions regarding their needs and perceptions of the surrounding habitat, and it is these decisions that ultimately give rise to the functional connectivity of the landscape (Tracey et al. 2013). Eurasian lynx is a highly territorial species and if individuals are to maintain their rights to a territory, they need to move fast and widely enough to advertise their presence over as much area and in as short intervals as possible. Movements within established territories of resident lynx are often cyclical/seasonal, with core areas of their home range being used more than the rest. Core areas usually have features and resources that are of high value to the lynx: abundant prey, preserved forests, potential den sites, low anthropogenic disturbance, etc. Home ranges are traversed throughout the animals' lives to mark, hunt and raise their young. Mothers with young usually stay near the natal den from the end of May to the first half of July and then roam the surrounding areas in search of prey.

GPS tracking in Dinaric mountains revealed movements of the lynx were primarily affected by daytime period, time since the last kill/den translocation, lynx demographic category, and their interactions (Krofel et al. 2013). The lynx tended to stay closer to the prey immediately after the kill, but were found increasingly further away, especially during the day, as the time progressed. This effect was especially pronounced in the females with immobile kittens, but was practically nonexistent in the subadult male. There was a notable difference in movement pattern of female lynx during the consumption process in the period of denning (Krofel et al. 2013). While their kittens were immobile, the females were frequently found further away from the kill compared to when they were alone or had mobile kittens, as they kept regularly returning to the den site. This was particularly the case during daytime, when the females spent a lot of time at the den site.

A home range is the area in which an animal lives and moves on a periodic basis. It is among the most basic of ecological parameters that is regularly described for a given species. An understanding of the requirements for use of space is fundamental for species management and conservation (Schwartz 1999). Furthermore, home range size is one of the most important parameters in producing population estimates. It is important to know how much space individuals need when estimating potential carrying capacities to plan conservation or recovery programs (Schmidt et al. 1997). Home range size is not easy to determine. One big problem is that home ranges vary greatly between interspecific and intraspecific samples. While some interspecific variations in home range can be explained in body mass and feeding styles (Guarino, 2002) in many cases patterns of space-use within species vary by factors of 10 to 1000 (Gompper and Gittleman 1991). Another problem is the variety of concepts, methodologies and estimators used to determine home ranges within and between species. The simplest estimator of a home range from a set of location data is the minimum convex polygon (MCP) (Mohr 1947) that has been widely used in Eurasian lynx studies, although it has many drawbacks including often overestimating the size of home ranges (Burgman and Fox 2003). The other estimators, especially in more recent studies, that have been frequently employed for constructing utilisation distribution home ranges in lynx are the so-called (fixed or adaptive) kernel density estimators (Worton 1989, Burgman and Fox 2003).



Dispersal

Dispersal is any movement of individual organisms in which they leave their home area, sometimes establishing a new home area. It is a life-history trait that influences genetic diversity, demographic viability of metapopulations (e.g. by increasing fitness) and range shifts (Tesson & Edelaar 2013) and is a crucial parameter in population dynamics, especially for threatened subpopulations within a metapopulation (Levins 1970, Hanski 1999). Dispersal alone can contribute to the recovery of a population if the reasons for decline are demographic or genetic in nature. Ultimate mechanisms most likely to affect dispersal are environmental variation and demographic structure. Direct mechanisms include genetics, competition, individual fitness and (breeding) habitat selection. These act through the fitness traits of survival and reproduction. If dispersal enhances these functions, it will be selected for independently of whatever proximate factors may serve to trigger it (Shields 1982). Another evolutionary issue is the fitness that often follows successful colonisation of empty habitat or the discovery of new habitat beyond the species' current range. Possibility of inbreeding or outbreeding depression are also potential concerns (Shields 1982). A final evolutionary issue concerns the maintenance of an appropriate level of genetic variability in a population (e.g. Cooper and Kaplan 1982). This is often seen as a population-level process involving the long-term probability of demic survival and reproduction. A distinction can be made between reproductive dispersal, i.e. the subsequent movement between sites or groups, and natal dispersal, i.e. the movement of an individual from its place of birth or previous breeding site to the site where it potentially reproduces (Zimmermann 2004). Ultimate factors are the selective forces that determine the evolution of behaviour. The most important factors that drive an individual into a dispersal are: genetic predisposition to disperse, local population density, habitat change, age of the individual, reproductive status and disturbance perturbation (Zimmermann 2004). The decision to stop dispersal may involve various elements of habitat or patch selection, such as attraction of conspecifics, habitat quality or physiological factors (Wiens 2001).

The chances for successful dispersal depend on the connectivity of the landscape and is consequently decreased in intensively used landscapes i.e. matrix by barriers mostly imposed by humans, such as traffic infrastructure and the loss of suitable habitat (Schadt et al. 2004). Dispersal allows a species to recolonize former habitats after severe range depression. Natal dispersal rate and dispersal distances are generally male biased in mammals and female biased in birds (Greenwood 1980, Dobson 1982, Clarke et al. 1997). However, the significance of dispersal for the spread of a population is less obvious in felids. Natal dispersal patterns are generally male biased for large solitary felids (Smith 1993, Beier 1995, Maehr et al. 2002), whereas the patterns are less clear among the four species of the Lynx genus, with no clear patterns within species and findings ranging from male biased dispersal (Mowat and Slough 1998, Mowat et al. 2000, Schmidt 1998, Janec̣ka et al. 2007) to male and female lynx dispersing equally far and with equal frequency (O'Donoghue et al. 1997, O'Donoghue et al. 1998, Ferreras et al. 2004, Zimmermann et al. 2005, Campbell and Strobeck 2006). The long-range dispersal of Eurasian lynx in their second year of life is sex-dependent. Lynx kittens stay with their mother on average for 10 months, after which they disperse. Dispersal age usually varies from 8 to 24 months (Breitenmoser et al. 1993; Schmidt 1998; Zimmermann et al. 2005; Samelius et al. 2012). While females are philopatric and only occasionally travel long distances, such long-distance movements (often up to several hundred kilometres) are more common in males (Samelius et al. 2012, Herrero et al. 2020). This dispersal pattern in lynx (and other cat species) prevents inbreeding and is also important for the exchange of genetic information and thus for ensuring the genetic health of populations. Dispersal is also associated with the expansion of a species' range (Thompson and Jenks 2010), which is particularly important for the recolonization of areas where the species has been eradicated. In this respect, it is necessary to maintain or achieve connected populations and suitable habitats to ensure the prevention of inbreeding and to ensure a high level of genetic diversity and thus long-term survival. Outside the populations of the large and continuous boreal forests in Asia, lynx

populations exist in the form of meta-populations with partly unknown connectivity of sub-populations and exchange of individuals.

A study comparing dispersing lynx from populations in the Nordics, Baltics, and Dinaric Mountains as well as Central Europe found that the mean dispersal distance was 39 kilometres, and 68% of dispersing lynx settled within 50 kilometres (Molinari-Jobin et al. 2010) while study of large dataset of GPS tracked reintroduced and wild dispersing lynx showed median dispersing distances of 84 and 83 kilometres (Meyer et al. In preparation). Lynx tend to establish home ranges adjacent to those of other lynx (Zimmermann et al. 2005), which affects their likelihood of establishing new colonies. Thus, while a lynx population may expand in spatial size, solitary lynx are unlikely to disperse and establish entirely new, separate populations (Zimmermann et al. 2007).

Between 1988 and 2001, a comprehensive study of the spatio-temporal behaviour of subadult lynx in two reintroduced populations was conducted in Switzerland (Zimmermann 2004, Zimmermann et al. 2005, Zimmermann et al. 2007). The study was based on telemetry and other data from 39 juvenile lynx; 22 in the northwestern Swiss Alps and 17 lynx in the Jura Mountains. The lynx became independent at the age of 9.3 - 10.6 months (there was no significant difference between males and females). Mothers usually left their kittens at the edge of their territory, making excursions to the other side of their territory or even out of their home range. In most cases, the mother appeared to have abandoned the young. The reason for the separation could be the female's feeling of not being able to catch enough prey for her kittens (Molinari and Molinari-Jobin 2001). Various aspects of spatio-temporal behaviour suggest that disintegration of litters of free-ranging lynx is not caused by aggression of the female parent, as claimed by Stroganov (1962) and later by Jonsson (1984). After separation, the subadult animals usually stayed a few days near the place where the separation took place and then moved on (Zimmermann 2004). Dispersing lynx were recovered mean=41.2 km (n=14) (in Jura Mountains) and mean = 24.3 km (n=13) (in North Western Swiss Alps) away from their point of origin. In Central Europe, Eurasian Lynx dispersal distances are substantially shorter than those in Scandinavia, although individual variation is considerable. In Central Europe, males dispersed 4.5–129 km, compared to 32–428 km in Scandinavia (Breitenmoser et al. 1993; Schmidt 1998; Zimmermann et al. 2005; Samelius et al. 2012). Females in Central Europe dispersed 2–81 km compared to 3–215 km in Scandinavia (Samelius et al. 2012).

For some subadults the researchers were able to document a transient home range but most subadults established a definitive home range directly after their dispersal. Subadults from the north-west Swiss Alps and the Jura Mountains appeared to have the same dispersal potential as there were no observed differences between the two areas in the total and maximum distances dispersed. However, a larger proportion of individuals in the north-west Swiss Alps, all males, moved through unfavourable habitat but all stopped at fenced highways and turned back, except one male, which left the area. The apparent reduced ability of subadults to cross barriers led to circular dispersal (Zimmermann et al. 2007). Within the study, they did not detect any positive density dependent effects in lynx dispersal and hence could not confirm the hypothesis that high population density encourages the expansion of the population.

Similar study of various aspects of lynx natal dispersal was carried out in Scandinavia by comparing dispersal patterns of 120 radio-marked lynx in two study areas in Sweden (Sarek and Bergslagen areas) and two study areas in Norway (Hedmark and Akershus areas, Samelius et al. 2012). They found, contrary to the Swiss study, that male lynx dispersed farther than female lynx with mean dispersal distances of 148 and 47 km for male and female lynx that were followed to the age of 18 months or older. In fact, female lynx often established home ranges that overlapped or partly overlapped that of their mothers. Similarly, the dispersal rate was greater among male lynx than among female lynx, with 100% of the males dispersing compared with 65% of the females dispersing.

Methodological approaches to study habitat suitability, connectivity, and viability of lynx populations

Defining important areas for conservation based on recognized species' habitat preferences is crucial for ensuring populations' viability and persistence in a given geographical area. This is equally true for existing populations and their present ranges as is for their future ranges. To assess given species' habitat preferences and define areas of importance, constructing habitat suitability models provides a crucial first step. Habitat suitability models (also referred to as habitat distribution models, resource selection functions – Guisan et al. 2017) are a widely used analytical tool that quantifies the relationship between the distribution of studied species (populations) in a given geographical area and various environmental variables that might contribute to their choice of habitat. Apart from their role in spatial planning for prioritisation of core habitat patches for conservation of present or future species' distribution, they also provide a basis for connectivity analyses and assessment of possible connections to different populations – e.g. defining the most suitable area for establishing a stepping stone population and assessing connectivity between that and surrounding core population areas in a metapopulation scheme.

Habitat suitability models are especially important in species that appear in low densities across large extents and are difficult to spot due to their cryptic nature which makes acquiring their actual distribution in space practically impossible – as holds true also for large carnivores (Zimmermann and Breitenmoser 2002). Thanks to the rapid development of telemetry technology and modelling techniques, it is possible to get good estimates of their potential distribution and habitat preferences. Next to generalised linear (logistic regression) models (e.g. Zimmermann and Breitenmoser 2002; Zimmermann and Breitenmoser 2007; Schadt et al. 2002a; Kramer-Schadt et al. 2004; Signer 2010; Skrbinšek 2004; Cristescu et al. 2019; Potočnik et al. 2020; Hemmingmoore et al. 2020), ecological niche factor analyses (e.g. Zimmermann 2004; Basille et al. 2009; Huck et al. 2010) and other statistical methods, machine learning algorithms have proved to provide an excellent tool for habitat suitability modelling. In the field of large carnivore spatial research, MaxEnt (Phillips et al. 2006; Phillips and Dudík 2008; Becker 2013 and Oeser et al. 2023 for the Eurasian lynx), Random Forest (Breiman 2001; Ripari et al. 2022 and Oeser et al. 2023 for the Eurasian lynx) and Boosted Regression Tree (Friedman 2001) have been increasingly used and are also deemed as the three most powerful models currently available (Elith et al. 2006; Oeser et al. 2023; Valavi et al. 2021).

One particular advantage of machine learning algorithm-based habitat suitability models, like MaxEnt, is their use of presence-only data and ability to work with small datasets (Phillips et al. 2006), which is crucial for study of species like large carnivores. MaxEnt, used for construction of habitat suitability model for the purposes of these guidelines, works on



estimating the probability of distribution based on the probability distribution of maximum entropy constrained by the given data (environmental variables on observed occurrence points versus generated random background points) (Phillips et al. 2006). Habitat suitability models give a basis for estimating possible core and suitable habitat patches in existing populations' ranges (and therefore estimate the potential population size, environmental capacity) and in potential stepping stone populations' areas (and therefore estimating the possible size of stepping stone populations in the area, which could mean crucial information for viability analysis, as well as determining suitable sites for reintroductions). A broader scale of habitat suitability models is increasingly necessary in order to assess potential future distribution sites that could represent important connections (in terms of stepping stone populations' areas) between existing Eurasian lynx populations. However, extrapolation of existing habitat suitability models over large areas can be difficult due to environmental differences across geographical extent. Using largest possible datasets and testing different modelling techniques, preferably including machine learning algorithms for large-scale habitat suitability models (like it was done in Oeser et al. 2023) might be the solution for a sound ecologically informed basis for spatial planning and management at the metapopulation level.

Once the habitat patches are defined, it is important to assess the connectivity between them. Connected paths ensure enough gene flow among parts of populations or between populations, avoiding splitting them into separate segments that become more isolated and prone to (local) extinction due to loss of genetic variability (Frankham et al. 2010), which is especially important also for the Dinaric population of Eurasian lynx considering its high levels of inbreeding due to small (and related) reintroduced population and prolonged isolation (Sindičić et al. 2013; Skrbinšek et al. 2019). Connectivity analyses can be done on the level of populations in order to evaluate the permeability or fragmentation of the landscape in population's range or on the level of metapopulations to evaluate the possible gene flow among the remote populated patches. The latter is important especially in determining suitable patches for reintroductions or relocations for establishing stepping stone populations, checking whether they are within range (distance and cost-wise) for dispersing individuals and thus ensuring the long term viability of (meta)populations. Crucial corridors or potential bottlenecks can be defined between habitat patches that need to be protected or established in order to ensure connectivity between those patches, which provides important information for spatial planning in management and conservation of species in study.

Apart from least cost path (LCP) analyses, connectivity models based on circuit theory (McRae et al. 2008) have increasingly been used in the past years. Incorporating random walk theory (Newman 2005), they can provide a more accurate description of possible successful dispersal movements through a previously unknown landscape, in contrast to LCP analyses, which assume knowledge and overview of the landscape (McRae et al. 2008). The algorithms used in circuit theory based connectivity models use resistance surfaces that define the costs of individual's movement across different parts of landscape and focal nodes (habitat patches or occurrence points) in case of Circuitscape (Shah and McRae 2008; Anantharaman et al. 2020) or a moving window with a defined radius (based on known dispersal distances) to iterate the Circuitscape algorithm across the landscape in the case of Omniscape (McRae et al. 2016; Bezanson et al. 2017). The output is a cumulative current flow map which considers all possible paths, where we interpret current density as the probability of the individual moving across a given location through a random walk across the landscape (McRae et al. 2008). Corridors are then defined as high current density at pinch-points where conservation actions are crucial in maintaining or establishing connectivity for a viable (meta)population. A good example is using connectivity models for planning animal crossings across barriers such as highways, often impeding connectivity between habitat patches, where intersections of corridors and linear barriers present sites where mitigation actions are crucial (as discussed in Kuralt et al. 2023).

An important notion to take into account when designing management and conservation actions is the species' dispersal characteristics. Dispersal, defined as the movement from the site of origin to the site of reproduction or new settlement (Howard 1960), is an important life-history trait that concerns not only the dispersing individual but also the population and the species as a whole (Tesson and Edelaar, 2013), especially with regard to sufficient gene flow between (isolated) populations to prevent inbreeding and the resulting risk of local extinction (Woodroffe 2003). Dispersal allows individuals to colonise new areas and connect populations into a metapopulation to ensure their long-term survival. Understanding dispersal movements and their prerequisites is crucial for effective conservation management, such as protecting and enhancing landscape connectivity for dispersing individuals, especially in fragmented and human-dominated landscapes (Woodroffe 2003).

While direct data on dispersers through telemetry studies of dispersing individuals is immensely important, it is often difficult to catch and tag dispersing animals within a population. Thanks to large databases of telemetry data, it is possible to identify dispersal movement through various methods, one of the widely used being the net square displacement (NSD) method, which uses the straight-line distance between the starting and each subsequent

location for the movement of each individual – the shape and slope of the curve can explain the movement type of the observed individual, with the dispersal fitting a logistic regression model (Bunnefeld et al. 2011) and thus showing a positive NSD slope over time (Meyer et al. unpublished). Additionally, data from translocated animals (which are often equipped with a GPS collar) that showed exploratory behaviour upon release (also named post-release dispersal) (Topličanec et al. 2022) or long-distance exploratory movements of remnant or translocated animals can be used as a proxy for dispersal movement and consequently immensely useful in creating a large enough dataset of extra-territorial movements for further analyses (as was done in the study made by Meyer et al., unpublished).

As space-use can often differ between resident and dispersing individuals (dispersers being known as using also sub-optimal habitat when traversing the landscape, e.g. Hemmingmoore et al. 2020), knowledge of dispersal characteristics is also important in constructing habitat suitability models or designing resistance surfaces for future connectivity analyses. Connectivity analyses that consider dispersal abilities of the studied species can provide an even better ecologically informed basis for spatial planning and translocation actions to establish a well connected network of stepping stone and core populations with sufficient natural gene flow provided through dispersal for a viable metapopulation.

Another important tool informing management and conservation strategies is population viability analysis that can simulate and predict the viability of the populations through time which provides crucial information on long term viability of established or potential (meta) populations. This involves determining the populations' demographic changes in the future, their survival rate under different scenarios, or identifying variables that are important for their population growth, which may prove crucial in determining future management steps or guidelines (genetic or spatial) for vulnerable populations, including reintroduced or reinforced ones (e.g. Pazhenkova and Skrbinšek 2021; Sanchez et al. unpublished; Pazhenkova and Skrbinšek 2024, unpublished; Potočnik et al. 2009; Heurich et al. 2018; Kramer-Schadt et al. 2005). Individual-based genetic-demographic models (as recently done for the Dinaric and SE Alpine population by Pazhenkova et al. unpublished and Pazhenkova and Skrbinšek, 2024) can be used to evaluate the success of past translocations (reintroductions and reinforcements) and inform future genetic management strategies (e.g. additional reinforcements) in terms of predicted long-term viability of populations based on reduction of inbreeding and enhanced genetic variability (Pazhenkova and Skrbinšek 2021, 2024; Pazhenkova et al. unpublished). In the case of the Dinaric population of Eurasian lynx, Pazhenkova and Skrbinšek (2021, 2024) have shown that even though recent reinforcements have increased the probability of population survival, the success is short lived and would need additional reinforcements of 5-10 animals every 10-20 years to maintain a viable population if it continues to live in isolation from surrounding populations. A spatially-explicit individual-based model of population viability recently done on the Alpine populations (Sanchez Arribas et al. unpublished), for example, showed an improvement in the viability and connectivity in the established SE Alpine population and predicted the most reliable patches for future establishment of stepping stone populations together with the minimum number of released individuals in order to connect Alpine populations into a viable metapopulation.

Other important variables that can be simulated and predicted through population viability analyses are factors leading to lynx mortality (such as poaching or traffic mortality) which should also be addressed in future management plans (Sanchez Arribas et al. unpublished, Pazhenkova et al. unpublished).

8 Modelling habitat suitability and connectivity for lynx in the Alps, Dinarics and Balkan region

Habitat suitability modelling and distribution of core and other suitable habitat patches

For the purposes of these analyses, a habitat suitability model was created using MaxEnt machine learning algorithm for a large study area ranging from Jura and the NW Alpine lynx populations on one side and Balkan and Southern Carpathian lynx populations on the other. Telemetry data from 42 individual lynx (from Dinaric, SE Alpine and Kalkalpen populations) were used as occurrence points on the background of five environmental variables – altitude, human footprint index, tree cover density, surface roughness and aspect. The model was later used to define highly suitable habitats, termed 'core' and other 'suitable habitat' patches, based on the suitability values at occurrence points (0.68) and the arbitrarily set threshold (0.5), respectively, including only patches larger than 10 km² to avoid using small fragments of core or other suitable habitat. The constructed habitat suitability model (Figure 1) shows that less populated, forested areas at medium altitudes are preferred, as high altitudes pose a natural barrier limiting their movement while low altitudes are usually densely populated. It shows large patches of suitable habitat in the massifs of Balkan peninsula, stretching from Dinaric mountains in the northwest to Pindus mountains in the south, to the edge of Carpathians and Balkan mountains in the east

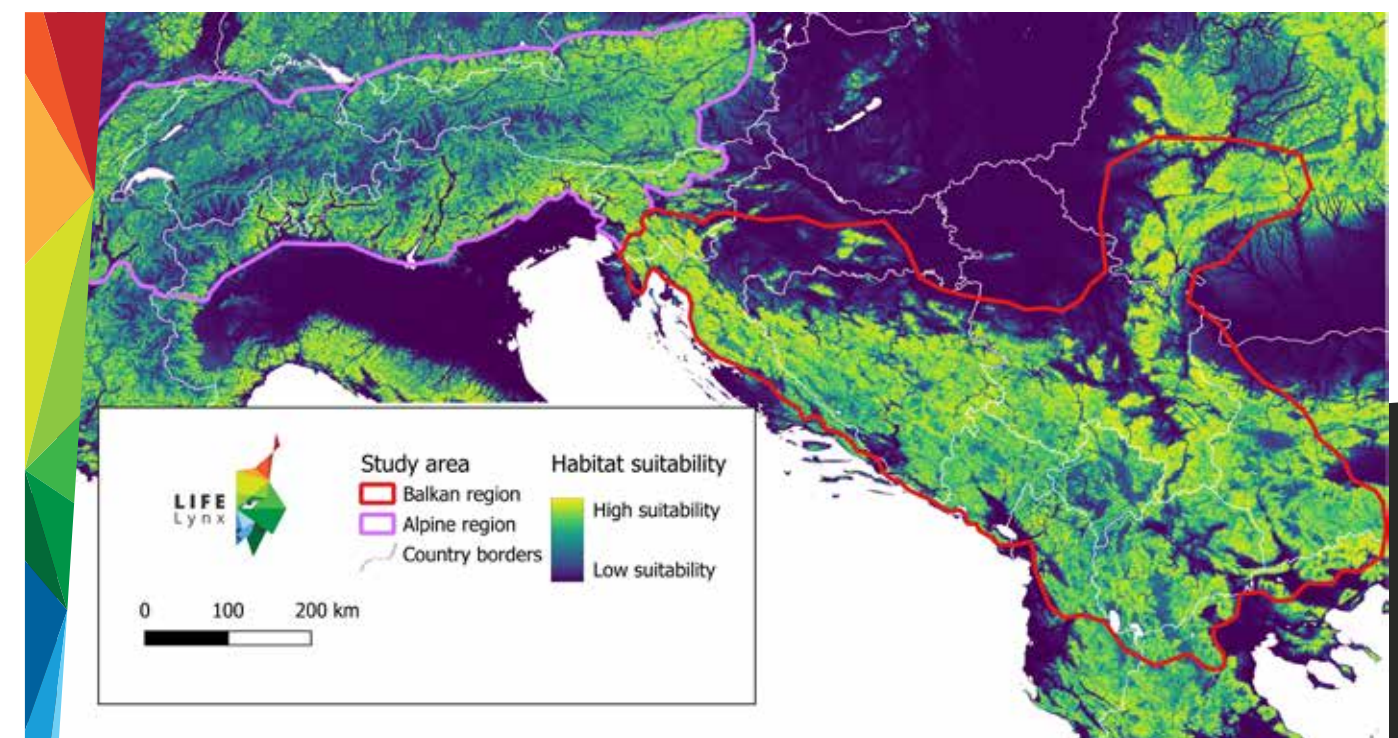


Figure 1. Habitat suitability model for Eurasian lynx in Alpine (purple outline) and Balkan (red outline) region.

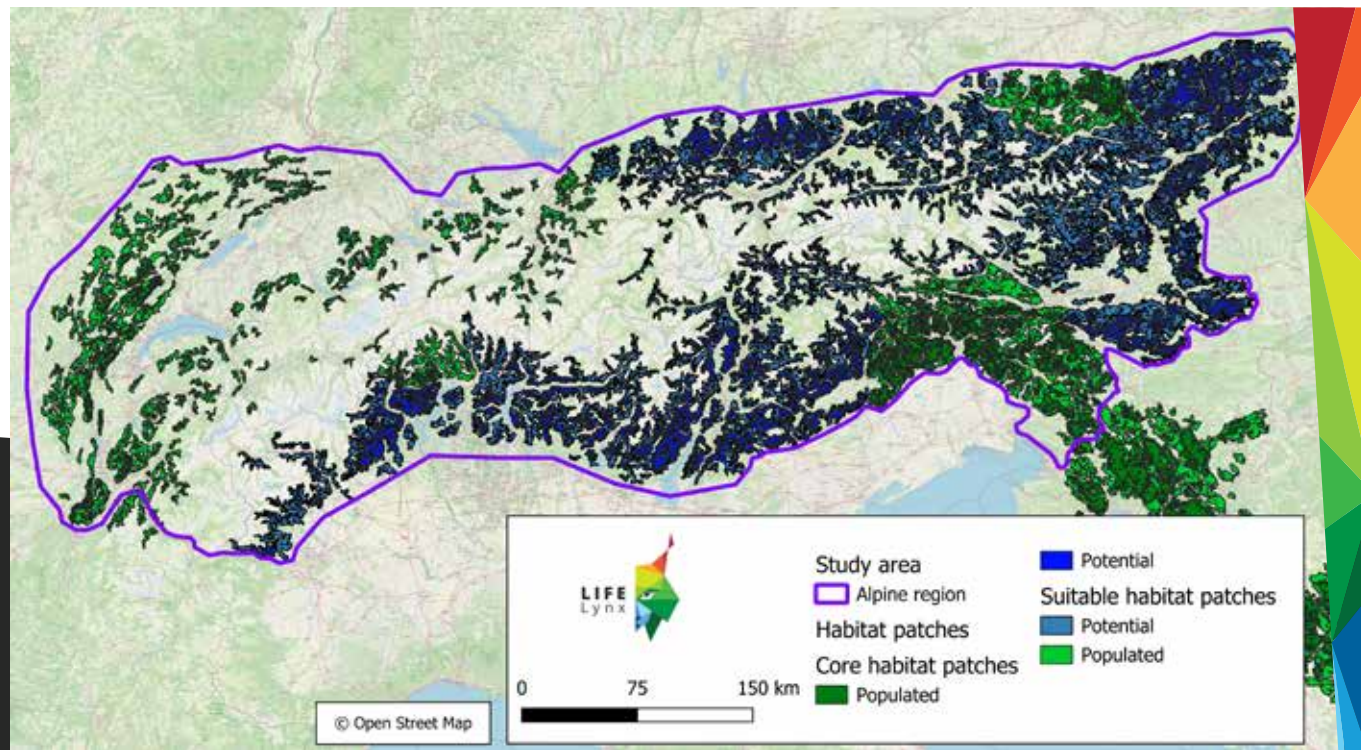


Figure 2. Suitable and core habitat patches for Eurasian lynx in the Alpine region. Populated patches are shown in green, potential patches in blue, both with darker tones for core and brighter for suitable patches.

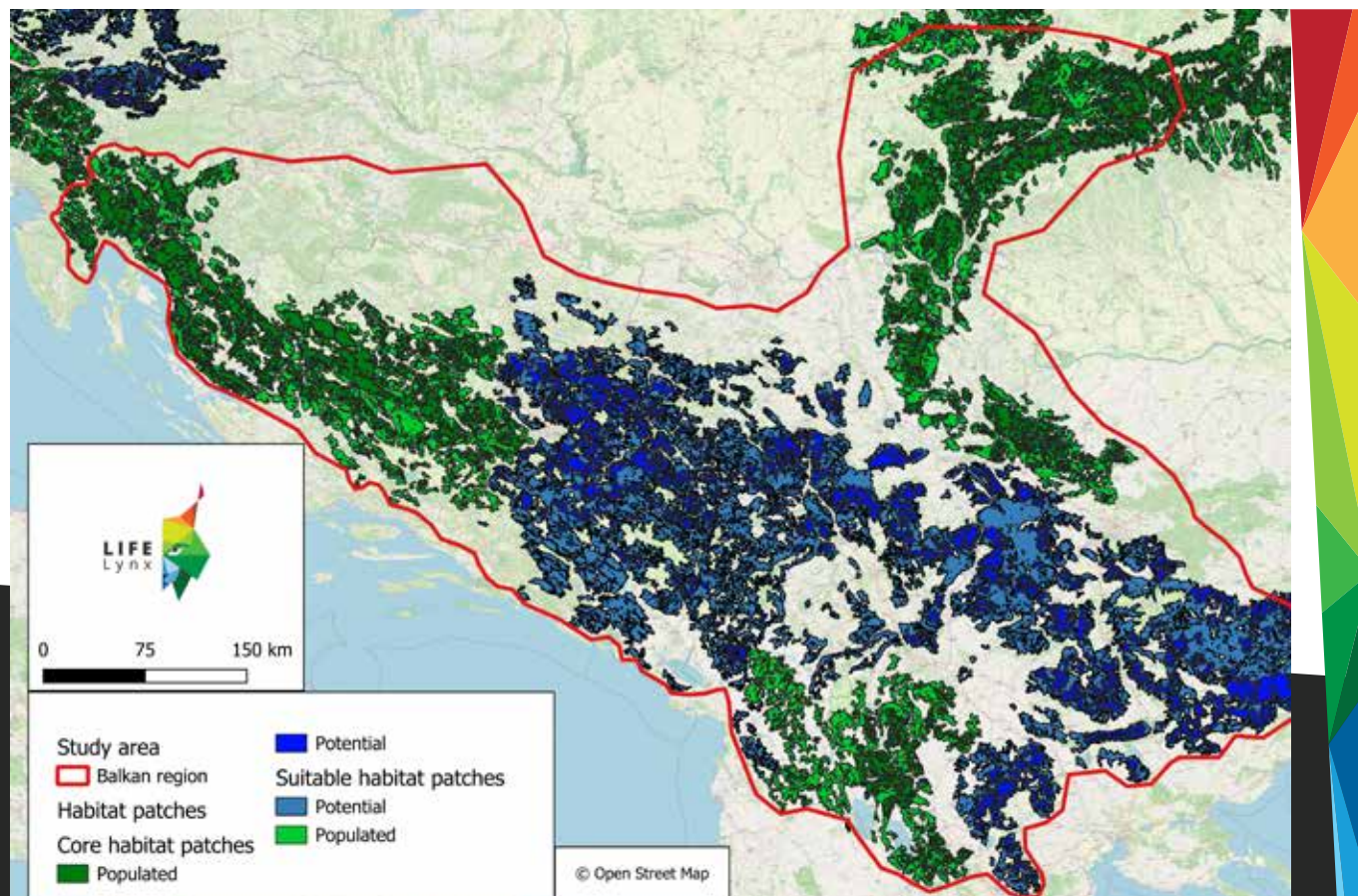


Figure 3. Suitable and core habitat patches for Eurasian lynx in Balkan region. Populated patches are shown in green, potential patches in blue, both with darker tones for core and brighter for suitable patches.

and Rhodope mountains in the southeast. Dinaric and other Balkan regions showed more suitable habitat for lynx compared to Oeser et al. (2023) model, however since our model was created using local data it might indicate better fit for that region. In the Alpine region, it shows smaller patches of suitable habitat on the northern and southern edges of the Alps, showing belts of suitable habitat below high altitude mountain ridges and above the valleys. The difference possibly resides in lynx habitat in the Alpine region being restricted by heavily populated valleys on one side and high altitude mountain ridges on the other side, whereas Dinaric mountains are less densely populated even at lower altitudes.

Populated and potential stepping stone areas	Core habitat (km ²)	Other suitable habitat (km ²)	No. patches (core / suitable)	Range of patch sizes [km ²] (core / suitable)	No. patches >= 200 km ² (core / suitable)	No. females (core / suitable) by area	No. males (core / suitable) by area	No. females (core / suitable) by patches	No. males (core / suitable) by patches
Jura and NW Alps	746.5	9348.25	25	10.25 – 131.4999	0	5	3	0	0
			103	10 – 3250.25	7	68	44	43	24
Kalkalpen	520.25	2135.5	8	10.25 – 323	1	3	2	1	1
			1*	2135.5	1*	13	9	13	9
SE Alps	2490.75	6932.5	16	11 – 865.9996	3	12	7	9	5
			1*	1426	1*	35	21	35	21
Dinaric	8142.5	22056	51	10.25 – 1327.75	10	45	36	31	24
			20	10.5 – 21265	1	123	99	119	95
Balkan	1491.93	8657.75	26	10.5 – 452.75	2	12	3	6	1
			7	11.25 – 7037.499	2	72	23	71	22
Western – Eastern Alps	7292.75	35493.99	121	10.25 – 12691.5	8	40	24	22	11
			78	10.5 – 5313.499	12	198	128	176	110
Northern Alps	1070.75	8106.5	17	10.25 – 506.75	2	6	4	9	4
			34	10.5 – 3312.57	3	48	32	36	23
Southern Alps	3479.25	14263.99	63	10.5 – 415.75	4	19	11	7	3
			33	10.75 – 5313.499	8	78	49	68	40
North-eastern Alps	2742.75	13123.5	41	10.25 – 1078.75	2	15	9	6	4
			11	12.5 – 12691.5	1	72	47	72	47
Dinaric - Balkan – S Carpathian (part)	14882.25	63528.02	157	10.25 – 1245.75	17	100	53	51	19
			56	10 – 43269.5	12	429	206	333	157

Table 1. Core and other suitable habitat areas, number of patches and their sizes and potential number of resident female and male lynx in populated and potential stepping stone areas. Data for the South Carpathian area is not shown due to using only a part of the whole area based on study extent.

Based on the habitat suitability model, we extracted core and other suitable habitat patches and categorised them into populated (based on lynx populations' distribution data of Kaczensky et al. 2021) and potential (possible stepping stone populations) habitat patches (Figure 2 and 3) that could present bridges between existing lynx populations. Similar to Schadt et al. (2002b), we also dissolved adjacent patches within 1 km distance and considered them connected as one. As already seen in the habitat suitability model (Figure 1), the patches in the Alpine region (Figure 2) are smaller and more fragmented than patches in the Balkan region (Figure 3).

We were able to assess the surface of core and suitable habitat in the populated and potentially populated areas and estimate the number of territorial individuals (male and female separately) that could reside in these patches or areas (similar to Kuralt et al. 2023), using data of home range sizes of Eurasian lynx from literature or accessible telemetry data for the population in question (Breitenmoser et al. 1993; Breitenmoser-Würsten et al. 2001; Potočnik et al. 2020; Kuralt et al. 2023; Melovski et al. 2020) and using the averages of home range sizes of neighbouring populations for potentially populated areas. We clustered patches into 5 populated areas (Jura and NW Alps, Kalkalpen, SE Alps, Dinaric, Balkan) and 4 potential areas (N Alps, S Alps, NE Alps, Dinaric-Balkan-S Carpathian), as shown in Table 1 and in Figure 4 and 5. Apart from determining core and suitable habitat areas, number of patches, their size ranges and number of possible individuals these patches or areas can hold (shown in Table 1), we also show core and suitable habitat areas in each country for respective population areas (Figure 4 for Alpine and Figure 5 for Balkan region).

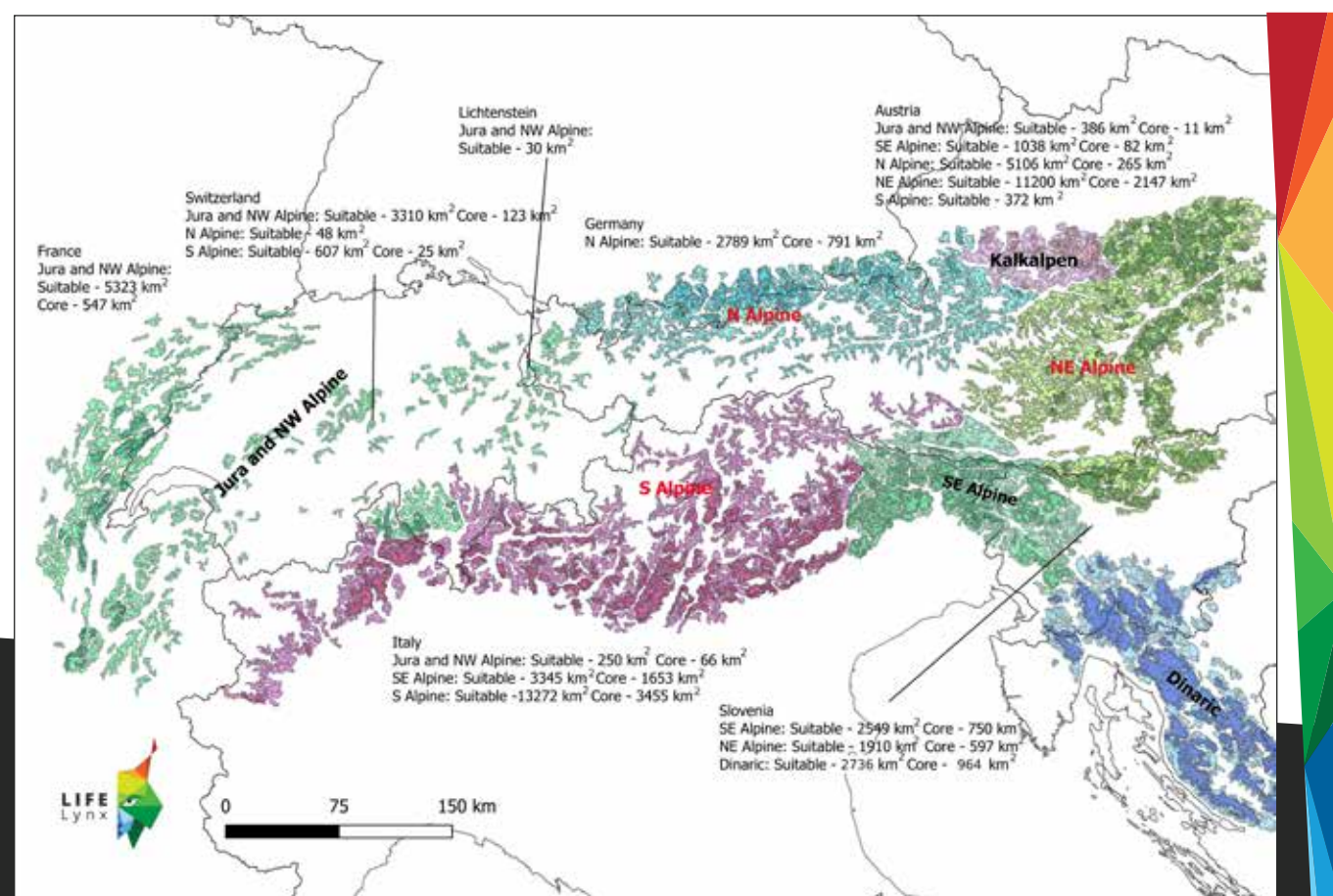


Figure 4. Core and other suitable habitat areas in countries for respective population areas in the Alpine region. The areas represented are only part of the areas in question for this study, other populated or potential population areas (such as Vosges mountains, BBA population or potential suitable areas in the Apennines) are excluded.

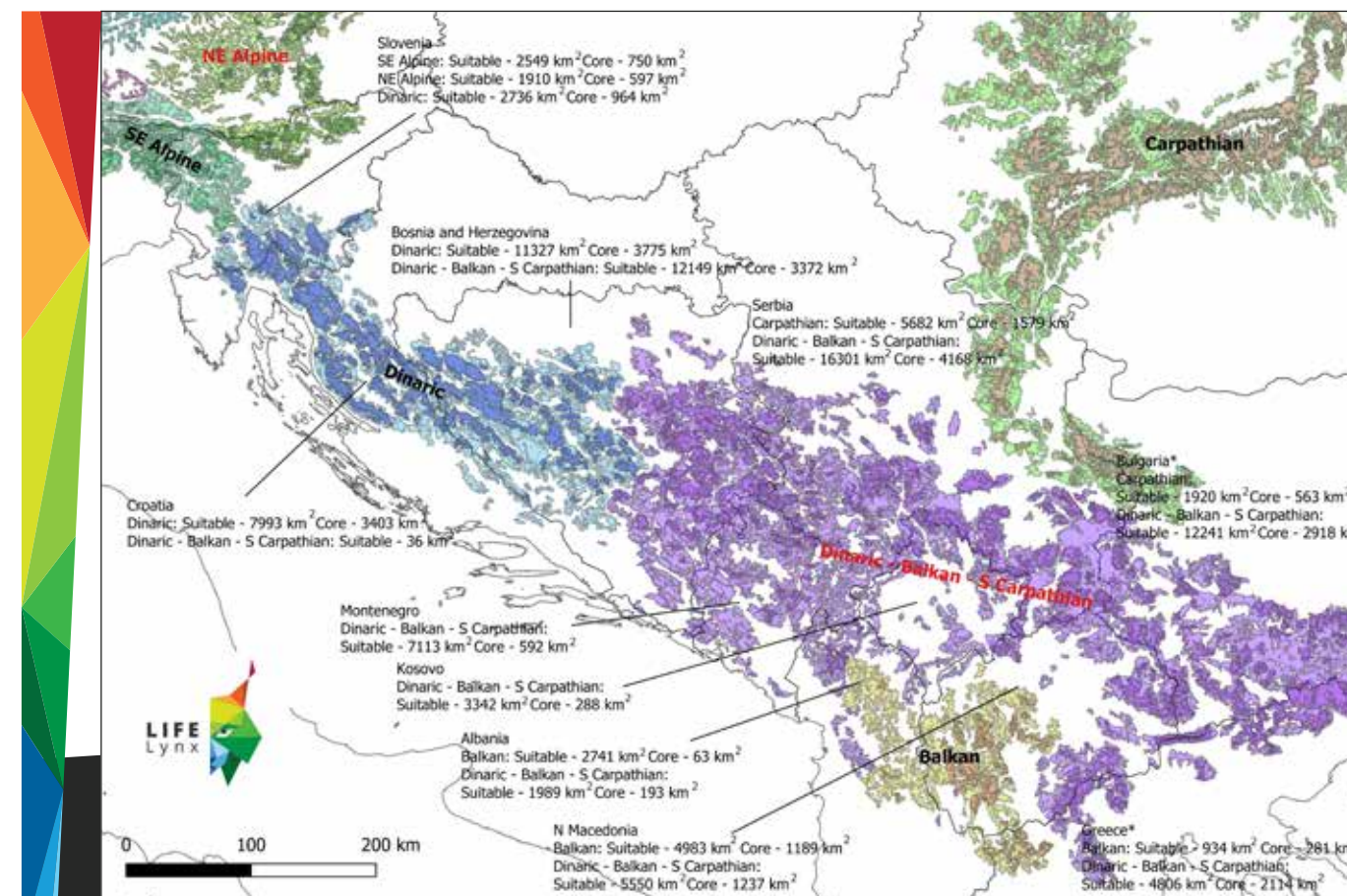


Figure 5. Core and other suitable habitat areas in countries for respective population areas in the Balkan region. The areas represented are only part of the areas in question for this study, other populated or potential population areas (such as suitable patches in Slavonia in Croatia or in eastern Slovenia) are excluded. Suitable and core areas in Bulgaria and Greece were only partially included in this study so the resulting areas should be considered with caution.

Extra-territorial and non-territorial movements

To analyse the extraterritorial movements of individuals from telemetry studies within the LIFE Lynx project, we used the lsmnsd package in R (Bastille-Rousseau et al. 2016) to cluster the movement data according to net square displacement (NSD) values. This approach was later combined with visual inspection of tracks and all extraterritorial/non-territorial movement paths were extracted and further analysed (as explained in Mlinarič et al. in preparation). Extraterritorial or non-territorial movements were categorised as follows: natal dispersal (when young lynx leave their mother's home range on their way to independence), post-release dispersal (exploratory movements of translocated lynx from release until home range/territory establishment, in some cases also between temporary home ranges) and excursions (a round-trip exploratory movement of territorial lynx outside of its territory), the latter being of particular interest during the mating season (February to early April) and thus called mating excursions.

Out of 30 individuals, 4 were considered territorial and showed no extraterritorial or non-territorial movements. Eight were dispersing from their mothers' home ranges, 4 in the Alps (see also Figure 6) and 4 in the Dinaric region (see also Figure 7) – the total length of their dispersal paths (sometimes divided into several sections by temporary home ranges) ranged from 96 km (Neža, Dinaric) to 860 km (Flori, Alpine); more information on dispersal paths can be found in Table 4 below. In the case of translocated lynx, 10 out of 15 individuals showed post-release dispersal movements (in some cases also divided into

several segments through temporary home ranges), ranging from 74 km (Blisk, Dinaric - Slovenia) to 481 km (Kras, Dinaric - Croatia), shown in Figure 8 for individuals released or resettled in Slovenia and in Figure 9 for individuals released and resettled in Croatia. The results also roughly correspond to post-release exploratory movement analysis done on the same (but not all) individuals by Topličanec et al. (2022) and Hočevár et al. (2024). Excursions were detected in 12 individuals, both remnant and translocated alike, with many individuals making multiple excursions throughout the tracking period, - with translocated lynx Katalin (Dinaric - Slovenia) leading the race with 13 recorded excursions.

Name of individual	Extra-territorial type	Total length [km]	Total distance [km]	Time frame
Mihec (R - M)				
e	Excursion	126.02	28.07	8.3.-20.3.2021
Klif (R - M)				
e1	Excursion	134.06	35.26	17.3.-7.4.2022
Bojan (R - M)				
e1	Excursion	33.72	23.98	17.1.-20.1.2020
Maks (T - M)				
e1	Excursion from temporary home range	303.67	76.28	26.11.2020-15.2.2021
Goru (T - M)				
e1	Excursion	223.68	57.46	1.3.-6.4.2020
e2	Excursion	219.07	43.68	19.2.-18.3.2021
e3	Excursion	126.61	25.49	8.3.-18.3.2022
Blisk (T - M)				
e1	Excursion	100.13	26.57	21.3.-6.4.2023
Katalin (T - M)				
e1	Excursion	71.85	36.35	11.3.-11.3.2021
e2	Excursion	79.27	32.82	15.3.-22.3.2022
e5	Excursion	59.12	36.18	17.3.-19.3.2023
e6	Excursion	47.75	26.14	4.4.-6.4.2023

Table 2. Long-distance exploratory movements – excursions of lynx, collared in the course of LIFE Lynx project. Total length represents the length of the extra-territorial movement path, total distance the distance between home range centroid and the farthest point of the extra-territorial movement path. Exploratory movement is shown in remnant (R) and translocated (T) individuals. In this case, only males (M) showed long-distance exploratory movements and all except Maks could be said to go on mating excursions.

The total length of excursion paths ranged from 20 km (Maks, Dinaric - Slovenia, excursion from a temporary home range) to 304 km (also Maks, excursion from a temporary home range). We also measured the total distance of extra-territorial movement paths as the distance between the centroid of home range and the furthest point of the path. Paths (post-release dispersal and exploratory) that had a total distance greater than 20 km were categorised as long-distance and are also listed in Tables 2 and 3 below. Long-distance excursions were recorded for individuals residing in Slovenia (or had a transboundary territory, as was the case for lynx Bojan) and are shown in Figure 10.

Name of individual	Extra-territorial type	Total length [km]	Total distance [km]	Distance start – centroid [km]	Time frame	Comments
Doru (T - M)						
pd	Post-release dispersal	146.85	44.39	41.5	5.5.-17.6.2019	
Emil (T - M)						
pd	Post-release dispersal	352.8	54.17	25.93	15.5.-1.10.2021	*not longitudinal but more polygonal movement
Kras (T - M)						
pd	Post-release dispersal	481.14	89.44	61.77	24.3.-17.7.2023	*not longitudinal but more polygonal movement
Lubomir (T - M)						
pd	Post-release dispersal	221.36	32	6.44	16.6.-29.8.2022	*first polygonal, then trip around until HR
Sneška (T - F)						
pd1	Post-release dispersal	26.69	19.99	19.99	26.4.-6.5.2023	
Alojzije (T - M)						
pd	Post-release dispersal	125.18	41.46	10.79	14.3.-24.4.2020	
Goru (T - M)						
pd	Post-release dispersion	113.25	40.6	15.97	14.5.-1.6.2019	
Katalin (T - M)						
pd	Post-release dispersal	207.41	58.88	25.43	31.3.-20.4.2020	

Table 3. Long-distance exploratory movements – post-release dispersal of lynx, collared in the course of LIFE Lynx project. Total length represents the length of the extra-territorial movement path, total distance the distance between established home range centroid and the farthest point of the extra-territorial movement path, fifth column of the table also shows distance from start to the centroid of established home range. Post-release dispersal was present in translocated (T) individuals, both male (M) and female (F).

Name of individual	Extra-territorial type [km]	Total length [km]	Total distance (mother HR / THR) [km]	Distance from center of natal HR / release site to centroid of HR / THR / end point [km]	Time frame	Comments
Andrej (A - M)						
d	Natal dispersal	857.9	31.911 (mother HR)	19.648 (mother HR centroid to latest point)	17.4.2023-24.3.2024 (ongoing)	*Not finished, but has some polygonal movements
Flori (A - M)						
d	Natal dispersal	860.26	52.011 (mother HR)	33.881 (mother HR centroid to latest point)	23.4.2023-22.3.2024 (ongoing)	*Not finished, but has some polygonal movements
Meri (A - M)						
d1	Natal dispersal to THR	12.7		12.816 (mother HR centroid to THR centroid) / 13.373 (start to centroid)	22.2.-24.2.2023	
e1	Excursion from THR	28.23	13.64		18.2.-21.2.2024	
d2	Dispersal from THR	106.87	16.875 (THR)	12.112 (THR centroid to end point)	10.3.-21.3.2024 (ongoing)	*Polygonal movement
Rozi (A - F)						
d1	Natal dispersal to THR	11.11	11.78 (mother HR)	8.596 (mother HR centroid to THR centroid) / 6.53 (start to centroid)	27.1.-1.2.2023	
d2	Dispersal from THR	23.89		4.672 (centroids) / 6.78 (start to centroid)	8.3.-14.3.2023	
d3	Dispersal from THR	28.83		13.564 (centroids) / 13.52 (start to centroid)	24.4.-15.5.2023	
d4	Dispersal from THR	296.08	16.179 (THR)	7.413 (THR centroid to end point)	15.10.2023-22.3.2024 (ongoing)	*Polygonal movement
Mala (D - F)						
d	Natal dispersal	134.14	9.228 (mother HR)	0.849 (mother HR centroid to end point)	28.4.-1.7.2020	*Polygonal but not distinctive HR
Neža (D - F)						
d1	Natal dispersal (attempt) / exploratory	40.64	11.929 (mother HR)		5.3.-16.3.2022	
d2	Natal dispersal (attempt)	95.97	11.794 (mother HR)	5.458 (mother HR centroid to end point)	6.4.-11.5.2022	*Killed
Valentina (D - F)						
d1	Natal dispersal (attempt) / exploratory	37.81	11.971 (mother HR)		4.3.-15.3.2022	

continue on the next page

d2	Natal dispersal	255.55	16.241 (mother HR)	11.948 (mother HR centroid to HR centroid) / 9.992 (start to HR centroid)	25.10.-26.12.2022	
Niko (D - M)						
d1	Natal dispersal	42.67	21.925 (mother HR)	23.043 (mother HR centroid to THR centroid) / 18.895 (start to HR centroid)	10.12.-24.12.2020	
d2	Dispersal from THR	47.15		32.412 (centroids) / 18.876 (start to centroid)	3.5.-19.5.2021	
d3	Dispersal from THR	26.08		25.33 (centroids) / 24.104 (start to centroid)	10.6.-18.6.2021	
d4	Dispersal from THR	103		54.503 (centroids) / 49.177 (start to centroid)	11.8.-3.9.2021	
d5	Dispersal from THR	55.28		27.026 (centroids) / 18.447 (start to centroid)	8.10.-19.10.2021	

Table 4. Dispersal movements of eight remnant individuals – from SE Alpine (A) and Dinaric (D) population, either female (F) or male (M). Total length represents the length of the extra-territorial movement path, total distance the distance between (natal or temporary) home range centroid and the farthest point of the extra-territorial movement path, where it is possible, and the distances between centroid of consecutive home ranges or between start/end point and the home range in question. The dispersal paths are segmented with several individuals as they showed home range movements (temporary home range – THR) between segments of dispersal movements and before establishing their home range (HR). In segments that do not present a "straight" line until the next (temporary) home range, total distances from centroids either of mother home range or temporary home range are calculated.

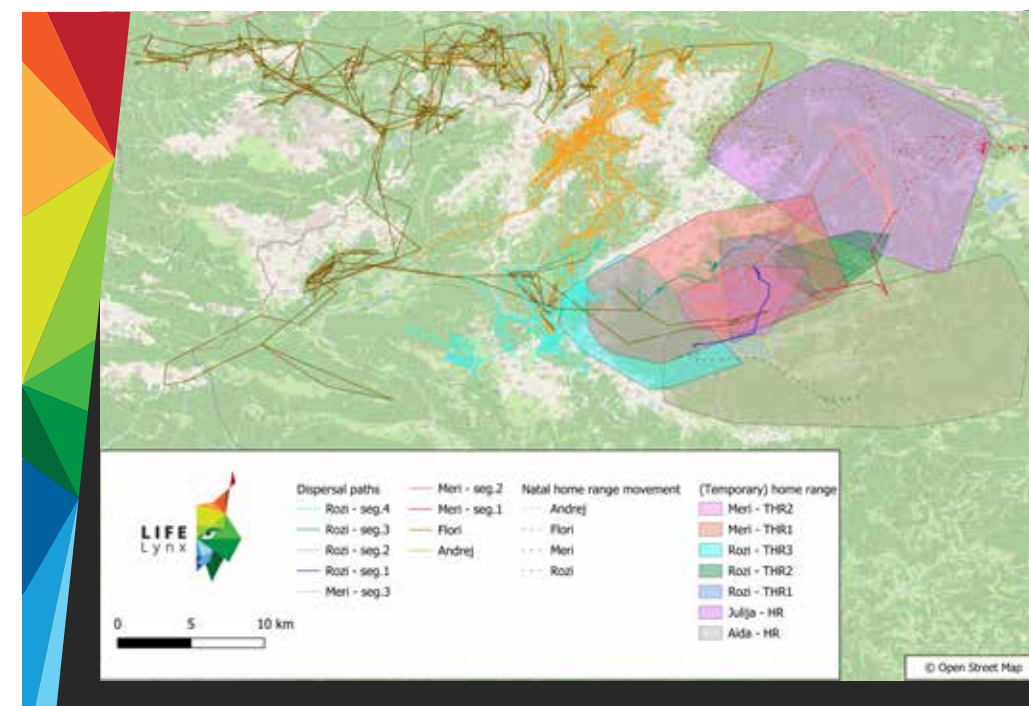


Figure 6. Dispersal paths of 4 individual lynx (Andrej, Flori, Meri and Rozi) in the Alpine region. In the case of Meri and Rozi, the dispersal path is segmented by temporary home ranges (shown as polygons). Mother home ranges (Julija for Andrej, Flori and Meri, and Aida for Rozi) are also shown as polygons on the map, together with paths of dispersing individuals still in natal home ranges (dashed lines).

Figure 7. Dispersal paths of 4 individual lynx (Mala, Niko, Valentina and Neža) in the Dinaric region. In the case of Niko, the dispersal path is segmented by temporary home ranges (shown as polygons). Last detected home range (THR5) is split in two parts (Slovenian and Croatian), with several paths (dark orange) crossing between them. Valentina and Neža attempted dispersal twice, the second resulting in (temporary) home range in Valentina's case and in mortality by poaching in Neža's case. Mother home range (Teja) is also shown as a polygon (dark brown) on the map.

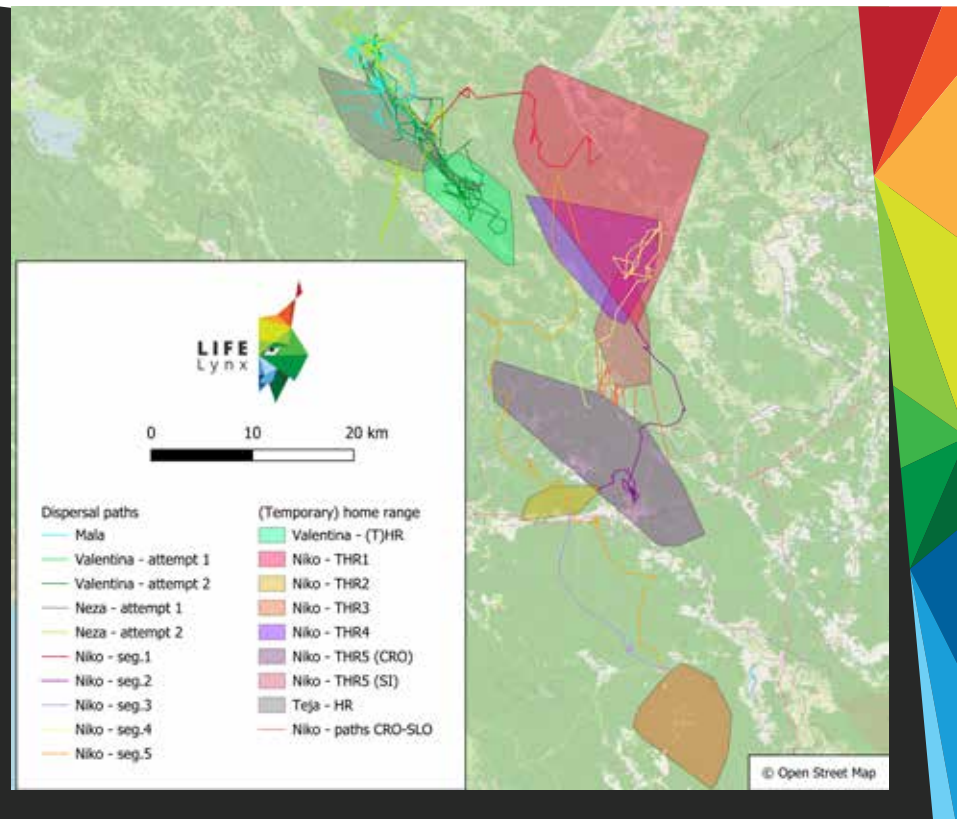


Figure 8. Post-release dispersal paths of 6 individuals released or later residing in Slovenia. Their established home ranges or temporary home ranges are shown as polygons. Sneška's and Boris' post-release dispersal paths are segmented by temporary home ranges, both also made a short excursion from the temporary home range.

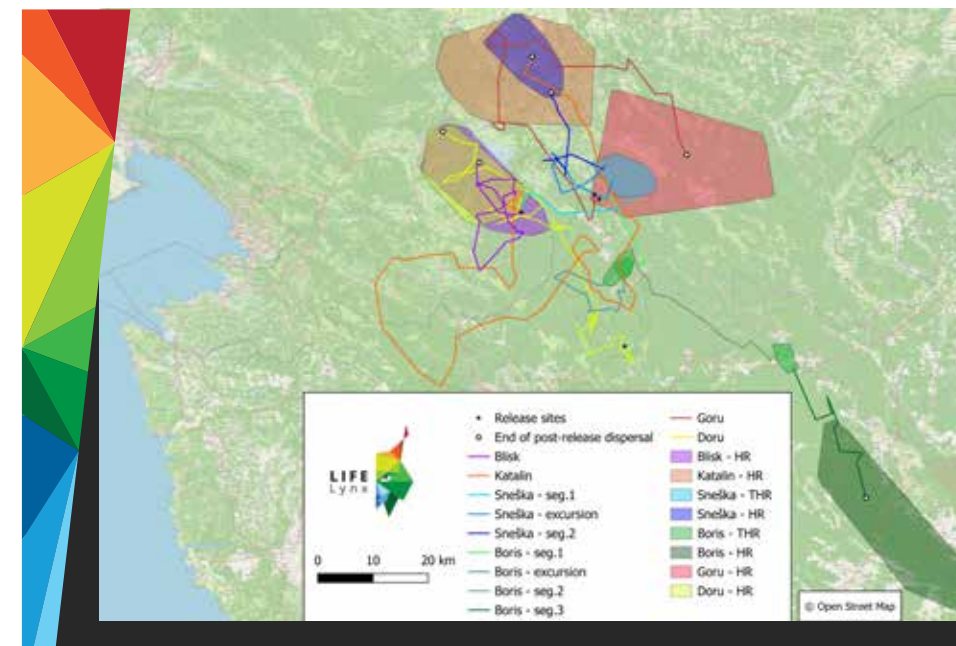


Figure 9. Post-release dispersal paths of 4 individuals released and later residing in Croatia. Their established home ranges are shown as polygons. Emil, Kras and Lubomir showed some polygonal movement that was not last long or was not concentrated enough to be classified as home range movement.

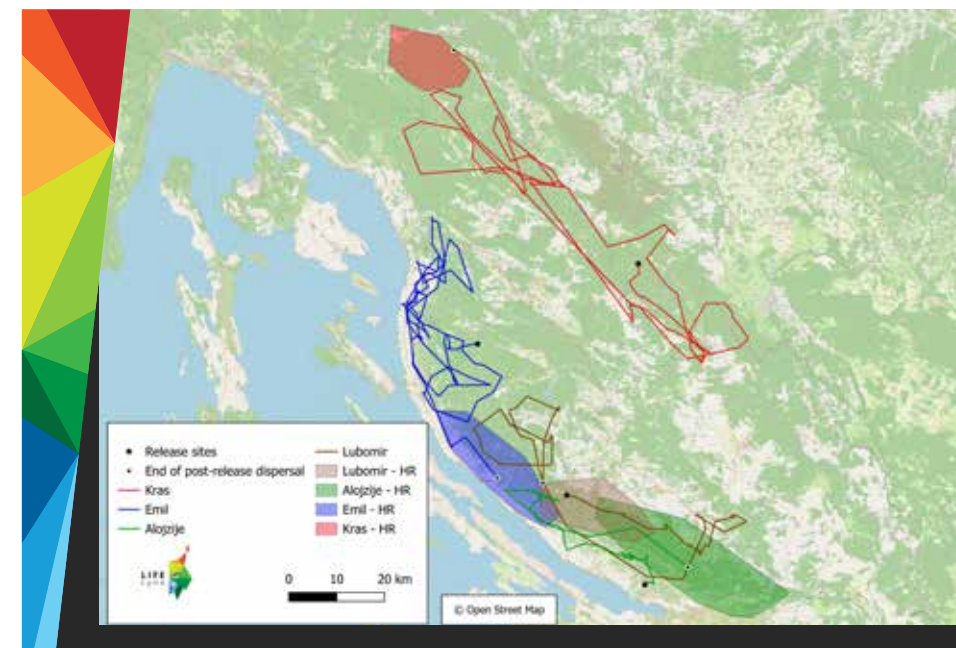
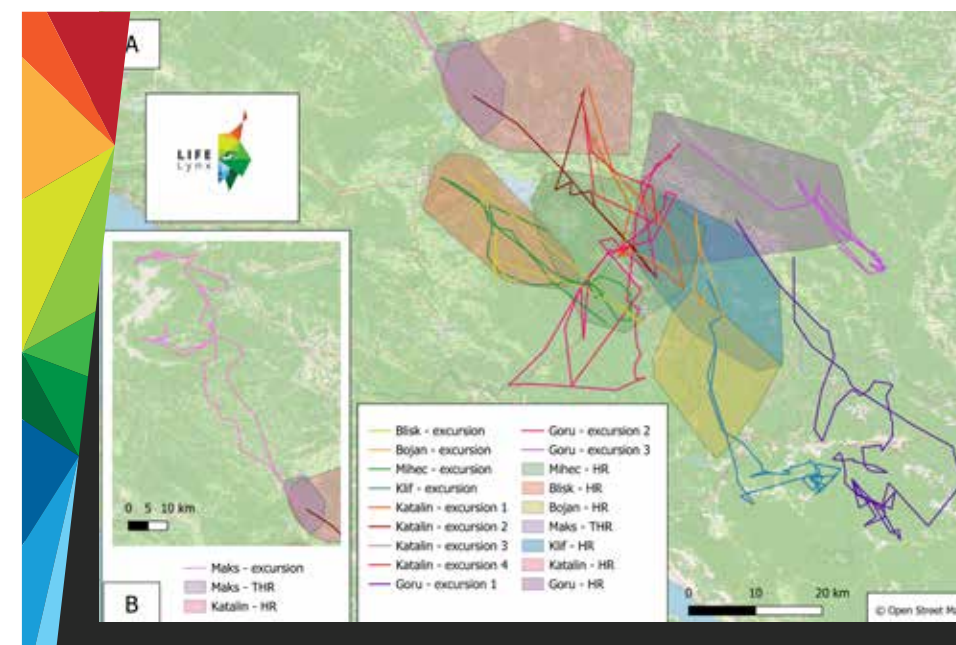


Figure 10. Long-distance excursions of 7 individuals. Their established (or temporary, in the case of lynx Maks) home ranges are shown as polygons. 11 paths are shown in part A, lynx Maks' excursion is shown separately in part B.



Connectivity

We conducted a connectivity analysis using two approaches – Omniscape algorithm (McRae et al. 2016; Bezanson et al. 2017) with a moving window radius set to 75 km (based on Kuralt et al. 2023 and Potočnik et al. 2020 information on longest dispersal distance of Eurasian lynx) and Grainscape package in R (Galpern et al. 2023). Resistance surface was created based on the habitat preferences from habitat suitability model and using the approach used in Kuralt et al. (2023). Motorway network was also included as a linear barrier, using the highest possible resistance value (100), with passages (bridges, tunnels, over- and under-passes and wildlife crossings) on the barrier reducing its resistance value. Resulting connectivity maps are shown in Figure 11 (Alpine region) and Figure 12 (Balkan region) for the output of Omniscape analysis, and in Figure 13 (Alpine region) and Figure 14 (Balkan region) combining both results from Omniscape and Grainscape analysis.

Omniscape (Figure 11, Figure 12) shows moderately high current density (landscape permeability) across larger suitable patches, meaning good connectivity with several possible pathways for individuals to choose when travelling across them, and low current density on unsuitable areas, meaning low connectivity or lower chances an individual would pass through them. However, the important information Omniscape current density maps provide, is the location of pinch-points or corridors where current density is high – these are seen in the case of smaller or narrower suitable patches, surrounded by otherwise unsuitable landscape, or between adjacent suitable patches, thus showing a possible corridor or path connecting neighbouring patches. If areas with moderately high current density call for large-scale protection of suitable habitat, corridors with high current density mean a need for management measures ensuring connectivity among and inside those suitable areas. The cumulative current value of 1.5 was taken as a threshold showing corridors or high current density areas (shown in Figure 13 and Figure 14).

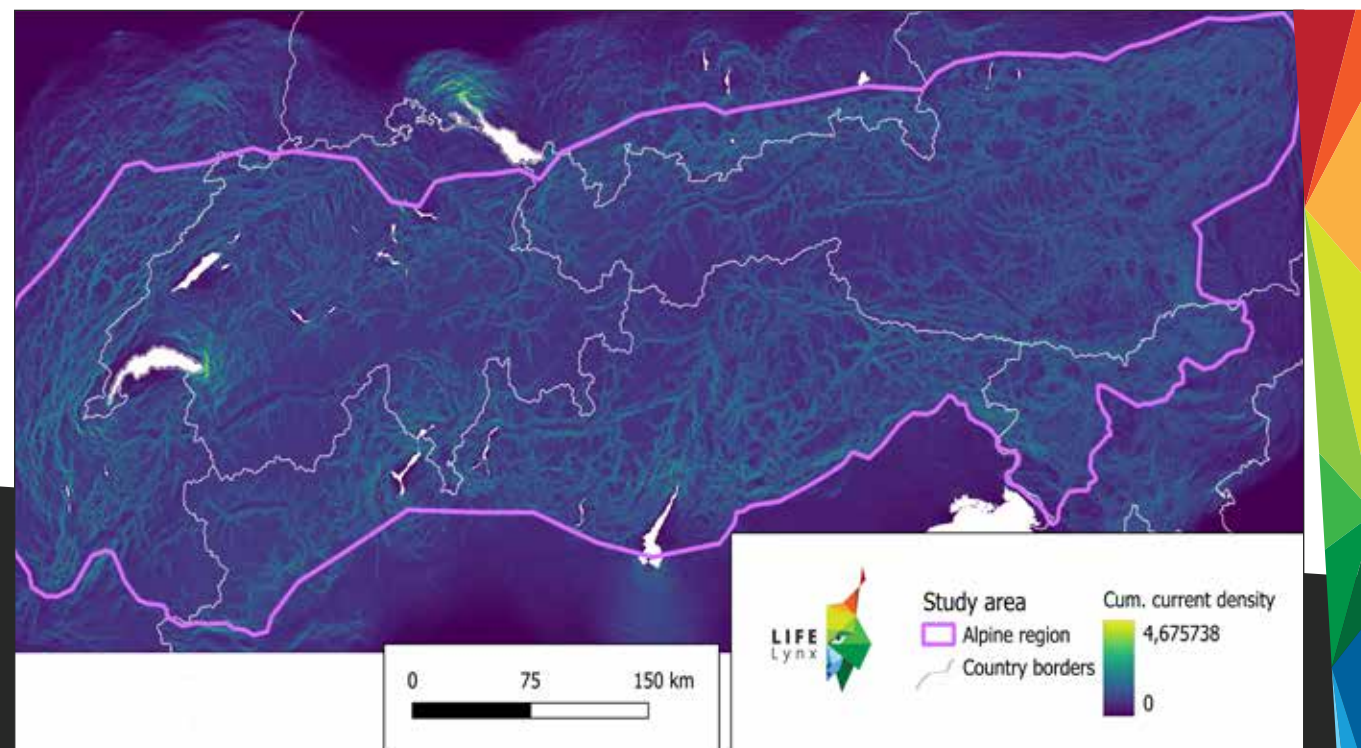


Figure 11. Omniscape connectivity results for the Alpine region. Cumulative current density, shown on the map, can be interpreted as the probability that a random walking lynx individual would pass through a specific cell on the map. High density thus means high chances of passing through, identifying corridors and narrow paths in need of protection.

For grainscape analysis, we used long-distance exploratory (excursions and post-release dispersal) tracks and entire dispersal tracks from lynx tracked during LIFE Lynx project, described above, together with data from 2 individuals from UlyCA2 project and 3 individuals from Kalkalpen population, in order to calculate cumulative costs of extra-territorial paths. Grainscape output provided least cost paths connecting suitable habitat patches with various cumulative costs, we extracted the paths with cumulative costs below 908 threshold – the median of cumulative costs extra-territorial paths – and the paths with cumulative costs below 5147 threshold – the value at 95th percentile of cumulative costs of extra-territorial paths. The results show 596 (below median threshold) and 796 (below 95th percentile threshold) least cost paths in the Alpine region (Figure 13) and 392 (below median threshold) and 520 (below 95th percentile threshold) in the Balkan region (Figure 14). The thresholded least cost paths show whether habitat patches could be connected through dispersal (either short-scaled dispersal movement, taken into account through the median threshold, or by exceptional long-distance dispersal, taken into account through 95th percentile threshold), and if so, where the most important corridors for connections are, providing crucial information on areas in need of protection. While the balkan region seems fairly well connected, especially due to large patches of suitable habitat, the alpine region shows a lack of connection between the western and eastern Alpine populations. The reason could lie in the barrier-like areas of low suitability in populated valleys or across high-altitude mountain ridges, as was already explained above.

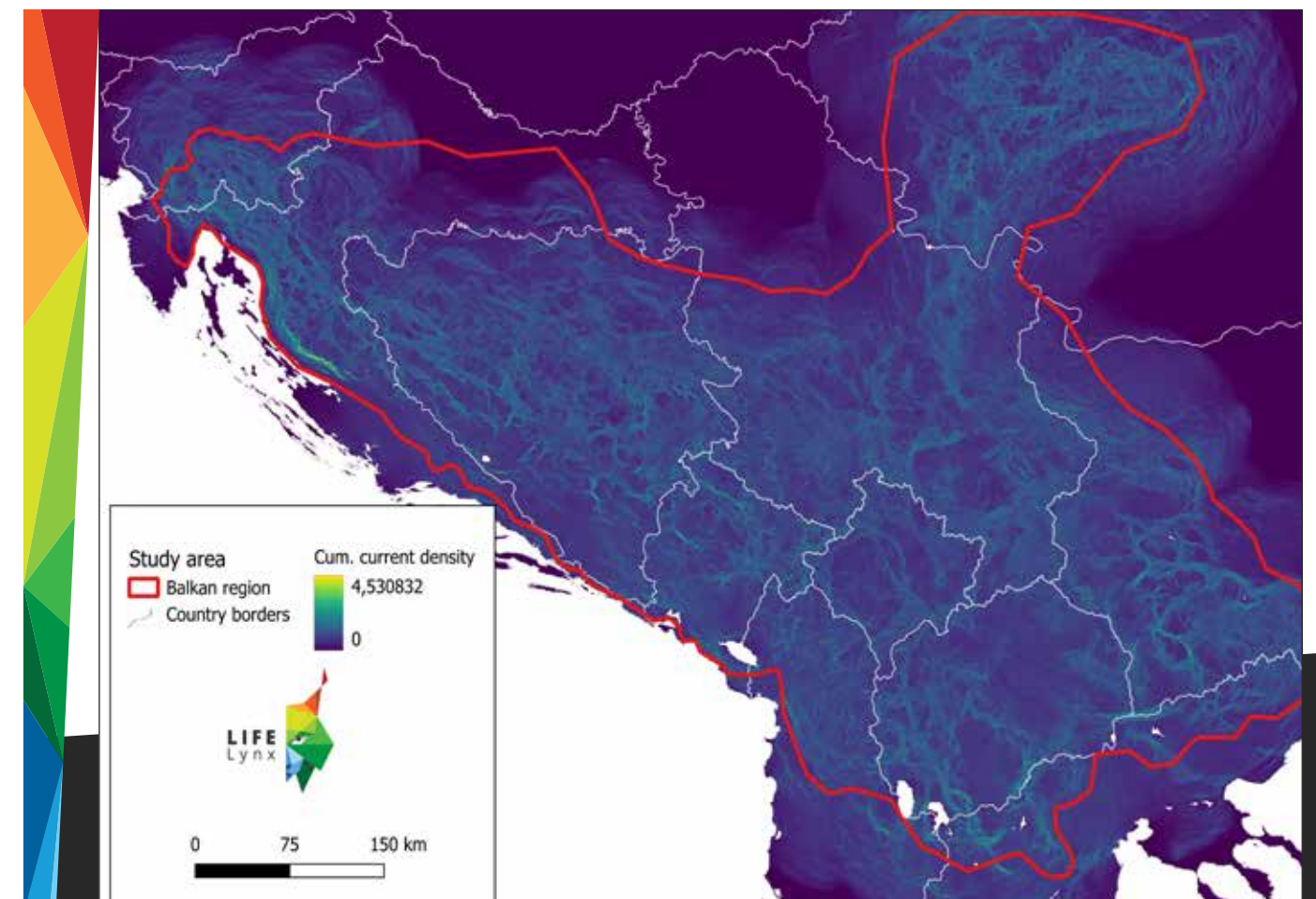


Figure 12. Omniscape connectivity results for the Balkan region. Cumulative current density, shown on the map, can be interpreted as the probability that a random walking lynx individual would pass through a specific cell on the map. High density thus means high chances of passing through, identifying corridors and narrow paths in need of protection.

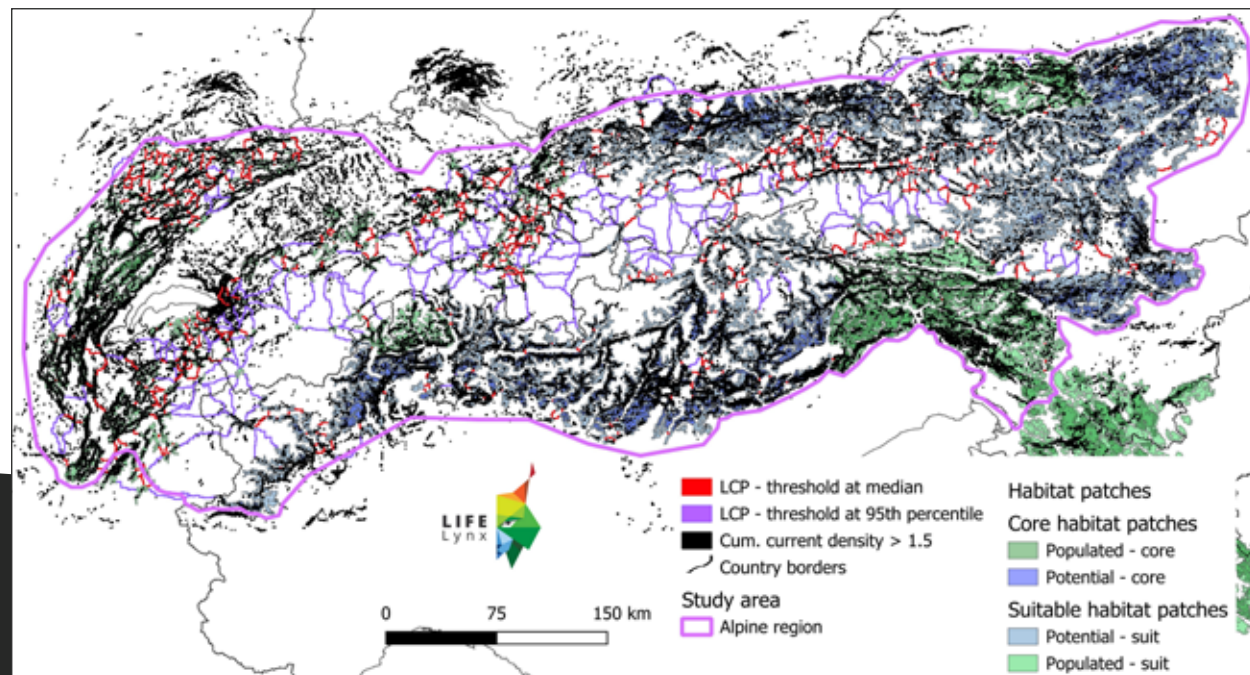


Figure 13. Connectivity of Alpine region. Results from Omniscape above the 1.5 threshold (black) and from Grainscape LCPs with thresholds at median (red lines) and 95th percentile (purple lines) of extra-territorial paths' cumulative costs are presented, together with populated and potential suitable and core habitat patches. The map shows less connections with shorter (median threshold) paths between West and East Alpine region, but the connection is established with longer (95th percentile) paths.

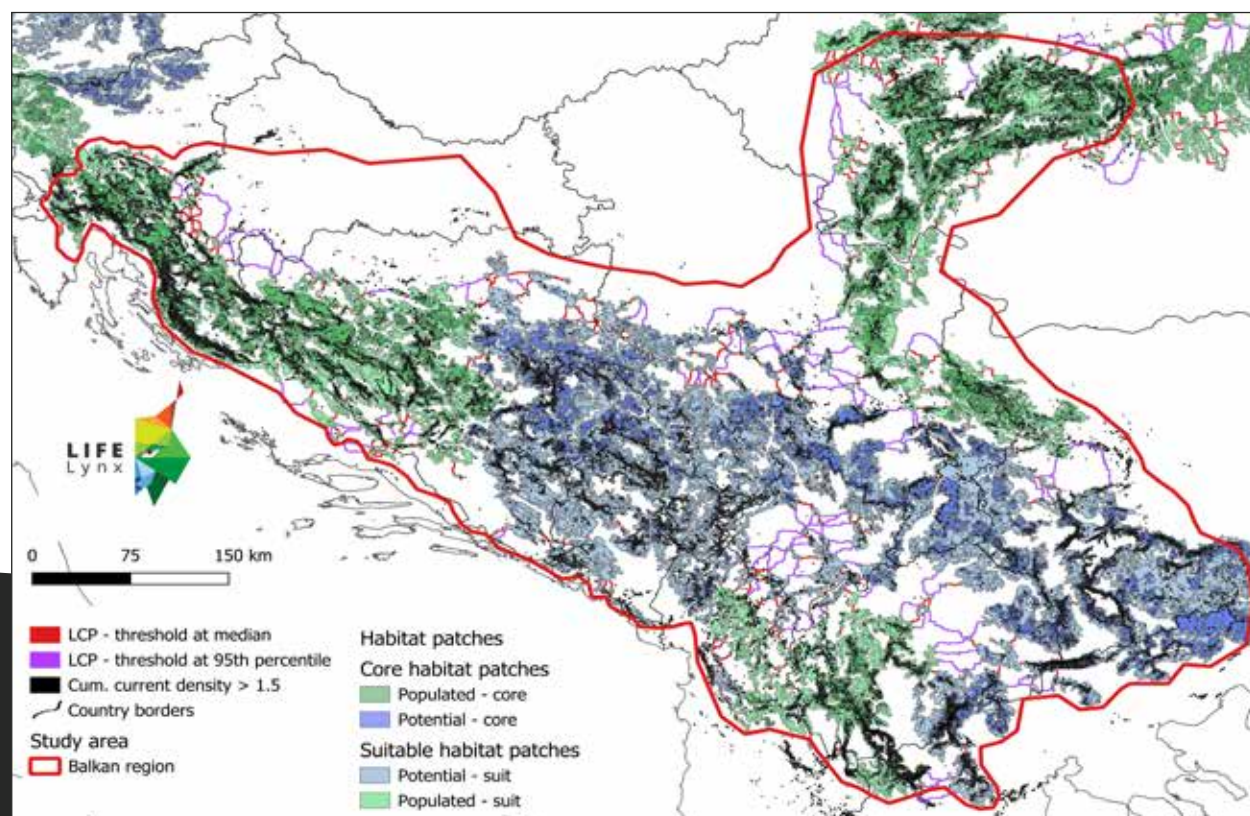


Figure 14. Connectivity of Balkan region. Results from Omniscape above the 1.5 threshold (black) and from Grainscape LCPs with thresholds at median (red lines) and 95th percentile (purple lines) of extra-territorial paths' cumulative costs are presented, together with populated and potential suitable and core habitat patches. Population patches are already seemingly well connected through large and abundant suitable patches.



Connectivity of potential stepping stone patches

The identification of potential areas for the establishment of stepping stone populations is an important step in the management strategy aimed at a metapopulation scheme. We chose the size of 10 home ranges of male lynx as a threshold for potential stepping stone population patch and obtained 5 patches in the Alpine region and 2 patches in the Balkan region with a sufficiently large and sufficiently connected area of suitable habitat. Their size and the area of core habitat within these areas are shown in Table 5.

Habitat patches [population region]	Suitable area [km ²]	Core area [km ²]
Alpine region		
Patch 1 [N Alpinel]	3146.7	759.7
Patch 2 [N Alpinel]	3312.7	277.7
Patch 3 [NE Alpinel]	12678.5	2742.7
Patch 4 [S Alpinel]	5313.5	1395.5
Patch 5 [S Alpinel]	3742	1250.7
Balkan region [Dinaric – Balkan – S Carpathian]		
Patch 1	43269.5	9947.7
Patch 2	11482.8	3413.5

Table 5. Potential stepping stone population patches with size larger than 10 lynx male home range sizes. Their suitable areas and core areas are provided, as well as in which population region they classify.

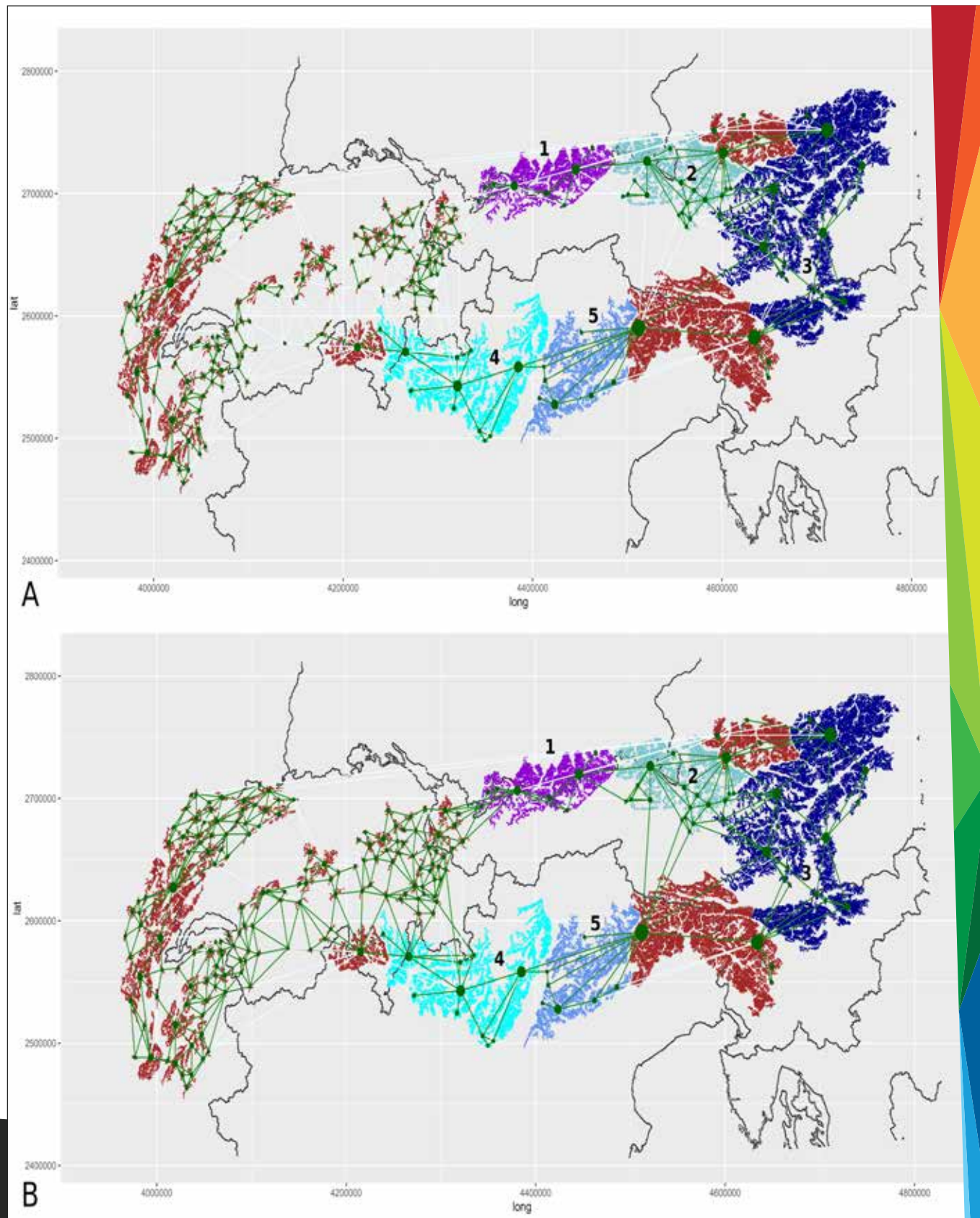


Figure 15. Schematic representation of connectivity between potential stepping stone population patches and populated patches in the Alpine region. Populated patches (dark red) are connected with potential patches (other colours) via LCP links below median threshold (A) or 95th percentile threshold (B). The green nodes represent centroids of smaller parts included in the populated or potential patches, their sizes represent the area of the parts. Green lines represent schematic LCPs between these nodes that are below the respective threshold, white lines represent those above. Patches in question are labelled with numbers that correspond to those in Table 5 above.

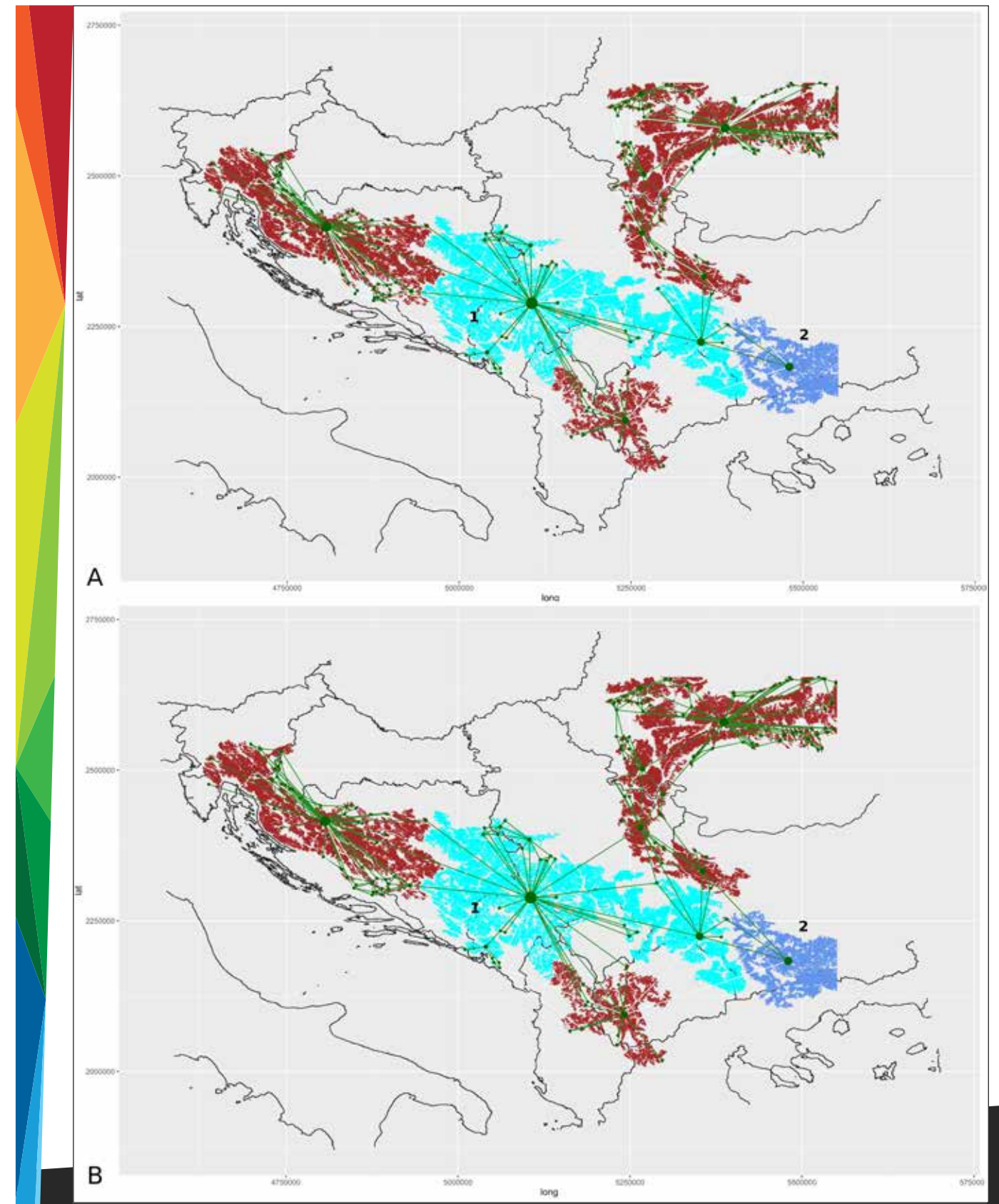


Figure 16. Schematic representation of connectivity between potential stepping stone population patches and populated patches in the Balkan region. Populated patches (dark red) are connected with potential patches (blue-purple) via LCP links below median threshold (A) or 95th percentile threshold (B). The green nodes represent centroids of smaller parts included in the populated or potential patches, their sizes represent the area of the parts. Green lines represent schematic LCPs between these nodes that are below the respective threshold, white lines represent those above. Patches in question are labelled with numbers that correspond to those in in Table 5 above.

We ran Grainscape with the above-mentioned thresholds for these patches (which Grainscape treats as several smaller patches) and plotted the resulting connectivity in Figure 15 for the Alpine region and Figure 16 for the Balkan region.

As seen previously (in Figures 13 and 14), West and East Alps are poorly connected through short dispersal paths, especially in the more fragmented northern side, while longer paths provide enough connections between potential and populated areas. In the Balkan region, on the other side, the areas already seem to be well connected due to large and abundant suitable patches, as mentioned above, even though the connections between Dinaric and Carpathian population is narrowed down in the eastern part to the potential suitable areas in south-eastern Serbia and western Bulgaria, at the western edges of Balkan Mountains.

An important point to consider when assessing connectivity are possible linear barriers that could impede landscape permeability and stop dispersers from reaching the adjacent populations or habitat patches. Motorways present such linear barriers that combine the effect of roads with increased mortality with perceived risk while also often being fenced and thus prevent individuals from crossing. Examination of the paths constructed with Grainscape analysis between all suitable patches and their intersections with highways provided an interesting perspective on the importance of available and suitable highway crossings, as shown in Table 6. There are a large number of crossings in the form of overpasses or underpasses that represent a narrow crossing (usually around 2 m) that already has its own traffic volume (primary, secondary or even tertiary roads) that could prove useful for lynx individuals (as in the case of lynx Maks and its regular crossings of the Ljubljana-Trieste highway (Seidl 2023)), however, such narrow crossings are usually not used and movement across highways is still limited. Potential corridors from connectivity analyses also provide important information on critical points where the construction of wildlife crossings is needed to improve landscape permeability.

Region and paths	Number of paths	Number of intersections with motorway	Number of crossings within those intersections	Number of crossings > 10 m / wildlife crossings
Alpine				
Median threshold	596	94	106	74 / 1
95th percentile threshold	796	144	178	125 / 1
Balkan				
Median threshold	392	34	34	28 / 1
95th percentile threshold	520	72	66	50 / 1

Table 6. Number of LCP paths from Grainscape analysis per region and per threshold setting with intersections with motorways and motorway crossings. As LCP paths have a resolution of 500x500 m cells, multiple smaller crossings can fall within one intersection between LCP path and motorway.

Another type of linear barriers that sadly do not provide a logical solution such as wildlife crossings are border fences, in this case especially important in the Balkan region due to externalisation of borders of European Union states and the moving of Schengen border more to the south – thus also urging states to implement measures like border fence construction. Like fenced highways, these too can mean a barrier that importantly impedes landscape permeability for large mammals, including Eurasian lynx (as seen in an example of lynx Niko in Figure 17) and measures limiting their construction, especially in suitable and core areas, are crucial.

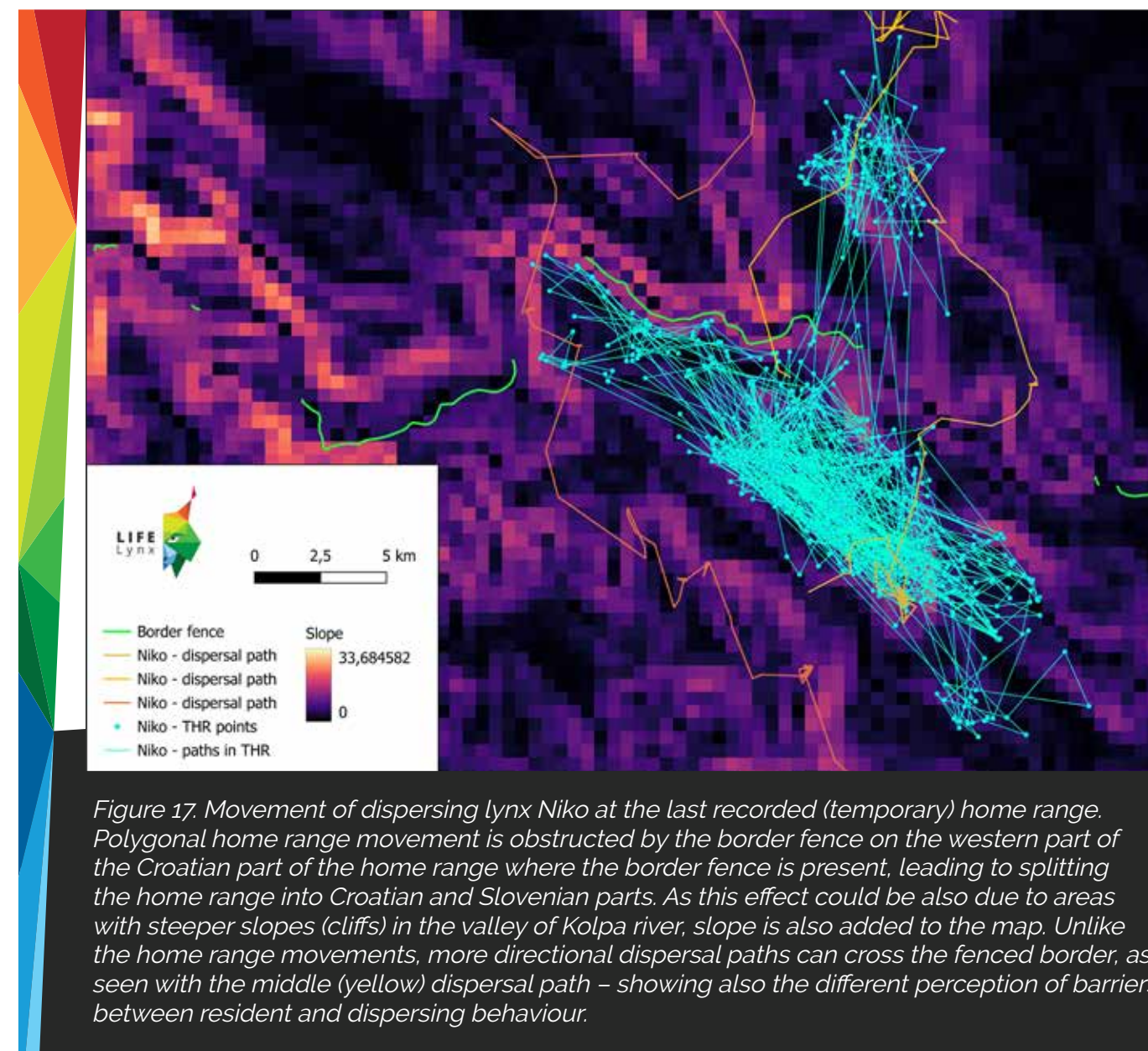


Figure 17. Movement of dispersing lynx Niko at the last recorded (temporary) home range. Polygonal home range movement is obstructed by the border fence on the western part of the Croatian part of the home range where the border fence is present, leading to splitting the home range into Croatian and Slovenian parts. As this effect could be also due to areas with steeper slopes (cliffs) in the valley of Kolpa river, slope is also added to the map. Unlike the home range movements, more directional dispersal paths can cross the fenced border, as seen with the middle (yellow) dispersal path – showing also the different perception of barriers between resident and dispersing behaviour.

9 Conclusions

The central and south-eastern European lynx populations are relatively isolated, and only limited movement occurs between some populations (Zimmermann and Breitenmoser 2007, Oeser et al. 2023). In the fragmented mountainous regions of the Alps, Dinarics and the rest of Balkan peninsula dispersal is constrained by barriers including high mountain peaks, deep valleys, canyons and glaciers, fenced highways, large rivers as well as settlements, agricultural, industrial and other urban areas. The ongoing refugee crisis in Europe has seen many countries rush to construct border security fencing to divert or control the flow of people (Linnel et al. 2016). The process of border fencing can represent an important additional threat to wildlife because it can cause additional fragmentation of habitat, thus reducing its connectivity and lower effective population size. All small and isolated populations of lynx are already suffering, or may suffer in the future, from the loss of genetic variation. Most reintroduced populations show low genetic diversity (Breitenmoser-Würsten and Obexer-Ruff 2003, Kaczensky et al. 2012, Schmidt et al. 2011, Sindicic et al. 2013, Mueller et al. 2022, Pazhenko and Skrbinšek 2024, Pazhenko et al. in preparation), which is due to inbreeding and genetic drift. But even isolated autochthonous populations – all of which experienced severe bottlenecks in the 19th and/or 20th century – can suffer from genetic deterioration if they remain isolated.

The existing highway network in Central and Western Europe poses a serious connectivity problem for the already fragmented and small reintroduced lynx populations. In particular, great efforts are being made to connect the Dinaric population in Bosnia, Croatia and Slovenia with the Alpine population in Italy. The highway connecting Ljubljana and Trieste is a permanent barrier with few crossing possibilities (Kuralt et al. 2023, Kuralt et al. in preparation, Sanchez et al. in preparation). Connecting the remaining Alpine populations (in Switzerland, France and Austria) remains a challenge and will probably mainly depend on translocations and reintroductions, as happened in the Kalkalpen National Park (Upper Austria) in 2011 and 2013 (Fuxjäger 2014). The most important area for the Alpine lynx population is in the north-western Alps (western Switzerland), followed by north-eastern Switzerland and the south-eastern Alps (Italy and Slovenia). These populations are the result of reintroductions in the early 1970s with very few founder animals, and both populations have reached a high inbreeding coefficient. Two other smaller nuclei are located in the Chartreuse (France) and in the Kalkalpen region (Schnidrig et al. 2016). There is still no reproducing lynx core in the German Alps and the closest lynx subpopulations are located in north-eastern Switzerland (distance 70 km) and Slovenia (distance 180 km), apart from the population in the Šumava ecosystem (Bohemian Forest), which is, however, separated from the Alps by open agricultural areas (Schnidrig et al. 2016). Although the Alpine lynx population is still far from being (genetically) viable, this is the only mountain range in Western and Central Europe that could harbour an isolated viable population given its suitable habitat. The Alps are therefore a future stronghold for the species and also crucial for connectivity with neighbouring populations, e.g. the Dinaric, Bohemian-Bavarian-Austrian, Black Forest and Jura populations (von Arx et al. 2021; Molinari-Jobin et al. 2021). The overarching goal is to establish a large Central European metapopulation (Bonn Lynx Expert Group 2021). However, the strong anthropogenic fragmentation of otherwise good habitat patches may require a partially managed metapopulation (e.g. assisted dispersal, genetic rescue, stepping-stones), which requires a range-wide strategy and reasonable cooperation between all range states concerned.

The situation in the south-western Balkans, within the current native range of the Balkan lynx, is still relatively well connected in terms of fragmentation. However, the non-EU countries are in a phase of rapid development to meet their increasing economic and energy needs. This potentially means fragmentation due to transportation (e.g. highways) and the construction of infrastructure for hydropower (artificial lakes on rivers). Due to the very mountainous terrain in the western parts of North Macedonia and eastern Albania, the main distribution patches of the Balkan lynx are bypassed by large infrastructure projects, but the future dispersal potential could be affected if such projects are implemented without crossing opportunities.

Inbreeding depression poses a serious threat to small populations as it leads to the fixation of deleterious mutations and a decrease in the survival probability. While the creation of connectivity and subsequent natural gene flow between populations is an ideal long-term solution, its practical implementation under real-life conditions is often challenging. The significant reduction in the inbreeding coefficient and increase in genetic diversity following translocations suggest that population reinforcement, as observed in the Dinaric lynx (Pazhenkova et al. 2024, Pazhenkova in prep.), can effectively mitigate the negative consequences of inbreeding. Stochastic modelling underlines the importance of genetic management, as simulations without translocations predicted a decline in population size and an increased risk of extinction within the next three decades. The population reinforcement efforts implemented as part of the LIFE Lynx project have significantly delayed the detrimental effects of inbreeding and genetic erosion, making a crucial contribution to the population's survival. Reinforcement of populations by translocating individuals from larger populations is proving to be a viable strategy for reducing inbreeding, increasing genetic diversity and potentially saving populations from extinction. However, the effectiveness of population reinforcement hinges on a thorough understanding of the genetic status of the target population and the long-term consequences of translocation, which can be achieved through close genetic monitoring. The selection of optimal translocation is discussed in more detail in Pazhenkova et al. 2024.

Lynx populations in the Alps and neighbouring areas have been demographically stable, but the lack of connectivity between these populations raises the question of whether they will survive in the long term without active management. Lynx translocations have been shown to be beneficial in small populations, as rescue effects by natural immigration have had minimal impact due to low local connectivity (Sánchez Arribas et al. 2023, in preparation). However, adding individuals in their model simulations did not result in sufficient connectivity between populations in the SE Alps and Dinaric populations to meet the 50/500 rule (Franklin 1980), suggesting that habitat fragmentation and human-associated risks hinder dispersal. Indeed, observations of lynx dispersing into new areas are rare (Drouet-Hoguet et al. 2021, Zimmermann et al. 2005, 2007). This finding underlines the need to create landscape corridors, assisted dispersal and the further connection of the populations through stepping-stone reintroductions (Molinari et al. 2021) to achieve metapopulation structures (McManus et al. 2015, Sharma et al. 2013). The creation and maintenance of a lynx metapopulation requires the cooperation of all affected countries in the area, which must be organised under the auspices of international treaties.

Balkan lynx has been intrinsically small for at least the past 150 generations (Bazzicalupo et al. 2022). Already experiencing few bottlenecks in the last 100 years, its genetic resistance is ever so weak in withstanding the rapid environmental change. The next steps of its recovery will most likely involve a genetic rescue mission in order to strengthen its genetic variability. Given that the Balkan lynx is genetically and taxonomically unique it has been questioned which subspecies is better candidate for such a measure, however using Carpathian males, mimicking recent gene flow, was suggested (Melovski et al. 2022).

Recent genetic studies (Gugolz et al. 2008, Cómert et al. 2018, Bazzicalupo et al. 2022) indicate a closer relationship with the Carpathian subspecies compared to the Caucasian subspecies, but analyses of ecological traits of the Balkan and neighbouring populations established quite clearly that the Carpathian subspecies has much better ecological fit for the phylogeographic and current genetic makeup of the Balkan subspecies (Melovski et al. 2022). IUCN/SSC Guidelines (2013) provide a clear direction on taking extreme caution when mixing different genetic lineages due to potential outbreeding depression. Historically, the lynx populations in the Alps, on the Balkan Peninsula and in the Carpathian region were interconnected (Kratochvil and Vala 1968). As a short-term and urgent measures, reinforcements in existing populations of Carpathian lynx and especially Balkan lynx should have been a paramount priority. Apart from further reinforcements, reintroductions and assisted migration/dispersal, the management goals should be directed also towards a natural connection of Dinaric - SE Alpine population with other lynx populations in Europe (Pazhenkova and Skrbinšek 2024). The population "stepping stone" established in the Julian Alps within the LIFE Lynx project served this purpose. The Julian Alps are within the average dispersal distance from the current lynx population in the Dinaric Mountains of Slovenia, but improving connectivity between these areas would help maintain adequate natural gene flow between the stepping-stone nucleus and the core population, for which permeability of the Ljubljana-Trieste highway is of particular importance (Kuralt et al. 2023, Pazhenkova and Skrbinšek 2024, Kuralt et al. in preparation, Mlinarič et al. in preparation).

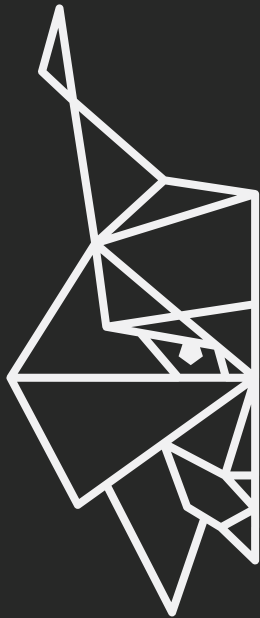
In the long term, further stepping stone nuclei should be created in the identified habitat patches in the Alps and the Balkans in order to connect the Dinaric-SE Alpine population with other, currently isolated lynx populations in the Alps (Molinari-Jobin et al. 2003) and with a Balkan lynx in the south. Our connectivity analysis of the habitat patches revealed that the Dinaric population and (remnant) Carpathian population from eastern Serbia and western Bulgaria could colonize the same large habitat patch extending from eastern Bosnia and Herzegovina to southern Serbia and serve as a stepping stone to the Balkan lynx population. This would create a functional meta-population across the southern Balkans, the Dinaric Mountains and the Alpine arc and ensure gene flow, reducing the need for further translocations from the Carpathians.



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