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CONTINENT-WIDE MODELLING OF POTENTIAL HABITATS AND CONNECTIVITY FOR THE EURASIAN LYNX (*LYNX LYNX*) IN EUROPE

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With 3 figures, 4 tables and 1 supplement
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Summary: Eurasian lynx (*Lynx lynx*) once inhabited almost the whole of the European continent. After facing nearly complete extinction about a century ago, they now form a more or less connected metapopulation with eleven broad-scale populations and numerous isolated habitat patches throughout Europe. Increasing public interest and a favourable legislative status by the EU give rise to hope for the return of the felide to parts of Central and Western Europe, where it is currently absent. In this context, a solid understanding of the overall suitability of the European landscape for a well-connected lynx population is crucial. Therefore, this work is looking into the current situation as well as potential habitats, ease of movement between those habitats, and potential future distribution, with the main focus on broad-scale spatial patterns. In addition to existing populations, eight habitat clusters were identified across Europe, using a modelling approach, rooted in a rule-based assessment accompanied by least-cost path identification, generating possible movement corridors. Key findings include large areas of potential habitat, yet overall low connectivity, with lynx movement restricted by a lack of forest cover as well as human land use, including mainly linear barriers like highways and dense road networks. This situation provides a number of challenges and opportunities for national and international conservation: The results clearly indicate that for a recolonisation of many parts of the European landscape reintroduction measures are indispensable in many parts of Europe. They also offer a first step towards a general understanding of how large carnivores like the Eurasian lynx might exist within a landscape increasingly shaped by anthropogenic actions and land use.

Zusammenfassung: Für lange Zeit war der Eurasische Luchs in weiten Teilen des europäischen Kontinents beheimatet, bis er vor etwa einem Jahrhundert beinahe vollständig aus diesen Lebensräumen verdrängt war und nur allmählich in seine ursprünglichen Verbreitungsgebiete zurückkehrte. Heute bildet er eine mehr oder weniger zusammenhängende Metapopulation mit elf großflächigen Subpopulation und zahlreichen isolierten Lebensräumen in ganz Europa. Steigendes öffentliches Interesse und ein positiver Rechtsstatus von Seiten der EU lassen auf eine Rückkehr des Eurasischen Luchses auch in Bereiche Zentral- und West-Europas hoffen, in denen er aktuell noch fehlt. In diesem Zusammenhang ist ein Verständnis der Eignung dieser Gebiete für eine ausreichend vernetzte Luchs-Population besonders wichtig. Hier untersuchen wir die aktuelle Situation, potenzielle Habitate, Möglichkeiten des genetischen Austauschs zwischen diesen Habitaten und zukünftige Verbreitungsmuster. Der Fokus liegt dabei auf großflächigen räumlichen Mustern. Durch die Erstellung eines regelbasierten Modells und eine Analyse der Least-Cost-Path-Verbindungen zwischen einzelnen Lebensräumen ist es uns gelungen, zusätzlich zu existierenden Population in Europa acht potenzielle Habitat-Cluster zu identifizieren, die durch ein Set potenzieller Bewegungskorridore verbunden sind. Insgesamt weist Europa große Flächen geeigneter Lebensräume auf; die Konnektivität dieser Habitate zeigt sich jedoch als gering. Dabei stellen ein Fehlen ausreichender Waldflächen, und die anthropogene Landnutzung die Haupthindernisse für die Verbreitung des Luchses dar. Lineare Barrieren wie Schnellstraßen und dichte Straßennetze spielen ebenfalls eine große Rolle. Der Schutz des Luchses ist demnach mit einer Vielzahl von nationalen und internationalen Herausforderungen verbunden, bietet aber auch Chancen für den aktiven Naturschutz. Unsere Ergebnisse unterstreichen, dass eine natürliche Wiederkehr des Luchses ohne aktive Eingriffe in vielen Teilen Europas nicht möglich sein wird. Sie stellen damit einen ersten Schritt in Richtung eines allgemeinen Verständnisses der Rolle von großen Raubtieren in einer zunehmend durch den Menschen geprägten Umgebung dar.

Keywords: habitat model, linkage-mapping, movement corridors, wildlife conservation, geographical information systems

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1 Introduction

Survival in a strongly human-dominated landscape is a problem faced by many species globally, and large, solitary, wide-ranging felids are especially affected (Dutta et al. 2016; Rabinowitz and Zeller 2010). Loss of connected habitat and increasing isolation of small populations with little genetic variability is for example experienced by tigers across their range in Asia (Dutta et al. 2016), or jaguars in South America (Rabinowitz and Zeller 2010). Similar problems have been present in Europe for decades, where large carnivores faced near continent-wide extinction until well into the 20th century (Kaczensky et al. 2012; von Arx et al. 2004). Today they are returning only very slowly to their historical habitats, heavily relying on a favourable legal protection status and active resettlement (Bouyer et al. 2015; Herdtfelder 2012; Kaczensky et al. 2012).

The Eurasian lynx is one of those returning large mammals. Historically, it was absent only from the Iberian Peninsula, where the Iberian species occurred (and still occurs in a small remaining population) and possibly from larger islands like Sicily (von Arx et al. 2004). Yet, while wolf and bear were able to maintain small populations throughout the 19th and 20th century, lynx became almost completely extinct in Central Europe as well as in Scandinavia, making a natural recolonization highly unlikely (Breitenmoser et al. 1998; Reinhardt et al. 2017; Rueness et al. 2003). Still, thanks to various reintroduction efforts starting with the first legal protection measures in the 1970s, the Eurasian lynx occurs in 27 countries today, including 17 EU member states (Fernández-Gil et al. 2018; Large Carnivore Initiative for Europe (LCIE) 2019). However, the structure of these populations is far from ideal: Large carnivores like the Eurasian lynx form isolated metapopulations across Europe, with only small areas where individuals can settle and breed, connected by corridors, crossing large parts of unsuitable land (Chapron et al. 2014). These conditions heavily restrict the natural ranging behaviour of those animals, and limit dispersal from their natal ranges. Yet, dispersing individuals are of crucial importance in maintaining the viability of populations because they have the potential to colonize new areas, increase genetic variation, and maintain gene flow (Dutta et al. 2016; Thomas 2000). Still, in the context of the current biodiversity crisis it is highly unlikely that the large carnivores of Europe will return to a continuous distribution area (Chapron et al. 2014). For proper conservation this means that an appropriate metapopulation management approach is needed.

This includes the creation or maintaining of wildlife corridors to ensure genetic exchange between populations and thus long-term survival. At the same time, the extension of existing habitat patches and creation of new habitats can be of great value. The chosen management approach therefore has to consider all possible strategies and combine them profitably (Breitenmoser et al. 2000; Davies-Mostert et al. 2010; Gray et al. 2016; Hetherington et al. 2008). In this context, this work strives to explore the overall connectivity of the European landscape for a healthy and viable populations of large carnivores, using the Eurasian lynx as a case study, with the focus on potential recolonisation of currently uninhabited habitats, and maximisation of the range area where possible and advisable, asking, how can populations of large carnivores thrive in the long run in a human-dominated landscape? Since past studies and habitat models (Mahdavi et al. 2020; Ovenden et al. 2019; Schadt et al. 2002a; b; Zimmermann and Breitenmoser 2007) focused mainly on the assessment of individual populations, countries, or regions, this work presents the first attempt in exploring the European landscape as a whole. In this way broad scale patterns, networks, and transboundary connections, which got less attention before, can be investigated. Circuit theory and least-cost corridor models were applied to map existing habitats important for connectivity, core areas and linkages for conservation.

2 Methods

2.1 Study area

Almost the whole of Europe was chosen as study area, yet, due to data shortages some countries had to be excluded, especially because the most recently released version of Corine land cover data, which was used as data basis, is not yet available in some parts of eastern Europe, including Turkey, Belarus and Ukraine, and data of similar resolution and detail for the excluded countries was not available.

Europe as a whole consists of a highly fragmented landscape, largely dominated by anthropogenic land use, with 4.2% artificial land and 22.2% cropland. Still, some forests remain across the continent and today 37.8% of the overall area is covered by woodland (Eurostat 2017; Statistical Office of the European Communities 2011). In recent years the importance of that ecosystem has been recognised and currently the expansion of forested areas exceeds overall loss to infrastructure building. Potentially this leaves some space for large, forest-dwelling carnivores like the Eurasian lynx, yet it has to compete with increasing human dominance and all forms of potentially threatening land use, including settlement, agricultural activities, highways, roads, and railways, as well as hunting and low public acceptance. As Europe consists of a multitude of biogeographical regions, natural conditions vary considerably across the continent as well (Statistical Office of the European Communities 2011). This variety is important, as it results in highly differentiated habitats for the Eurasian lynx and complicates the identification of habitat patterns and analysis of the European landscape attempted in this work.

2.2 Habitat model

The most common approach for modelling habitat suitability are empirical models based on telemetry data (Doswald et al. 2007). As they are often based on a few individuals and a very specific region, their results are limited and they have often been criticised in the past (Doswald et al. 2007). Another method, which was for example used by Schadt and colleagues in 2002 and Hetherington and colleagues in 2008 (Hetherington et al. 2008; Schadt et al. 2002a), is a rule-based approach. Our work aims to combine both methods to include data from across Europe into the model, making it more applicable for the whole of the continent. Essentially, our model is based on the ecological parameters governing lynx distribution, which were gathered from published studies, including telemetry measurements, and implemented into a spatial design to form an empirical habitat suitability model (Storch 2002). Subsequently, we identified habitat patches in a rule-based approach and assessed the underlying habitat model based on statistical values.

To guide variable selection, we consulted existing habitat models (e.g. Doswald et al. 2007; Hetherington et al. 2008; Schadt et al. 2002a), as well as the most recent studies on lynx behaviour (e.g. Cohen and Newman 1991; Lynx Trust UK 2017; Sunquist and Sunquist 2002) and conservation (e.g. Corsi et al. 1998; Podgórski et al. 2008) across a variety of European landscapes including, for example, the Alps and Jura Mountains (Becker 2013; Haller and Breitenmoser 1986; Zimmermann and Breitenmoser 2007) or Eastern Europe (Maanen et al. 2005; Rozylowicz et al. 2010). Also, studies on closely related species of the same genus and with similar biological characteristics (e.g. Bates and Jones 2007; Blazquez-Cabrera et al. 2018; Ferreras 2004; Gastón et al. 2016) were consulted with caution, based on the assumption that habitat selection might follow similar patterns. Studies on lynx interaction with human land use (Bunnefeld et al. 2006; Fahrig, and Rytwinski 2009; Filla et al. 2017) and behaviour in fragmented landscapes (Crooks 2002) were of special importance. From this information, a set of ten relevant parameters, which influence lynx habitat selection, was created and classified using Geographical Information Systems (hereafter GIS, specifically ArcGIS 10.7.1 (ESRI 2011)), in accordance with current knowledge on lynx habitat selection (Tab. 1 and Supplement I). The spatial raster data (sources summarized in Tab. 2) was resampled to a 100 x 100 m resolution, where necessary, based on the resolution of the Corine land cover data, which was the most relevant of the entering variables. A similar resolution proved adequate in previous models of similar design (e.g. Bates and Jones 2007). Other models used a coarser resolution (e.g. Hetherington et al. 2008). Each raster cell of size 100 x 100 m was given a value from 0 to 10 for each of the ten variables, representing the suitability of the cell based on the respective variable, with 0 meaning that the cell will most likely not be inhabited by lynx and 10 meaning that it consists of highly suitable habitat. This required a decision-making process in order to quantify existing qualitative data, similar to the one implemented by Beier and colleagues, developers of the GIS software Corridor design (2013). A similar approach was used by Bates and Jones (2007) for Canada lynx with valuable results.

In a second step, a weighting factor was chosen for each of the chosen variables, based on their relative importance for overall habitat quality, rated in accordance with most relevant literature: This factor determines how strongly the given variable influences lynx habitat selection in relation to all other variables. Values were chosen to add up to one and facilitate both, decision making in the assigning process, and mathematical operations later on (Tab. 1). This step is considered the weakest part of the model, as the weighting factor strongly influences the model outcome, yet cannot be based on empirical, quantitative data. Instead, we solely relied on previously published studies. Additionally, only variables were included, for which spatial data of sufficient quality for the whole of Europe was available. It has to be assumed that there are a multitude of other factors influencing habitat selection, which are not grasp-

Tab. 1: Variables influencing habitat suitability

Class	Variable	Weighting factor	Data basis for choosing weighting factor and classification
Environmental	Land cover	0.250	Bates and Jones 2016; Becker 2013; Corsi et al. 1998; Doswald et al. 2007
	Tree cover	0.100	Hetherington et al. 2008; Lynx Trust UK 2017; Rozylowicz et al. 2010; Podgorski et al. 2008
Topographical	Height	0.075	Becker 2013; Bouyer et al. 2015; Corsi et al. 1998; Doswald et al. 2007; Haller and Breitenmoser 1986; Maanen et al. 2005
	Slope	0.075	Becker 2013; Bouyer et al. 2015; Corsi et al. 1998; Doswald et al. 2007; Haller and Breitenmoser 1986; Maanen et al. 2005
	Aspect	0.075	Bouyer et al. 2015; Haller and Breitenmoser 1986
Human influence	Distance to human settlements	0.075	Bouyer et al. 2015; Filla et al. 2017; Zimmermann and Breitenmoser 2007
	Distance to large streets	0.100	Bunnefeld et al. 2006; Herdtfelder 2012; Fahrig and Rytwinski 2009
	Distance to frequently used railways	0.100	Bunnefeld et al. 2006; Herdtfelder 2012; Fahrig and Rytwinski 2009
	Population density	0.075	Cohen and Newman 1991; Crooks 2002; Fahrig and Rytwinski 2009
Competition	Competition	0.075	Bunnefeld et al. 2006; Sunquist and Sunquist 2002

able in GIS at this scale, including prey density, for instance, which has been successfully included into models of smaller scale (Doswald et al. 2007). We have to assume that prey density is closely linked to other variables like land cover or tree cover and can be omitted without distorting results, as those are strongly represented in the data.

2.2.1 Habitat variables

Land use and tree cover (Supplement I): As a forest dwelling species, Eurasian lynx mostly prefer forested areas which also provide sufficient prey densities with small ungulates, especially roe deer, being the main prey across Europe. Forest cover can therefore easily be identified as the most important source of resources and the main factor contributing to lynx distribution. In general lynx are found in both coniferous and broadleaved woodland, not preferring either form. In some cases, scrubs and rocks are inhabited alternatively, yet overall lynx habitat is mostly confined to woodlands. If lynx use open areas, they do so during the night, thus limiting the risk of encounters with humans (Breitenmoser et al. 2000; Hetherington et al. 2008; Zimmermann and Breitenmoser 2002).

Topography (Supplement I): Topography and relief is another important element in habitat selection, with lynx preferring mountain forests and rocky areas, probably due to their inaccessibility and low disturbance (Maanen et al. 2005; Rozylowicz et al. 2010). Here a seasonal change can be observed with most individuals seeking out lower areas in winter, following their prey and avoiding the deepest snows (Sunquist and Sunquist 2002). Usually, the Eurasian lynx's habitat includes a number of core areas with very little disturbance, where the lynx is found most of the time. They function as resting places as well as places for breeding and retreat areas for the young. Here, places protected from wind and rain with aspect south are preferred (Bouyer et al. 2015; Haller and Breitenmoser 1986).

Human influence (Supplement I): Similar to most large carnivores, Eurasian lynx tend to avoid areas of intensive human land use and prefer areas of low population density. Yet in some cases higher prey densities in relative closeness to anthropogenic disturbed areas cause lynx to seek out those areas as well (Bouyer 2015; Filla et al. 2017). In this context road networks play an important role as well, contributing to large parts to mortality risk, due to road accidents as well as increased accessibility for hunters (Herdtfelder 2012).

Tab. 2: Data basis for spatial data by variable

Variable	Data basis	Source
Land cover	Corine Land Cover 100 m	European Environment Agency 2018
Tree cover	Global Tree Cover 30 m	Sexton et al. 2013
Hight	Digital Surface Model 30 m	UGSG 2010
Aspect	Digital Surface Model 30 m	UGSG 2010
Slope	Digital Surface Model 30 m	UGSG 2010
Distance to highways	European roads	Open Street Map 2018a
Distance to railways	European railways	Open Street Map 2018b
Distance to human settlements	Corine Land Cover 100 m	European Environment Agency 2018
Population density	Global population density 1000 m	Center for International Earth Science Information Network - CIESIN - Columbia University 2016
Competition	Distribution Brown Bear	McLellan et al. 2017
Competition	Distribution Wolf	Boitani 2018
Competition	Distribution Wolverine	Abramov 2016
Competition	Distribution Iberian Lynx	Rodríguez and Calzada 2015

Competition (Supplement I): Even though humans have by far the greatest influence on lynx survival rates (Bunnefeld et al. 2006), it might be reasonably assumed that lynx might also avoid areas where other large carnivores might provide competition for resources.

In order to combine variables, we chose the weighted geometric mean, with x being the suitability value for each variable and w being the weighting factor:

$$\bar{x} = \left(\prod_{i=1}^{n} x_i^{w_i} \right)^{1/\sum_{i=1}^{n} w_i} \qquad \text{Eq.1}$$

This ensures that limiting factors (values of 0 or close to 0) have more influence on results and cannot be cancelled out by higher values.

2.2.2 Patch identification

We identified patches of suitable habitat meeting the spatial requirements of the lynx, following a rule-based approach and the basic assumption that forested areas make up the largest part of a residential lynx' home range. Yet, open land can be inhabited as well and residential lynx are willing to cross up to 1 km to reach another suitable woodland patch (Schadt et al. 2002a; b). For this reason, the identified forest patches were buffered by 500 m before excluding urban areas, water bodies, railways and large roads from the resulting habitats, since they were considered edges which will not be included into their home range by resident lynx. The final rule considered was home range size, which can vary between regions. To include those spatial variations into our model, Europe was split into eight natural regions and a minimum home range size was chosen for each of those regions based on existing data (Breitenmoser-Würsten et al. 2001; Huber et al. 1995; Linnell et al. 2001; Niedziałkowska et al. 2006) (Tab 3). In some cases, we had to make assumptions, transferring data from one geographical region to another, as there is no data available for regions which do not have an existing lynx population. Finally, patches which do not meet the minimum size required by resident lynx as home range were excluded. Here, two minimum patch sizes were relevant: patches large enough for one male and one female resident animal, which equals the minimum home range for male lynx, since habitats of male and female lynx can overlap, which leads to male home ranges encompassing female ones (Hetherington et al. 2008). On the other hand, home ranges of two lynx of the same sex tend not to overlap. Therefore, the minimum size for a patch large enough to support a whole population (20 individuals consisting of seven male and 13 female lynx (Hetherington et al. 2008)) equals the minimum size of 13 non-overlapping, female home ranges.

Suitability was rated for each patch based on the mean suitability value from the habitat model within the patch boundaries. Additionally, the number of

Tab. 3: Home range sizes of Lynx lynx across Europe. Data were not available for all regions of Europe, since monitored and investigated lynx populations exist only in some countries. In those cases, data was transferred from similar regions. In most cases home range sizes vary little, with the exception of the northern part of Europe, where large areas of available habitat cause lynx to expand their territory.

Bioregion	Male home range [km^2]	Female home range [km^2]	Source	Country	Patch size needed for a viable population (20 individuals) [km^2]
Alpine	159	106	48	Switzerland	1378
Arctic	952	425	49	Norway, Sweden	5525
Atlantic	248	133	50	Poland	1729
Boreal	952	425	49	Norway, Sweden	5525
Continental	248	133	50	Poland	1729
Mediterranean	200	177	51	Slovenia	2301
Pannonian	200	177	51	Slovenia	2301
Black Sea	200	177	51	Slovenia	2301
Steppe	248	133	50	Poland	1729

individuals the identified patches can potentially support were estimated, based on the home range requirements from Table 3, and the assumption that male and female numbers are about equal, with male home ranges encompassing female ones. A comparative approach assumed an average density of 0.75 lynx per 100 km^2, based on most recent density estimates from Jura and Vosges Mountains (Gimenez et al. 2019; Pesenti and Zimmermann 2013).

2.3 Connectivity Assessment

Species conservation in the fragmented mosaic of the European landscape includes not only the question, where potential habitats can be found, maintained, and potentially expanded, but also how to ensure exchange between those patches to avoid local extinction (Fahrig 2003). This is especially important for the Eurasian lynx as resident subpopulations are small and heavily dependent on migration and linkage to other patches for genetic exchange (Kramer-Schadt et al. 2011). To ensure this exchange a fundamental understanding of landscape connectivity, or "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993) is of crucial importance. Therefore, we defined corridors which connect the previously identified potential habitat patches, using the software Linkage Mapper (McRae 2013). Like most similar tools, Linkage Mapper is based on graph theory, using a set of nodes (or habitat patches), connected by links (or corridors). As input data Linkage Mapper requires habitat patches and a resistivity or friction map, a raster layer, specifying for each raster cell the willingness or physiological cost, with which the cell is crossed (McRae and Kavanagh 2017; Nordén 2016; Zeller et al. 2012). We created this map by inverting the existing habitat model, assuming that cells of higher suitability for resident lynx are more readily chosen by migrating lynx as well (Beier et al. 2013). The inverted habitat model was supplemented by including higher values for different types of roads, railways, and large rivers, with highways and rivers getting the highest resistivity of 100. Our underlying assumption was that those linear features represent barriers to dispersing lynx and increase mortality risk. Therefore, lynx is likely to avoid them and they have a much higher influence on movement than on habitat selection (Fig. 1). For a detailed description of how Linkage Mapper works see McRae and Kavanagh (2017). As a final step, the output raster map was truncated, a function which converts all cost weighted distance values above a given threshold to NoData, thus identifying areas which contribute the most to overall connectivity and can be called movement corridors (McRae and Kavanagh 2017). The optimal threshold for this can vary and was set to 1, in accordance with our data. In this way, we identified least-cost corridors in addition to the least-cost paths. This is of much value for conservation as migrating animals very seldom find the exact least-cost path (which is usually only one pixel wide), and the corridor is therefore of much greater importance. Results based on linear approaches are very limited in comparison, even though they are usually preferred, due to their simple applicability (Lynx Trust UK 2017). As the width of the result-

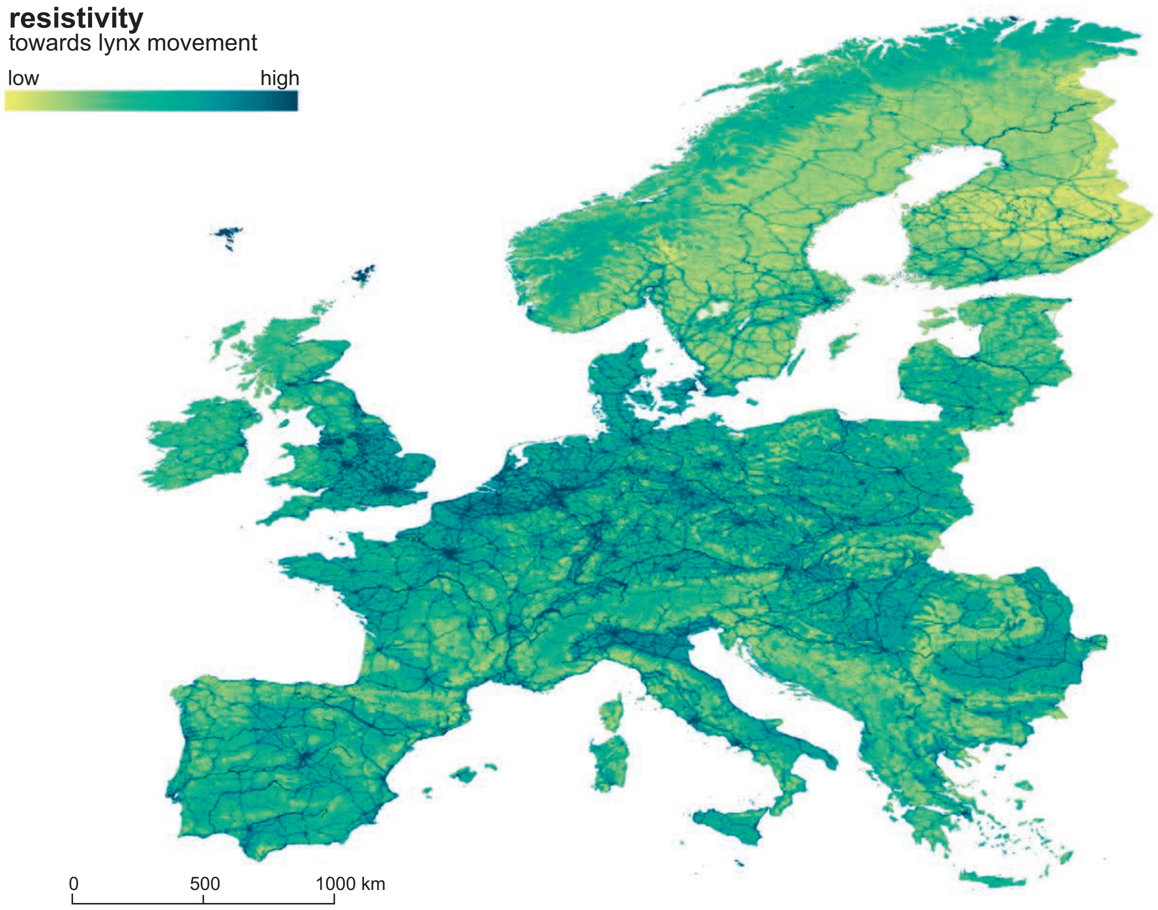

Fig. 1: Resistivity towards lynx movement. Dark areas indicate barriers and areas of high resistivity. Values are from 0 - 100 based on the inverted habitat model.

ing corridors is influenced by the selected threshold, they can only be interpreted in relation to each other.

This approach produced corridors which were in some cases biologically unreliable, due to limiting factors like corridor length or limited forest cover within the corridor. In order to determine which corridors might actually be used by migrating lynx and how this could affect future lynx distribution across Europe, we focused on those limiting factors for corridor selection by individual animals. Following the assumption that movement between patches is mainly explained by distance and intermediate habitat, we applied a rule-based approach, and identified a number of corridors which will most likely be used by dispersing lynx. We defined highways and large rivers as barriers limiting movement, while primary roads and railways could occasionally be crossed (maximum number: 3) (Zimmermann et al. 2007). As for the crossing of agricultural land presumptions were based on findings by Gastón and colleagues (2016), who made a clear distinction between crop types. Permanently irrigated land, non-irrigated arable land, and rice fields were therefore considered barriers, while vineyards, olive groves, and fruit trees were not. Average forest cover at dispersing sites noted by Palomares (2001) for Iberian lynx were 32 % and Gastón et al. 2016 found a clear preference of woodland cover for Iberian lynx as well. Squires et al. (2013) confirmed similar patterns for dispersing Canada lynx, which preferred areas of high greenness, while data for Eurasian lynx was not available. The value of 32 % was therefore chosen as minimum forest cover needed within the corridors. Urban areas were classified as unbridgeable, including a 500 m buffer this time, presuming that migrating lynx would avoid passing in relative closeness to human settlement (Bouyer et al. 2015; Filla et al. 2017; Zimmermann and Breitenmoser 2007). Limiting distance values for corridor selection were based on maximum dispersal distances found by Zimmermann and colleagues (2007) for the Jura Mountains and Swiss Alps and average distance values found by Zimmermann et al. (2007) as well as findings by Huck and colleagues (2010) for dispersing lynx in Poland. They were therefore set to 75 km euclidean distance and 87 km travelled path distance respectively. Minimum corridor width (300 m) was included as a limiting factor, and so was the edge-length of the corridor-patch connection, based on the assumption that corridors with a better connection to the respective habitat patch would be chosen more readily. Also, animals that evolved in landscapes with patchy habitat and risky matrix should also evolve the ability to detect suitable habitat from a distance, which is why it was assumed that the quality of the patch that could potentially be reached by using the respective corridor plays a minor role in path selection as well (Fahrig 2007). Based on these assumptions we identified a set of suitable corridors for lynx dispersal and a number of interconnected patches of suitable habitat.

3 Results

3.1 Potential habitat

We identified 321,408 km^2 as potentially suitable habitat for residential Eurasian lynx and successful lynx reproduction over Europe. Altogether the identified area would allow for an estimated maximum of about 2,400 individuals, presuming the maximum available habitat is used. The area is fragmented into 945 individual patches of varying size, with the largest connected patch (about 484,000 km^2) stretching over Northern Scandinavia and Finland (Tab. 4). There are patches situated almost across the whole of Europe, with every country having at least some portion of suitable habitat, which consists mostly of densely forested areas, in accordance with the habitat preferences of the lynx. Yet, there are some broad-scale spatial patterns discernible from the resulting map (Fig. 2) and a number of potential habitat clusters were identified from those patterns (summarised in Tab. 4). Additionally, there are suitable habitats of smaller size, yet large enough for a population in Portugal and across the Iberian Peninsula as well as across central France and Germany. Even relatively small islands like Corsica, Sardinia and Gotland consist of a portion of suitable habitat worth mentioning, while Ireland and England can offer only a few sparse patches. When compared to the current range, Figure 2 reveals that existing populations have space to expand as well. While currently only the Harz Mountains and surrounding regions are populated, other parts of the German Uplands offer suitable habitat as well, even though patches are further apart and smaller here, and in general ranking lower in mean suitability (Fig. 2). Further South the Alpine population is currently centred in Switzerland and France, but there is much space to expand to Austria and Italy. In accordance with habitat preferences, suitable habitat is mostly available in mountainous regions and uplands, while the lowlands offer very little suitable land. When considering the suitability of the patches themselves, a general pattern shows across the whole of Europe: In clusters consisting of a high number of spatially close patches the patches show higher mean suitability themselves, forming a promising network, while more widely spread, isolated patches have lower suitability in most cases. Considering suitability detached from the identified patches, it is noticeable that some areas are overall ranked high in suitability, yet offer no continuous habitat of sufficient size in which lynx could establish a home range (e.g. the British Islands). Here, tree cover and the presence of unfragmented forest patches are the main limiting factors.

Tab. 4: Potential habitat clusters across Europe and their potential population

Potential habitat cluster	Area of potential habitat	Potential maximum population size [individuals]*
Apennines and Southern Italy	58,622 km^2	440
Eifel and High Fens	18,531 km^2	139
Pindos Mountains	10,858 km^2	82
Pomerania	30,635 km^2	230
Pyrenees and Northern Spain	99,873 km^2	749
Rothaar Mountains	7,822 km^2	59
Scottish Highlands	11,444 km^2	86
Southern France	83,623 km^2	627

*assuming an average population density of 0.75 lynx per 100 km^2 (Gimenez 2019; Pesenti and Zimmermann 2013)

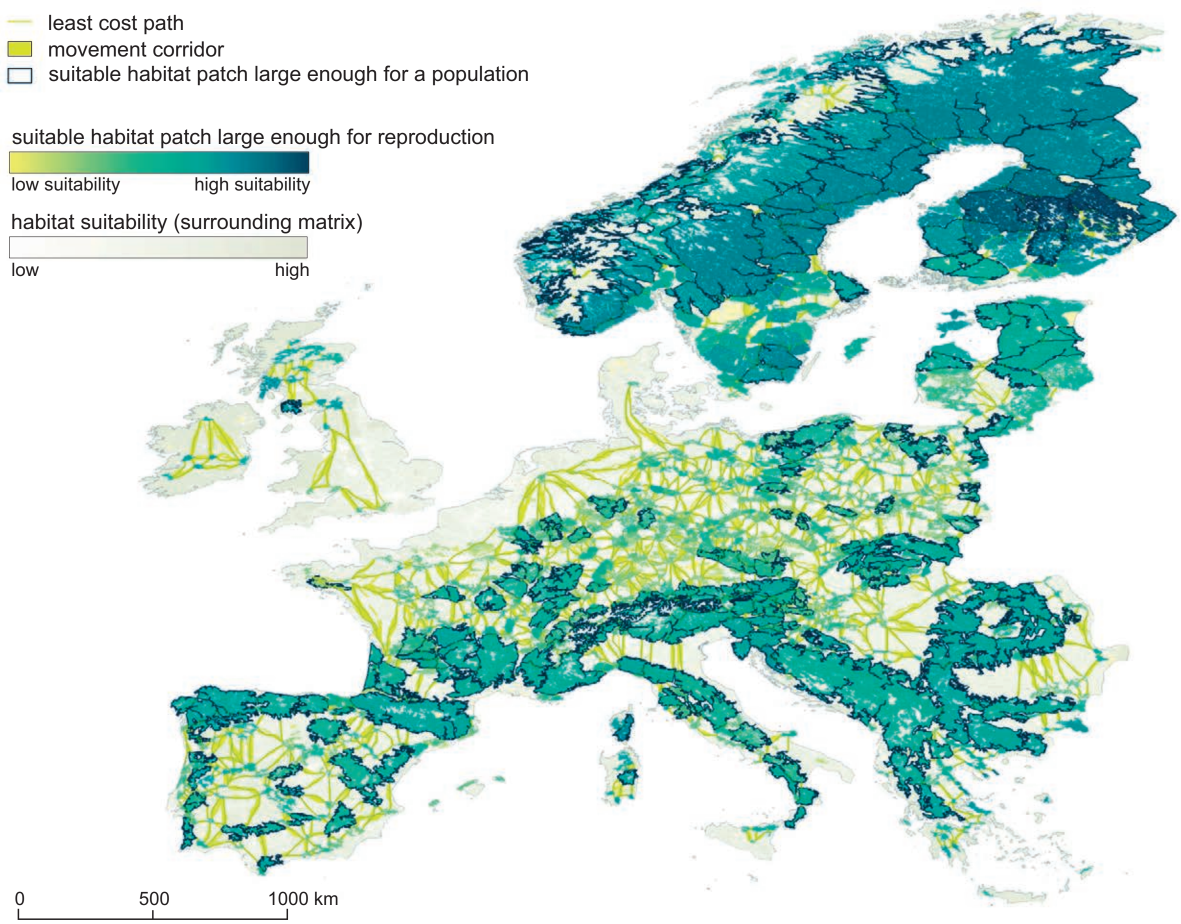

Fig. 2: Habitat model, potential habitat patches and connecting corridors for Lynx lynx in Europe. Potential habitat patches large enough for reproduction are shown in green, with darker colouring indicating higher suitability. Patches surrounded by a dark edge were identified as large enough to support a population (minimum of 20 individuals). Movement corridors connecting the patches are shown in yellow with dark lines indicating the least-cost paths.

3.2 Connectivity

Combined effects of high population density, extensive land use, highways, roads and railways result in a high fragmentation and overall low connectivity across Europe, with an average resistivity of 58.7 (of 100) (Fig. 1). Areas of high resistivity correspond to large parts with highly populated lowlands, while mountainous regions have lower resistivity. This indicates that human-made barriers tend to outweigh natural boundaries like mountain ridges in their effect on overall connectivity.

3.3 Potential dispersal corridors

A set of potential dispersal corridors of varying length and width was identified, linking the patches described above (Fig. 2). In this context, potential means that while those corridors represent the easiest way of movement for dispersing and migrating lynx, they themselves do not indicate how they might be used. In total 1 865 corridors were identified with an average length of 246 km (range: 3 - 6 171 km). In comparison to straight-line connections, least-cost paths take much longer routes almost across the whole of Europe, attesting to the overall high resistivity. Mean forest cover within the movement corridors is 21%, and thus much lower than found at dispersing sites of Iberian lynx (32%, Palomares et al. 2001). Also, 45% of the corridors cross at least one highway. Overall, these factors led to the identification of only 131 (7%) of the identified corridors as suitable for dispersing lynx (Fig. 3). Again, anthropogenic factors represented the main influence on connectivity here, with linear barriers (highways, road networks) exerting the highest influence. Land cover within the corridor was identified as a second

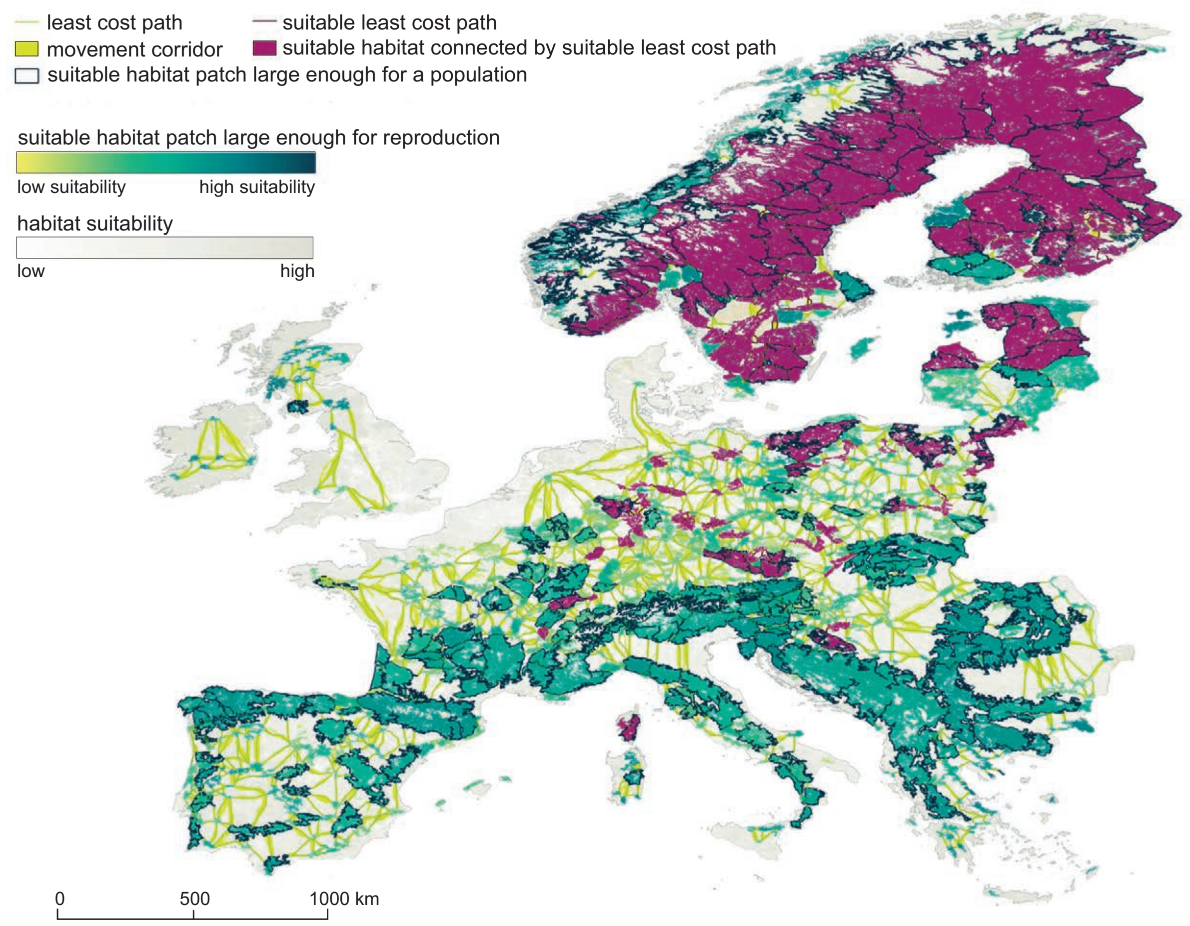

Fig. 3: Habitat model with suitable least cost paths. Colors indicate the paths which will most likely be used by dispersing lynx, as well as potentially connected habitat patches in this case. For detailed information on how these paths were chosen see Methods section. Patches surrounded by a dark edge were identified as large enough to support a population (minimum of 20 individuals).

major factor, with many corridors being excluded due to large patches of agricultural land limiting lynx movement.

4 Discussion

4.1 Suitability of the European landscape

Keeping the natural range of large carnivores like the Eurasian lynx stable or increasing, as called for in the EU habitats directive (European Union 1992), provides huge challenges for management and maintenance. The current population pattern across Europe shows that long-term populations of large carnivores thrive only in regions, where connected habitat for a sufficient number of individuals exists (Gray et al. 2016) and successful movement between habitat patches is possible (Thomas 2000). Maximising the number of individual animals and facilitating movement has therefore proven to be the most promising strategy to ensure long-term viability of a population. Yet, our results indicate that even though suitable habitat is available across Europe, most of this habitat will most likely not be colonised naturally, as distribution is limited by anthropogenic barriers and fragmentation. Because of the overall high resistance to movement (Fig. 2), we found the European landscape not particularly suitable for a lynx metapopulation. A number of cases where populations declined or ceased to spread due to inbreeding, low genetic variability and limited space seem to confirm this (e.g. Dinaric Mountains (Sindičić et al. 2013) or Jura (Zimmermann and Breitenmoser 2007)).

In general, small and isolated patches of suitable habitat are problematic. Yet examples from the past, like the successful reintroduction of lynx into the Harz Mountains, have shown that such patches can hold viable populations as well, given the opportunity for spreading into neighbouring habitats. Thriving populations in the centre of Europe (e.g. Harz Mountains, Swiss Alps) and the vast areas of suitable habitat detected across Europe give rise to hope. Regions like the Eifel and High Fens, where national parks and (eco-)tourism structures exist, into which the lynx could be integrated, are especially promising. Such concepts are successfully applied in the Harz Mountains, where the existing lynx population is utilised as a marketing tool by local businesses and authorities, increasing public interest and acceptance (Hetherington 2006). With the success of the Harz project as a role model, it is likely that further reintroductions will be attempted in future, to expand the lynx range across the German Uplands. Regions like the Rothaar Mountains were already reached by natural dispersal of individual animals, even though no permanent population could be established as of yet (Kaczensky et al. 2012; Large Carnivore Initiative for Europe (LCIE) 2019). Our results show that despite relatively high population density in these parts of Central Europe, individual patches are comparatively well connected. Other suitable regions, like the Apennines and Pindos Mountains, provide larger patches of habitat but will most likely not be reached naturally (Fig. 3) and depend on reintroduction, which is complicated by a lack of management structures, public knowledge and interest in some countries.

Also, in Southern Europe the Iberian Peninsula offers large proportions of suitable habitat, where other large carnivores like the wolf are already native. Still, introducing the Eurasian lynx to Spain must be viewed critically. Historically, the Iberian Peninsula was not populated by Eurasian lynx, since the Iberian lynx, a closely related species of the same genus, was native there. Today the Iberian lynx is highly endangered, with only a few patches of populated habitat remaining in the Southern part of the peninsula. Introducing the Eurasian lynx could sabotage current conservation strategies, which aim to recover the historical range across the whole of the Iberian Peninsula and (Gastón et al. 2016). Further information on the interaction between the species is necessary before any attempt can be made. Potentially the Iberian region is linked to identified potential habitats in Southern France, even though this link is not very strong, mostly due to large highways and a dense road network crossing the area. Yet, Southern France can easily be called the most promising region for lynx recolonization, with the largest proportion of suitable habitat identified throughout Europe and excellent natural conditions. With increasing numbers in the Western Alps (SCALP 2016) and a stable population in France, natural colonisation could be possible via the Massif Central. Population density and infrastructure is the main limiting factor in this region, with habitats in relative closeness to large cities and fragmented by highway and railway networks (Fig. 3).

To the North, the Scottish Highlands offer a comparatively small proportion of suitable habitat with potential linkage to habitat patches in northern England. This corresponds well with findings by Hetherington and colleagues from the year 2008 (Hetherington et al. 2008). Given the natural conditions, establishing a viable lynx population on the British Islands relies solely on translocation. Luckily, interest in reintroducing lynx to the United Kingdom, where it was once native, is high, with several proposed trial projects. However, no translocation has taken place yet, even though the Kielder Forest and the Galloway National Park have been identified as preferred reintroduction sites (Mayhew et al. 2017). Especially Galloway National Park in North Western England was classified as highly suitable and large enough for a viable population in this work as well. Reintroducing lynx here could potentially lead to recolonization, even though we identified more suitable and better-connected habitat further north, from which Galloway National Park is mostly isolated. Also, since the United Kingdom has currently no noteworthy populations of large carnivores, there are many unknowns and potential risks involved, related to the potential introduction of diseases with the projects and public acceptance. Only prior assessment of public position can give an insight into those potential conflicts (Mayhew et al. 2017). On the other hand, Scotland has an already thriving wildlife tourism sector which could potentially benefit from lynx reintroduction and thus raise public acceptance and inclusion into local economic structures (Hetherington 2006; Ovenden et al. 2019).

4.2 Fragmentation, barriers and limitations to distribution

Of vital importance for all efforts of conservation, connectivity management and successful recolonisation is a clear understanding of how large carnivores move in relation to their surroundings. In this context dispersal is the main process governing distribution patterns and closely linked to landscape connectivity and the establishing and persistence of populations. In the past, lynx dispersal proved sensitive to a number of factors. In our study, in most cases, anthropogenic barriers (roads, settlements, agricultural land) lead to a loss in connectivity. Natural barriers are less of a problem to migrating lynx. Yet, the most limiting factor can be identified as forest cover, which is with an average of 21% within the identified corridors much lower than the average 32% noted at dispersing sites of Iberian lynx (Palomares 2001) and also significantly lower than the average 68% of forest cover found in habitats occupied by resident lynx in Poland (Niedziałkowska et al. 2006). Other works confirmed this dependency on woodland as resting site and source of resources for dispersing lynx (Gastón et al. 2016; Schmidt 1998). This indicates that further insight into how forest is used by dispersing lynx and how much cover is needed would be of crucial value for gaining further understanding of overall connectivity. Also expanding forest areas across Europe and especially within the identified corridors would contribute a great deal to this connectivity. Luckily, this corresponds with the forestry goals of the European Union, facilitating realisation (Statistical Office of the European Communities 2011).

Another key limiting factor is distance, with an average corridor length of 246 km, which is longer than the average dispersal distance of the Eurasian lynx, especially for female lynx, who tend to stay in relative closeness to their natal habitats (Palomares 2001; Zimmermann et al. 2005; Zimmermann and Breitenmoser 2007). The creation of small habitat patches (so-called stepping stones) for short-term residing could aid to patch connection. Past studies showed that such stepping stones could reduce mortality while dispersing as well, yet they have to be large enough to provide sufficient cover, since small stepping stones could have negative effects, by distracting dispersing lynx from more suitable habitat (Bouyer et al. 2015; Kramer-Schadt et al. 2011).

Our results clearly support the hypothesis from past publications (e.g. Becker 2013), stating that natural population spread of lynx will most likely be insufficient to establish an interconnected, continent-wide population, even if more suitable habitat and stepping stones could be created. Relocation measures are therefore indispensable. In the past, national parks and other protected areas have been of high importance as reintroduction sites. However, in most parts of Europe such protected areas are too small in size to be sufficient for the huge spatial requirements of the lynx (Linnell et al. 2001). Therefore, even though protected areas are possibly of help during the first years after reintroduction, population development and management has to be viewed separately. In most cases, the identified patches of suitable land were connected by one path only, allowing for very little flexibility in this management and planning process. However, this also indicates that efforts to maintain or increase connectivity should concentrate on a limited number of crucial areas. Reintroducing lynx is a long-term process and conflicts and mortality risks, as well as population development, have to be monitored continuously, even decades after the initial release (Hayward and Somers 2010; Huber and Kaczensky 1998). Undeniably, the lynx is an excellent target species for European conservation, which gives the rare opportunity to actively aid the recolonization of whole regions by a large mammal. Now, the question remains, if this chance will be taken.

4.3 Strengths and limitations of the approach

With the help of the habitat model and movement corridors solid maps were compiled, giving answers to the questions proposed in our work. Yet, in the process of creating those maps, a number of assumptions and decisions had to be made, based on the available information on biological traits and behaviour of the Eurasian lynx. Building a resistance surface, which formed the key element of this study, is usually not possible to be entirely based on empirical data. As with any other model, both habitat, and connectivity analysis depend on certain subjective choices made by the modeller (Dutta et al. 2016). Additionally, the large scale of our analysis and the comparatively low resolution of the input data on lynx movement behaviour and habitat preferences proved challenging. Simplifications due to data shortage and lack of information may therefore influence the results a great deal and has to be discussed here. For species with little known behavioural characteristics our approach is not practical. A major factor which may influence lynx distribution, and was only partly considered here, is for example the behavioural flexibility of the lynx and its capability to adapt to new landscape conditions (Bouyer et al. 2015; Kramer-Schadt et al. 2005). This capability may for example cause it to use new habitats not included in the model, or to overcome dispersal barriers previously considered insurmountable. In general, it is believed that such adaptation is one of the factors that contributed to the recovery of some lynx populations in Central Europe in recent years (Červený et al. 2019). Still, there are many uncertainties concerning such changes in behaviour. In general, the results come with the shortages experienced by most modelling approaches, including uncertainties as well as possible misinterpretation or remoteness from reality (Synes et al. 2016). Still, a comparison of our identified habitats with current range data (Large Carnivore Initiative for Europe (LCIE) 2019) shows relatively high conformance, confirming the applicability of the approach for identifying potential habitats for Eurasian lynx or similar, solitary, forest-dwelling species.

5 Conclusion

Our analysis shows that, despite high human use in this landscape, Europe as a whole offers potential for lynx populations and there are some opportunities to maintain connectivity within parts of the European continent. Still, overall connectivity between habitat patches proved to be low and insufficient for a continent-wide (meta-)population. Even though some of the current populations have space for potential range spreading, it is unlikely that new habitats will be colonised without active anthropogenic help in form of recolonization and translocation measures, as well as the creation of wildlife corridors and stepping stones. Here we show that the main factors lowering connectivity are a lack of woodlands, especially within potential movement corridors, and human-made barriers, including mainly road networks. We also show that distance between habitats is a key problem. According to our habitat model, the most promising habitat clusters in Europe not yet colonised by Eurasian lynx are Southern France and the Scottish Highlands, and, most prominently, some parts of the German Upland, including the Eifel and Rothaar Mountains. While Scotland can only be colonised with the help of reintroduction, the other clusters potentially have natural connections to existing habitats. Still, no population spreading into those regions has occurred until now. Considering the fast spread of the Harz Mountains population however, the most likely natural recolonization is the occupation of other parts of the German Uplands from this core area. Additionally, Southern Europe offers large parts of suitable habitat. While those habitats are on average larger in patch-size and more suitable, compared to those in Central Europe, they are also less connected to existing populations. Additionally, introducing the Eurasian lynx to Spain is currently not advisable, due to potential competition with the native and threatened Iberian lynx. However, the quality of the model can only be measured by further insight into how Eurasian lynx use the landscape, and field-observations aiming beyond the theoretical overview proposed here. Nonetheless, our findings may act as a first step in developing an interdisciplinary, international management strategy. Even though the scope and the huge spatial extent of our work did not allow for much detail, it did succeed in creating a general understanding of the lynx's place within Europe. Understanding of such kind is of crucial importance, considering large mammals and their struggle within fragmented, human-dominated landscapes in general.

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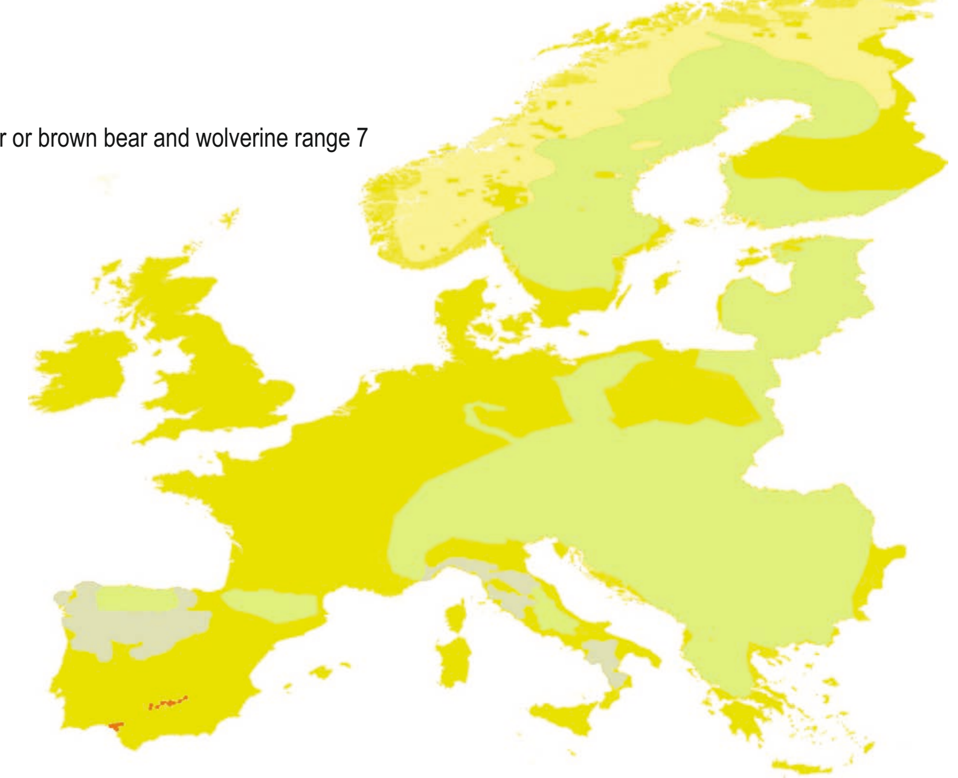
Modelling habitat suitability for Eurasian Lynx - input layers and modelling process

input layers

competition

competition
weighting factor: 0.075

suitability
- 🟧 Iberian lynx range 1
- 🟨 wolf, wolverine and brown bear range 6
- 🟩 wolf and wolverine, wolf and brown bear or brown bear and wolverine range 7
- ⬜ wolf, wolverine or brown bear range 8
- 🟨 no other large carnivore range 10

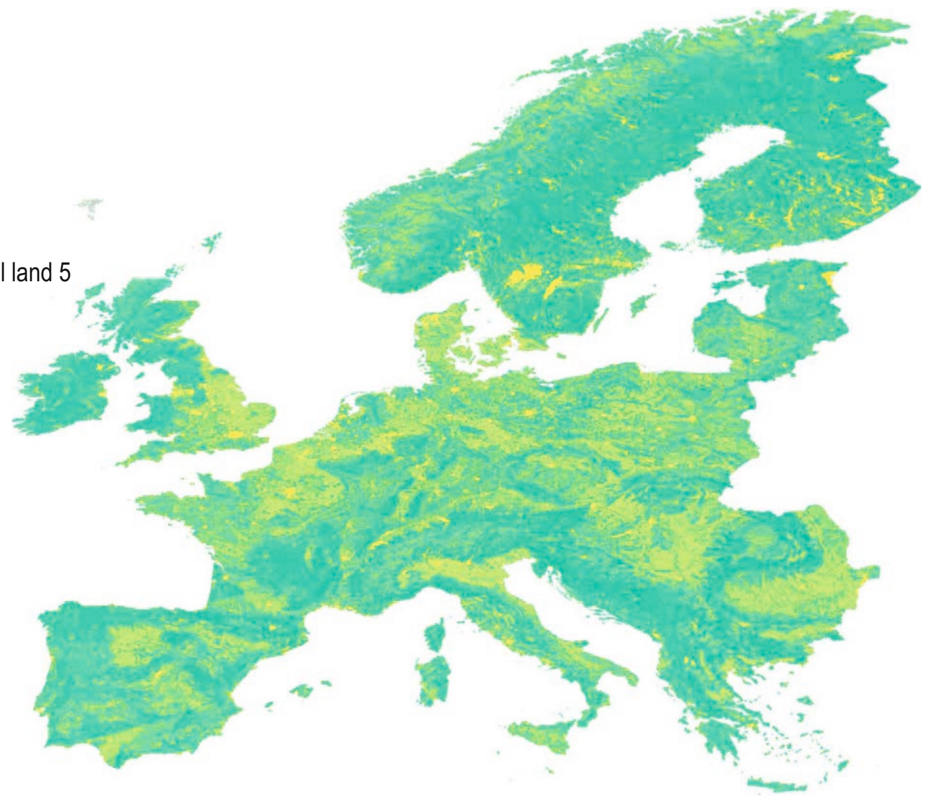


Data sources: RODRÍGUEZ and CALZADA 2015; ABRAMOV 2016; BOITANI 2018; MCLELLAN 2017
Data basis for choosing weighting factor and classification: BUNNEFELD et al. 2006; SUNQUIST and SUNQUIST 2002

environmental

land cover
weighting factor: 0.25

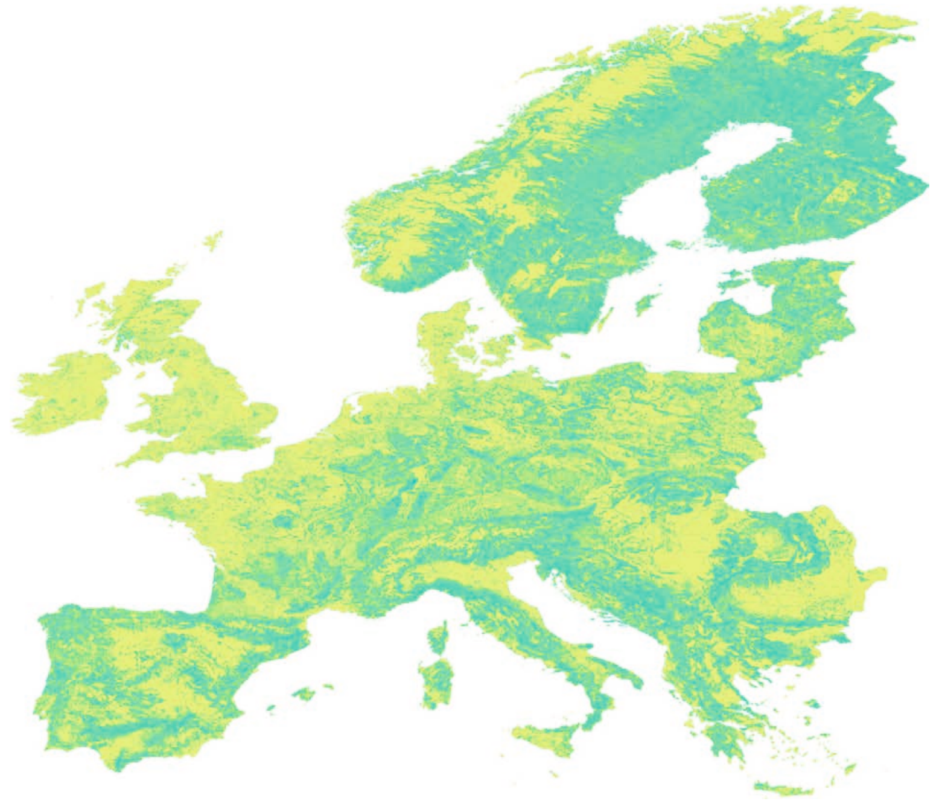
suitability
- 🟨 water bodies, urban areas 0
- 🟨 green urban areas 1
- 🟩 arable land, coastal wetlands 2
- 🟩 open land with little or no vegetation3
- 🟩 permanent crops 4
- 🟩 inland wetlands, heterogenous agricultural land 5
- 🟩 shrubs 6
- 🟩 pastures 7
- 🟩 forests 10



Data sources: European Environment Agency 2018
Data basis for choosing weighting factor and classification: BATES and JONES 2016; BECKER 2013; CORSI et al. 1998; DOSWALD ET AL. 2007

tree cover
weighting factor: 0.1

suitability
- 🟨 0 - 10% 1
- 🟩 10 - 20% 5
- 🟩 50 - 100 8
- 🟩 20 - 50 10



Data sources: SEXTON et al. 2013
Data basis for choosing weighting factor and classification: HETHERINGTON et al. 2008; LYNX TRUST UK 2017; ROZYLOWICZ et al. 2010; PODGORSKI et al. 2008

topographical

aspect
weighting factor: 0.075

suitability
- 🟩 north 3
- 🟩 east 4
- 🟦 west 8
- 🟦 south 10

Data sources: USGS 2010
Data basis for choosing weighting factor and classification: BOUYER et al. 2015; HALLER and BREITENMOSER 1986

slope
weighting factor: 0.075

suitability
- 🟩 0 - 5% 4
- 🟩 5 - 20% 6
- 🟦 20 - 50% 8
- 🟦 50 - 90% 9

Data sources: USGS 2010
Data basis for choosing weighting factor and classification: BECKER 2013; BOUYER et al. 2015; CORSI et al. 1998; DOSWALD et al. 2007; HALLER and BREITENMOSER 1986; MAANEN et al. 2005

hight
weighting factor: 0.075

suitability
- 🟨 more than 5500 m 0
- 🟩 2000 - 5500 m 2
- 🟩 1000 - 2000 m 4
- 🟩 less than 500 m 8
- 🟦 500 - 750 m 9
- 🟦 750 - 1000 m 10

Data sources: USGS 2010
Data basis for choosing weighting factor and classification: BECKER 2013; BOUYER et al. 2015; CORSI et al. 1998; DOSWALD et al. 2007; HALLER and BREITENMOSER 1986; MAANEN et al. 2005

human influence

distance to human settlements
weighting factor: 0.075

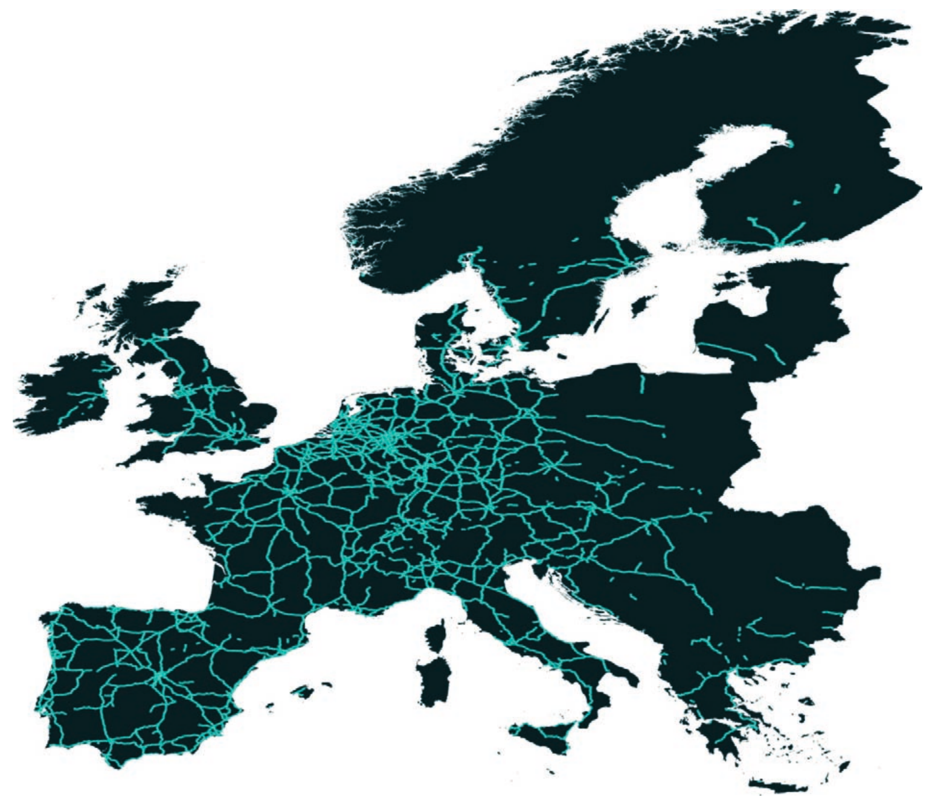
suitability
- 🟩 less than 500 m 1
- 🟩 500 - 2000 m 3
- 🟦 more than 5000 m 8
- ⬛ 2000 - 5000 m 10

0 500 1000 km

Data basis for choosing weighting factor and classification: BOUYER et al. 2015; FILLA et al. 2017; ZIMMERMANN and BREITENMOSER 2007

distance to highways
weighting factor: 0.1

suitability
- 🟩 less than 500 m 1
- 🟩 500 - 1000 m 2
- 🟩 1000 - 5000 m 4
- ⬛ more than 5000 m 10



Data sources: Open Street Map 2018a
Data basis for choosing weighting factor and classification: BUNNEFELD et al. 2006; HERDTFELDER 2012; FAHRIG and RYTWINSKI 2009

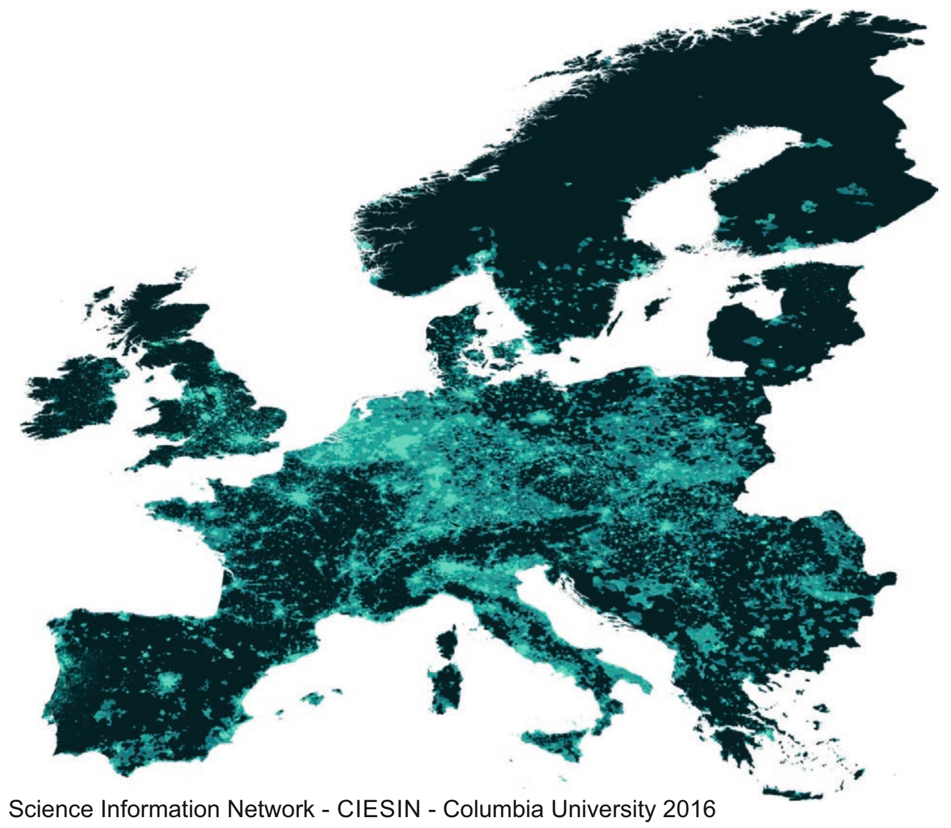
distance to railways
weighting factor: 0.1

suitability
- 🟩 less than 500 m 1
- 🟩 500 - 1000 m 2
- 🟩 1000 - 5000 m 4
- ⬛ more than 5000 m 10

Data sources: Open Street Map 2018b
Data basis for choosing weighting factor and classification: BUNNEFELD et al. 2006; HERDTFELDER 2012; FAHRIG and RYTWINSKI 2009

population density
weighting factor: 0.075

suitability
- 🟩 more than 500 people per square km 1
- 🟩 100 - 500 people per square km 4
- 🟦 50 - 100 people per suare km 6
- ⬛ less than 50 people per square km 10

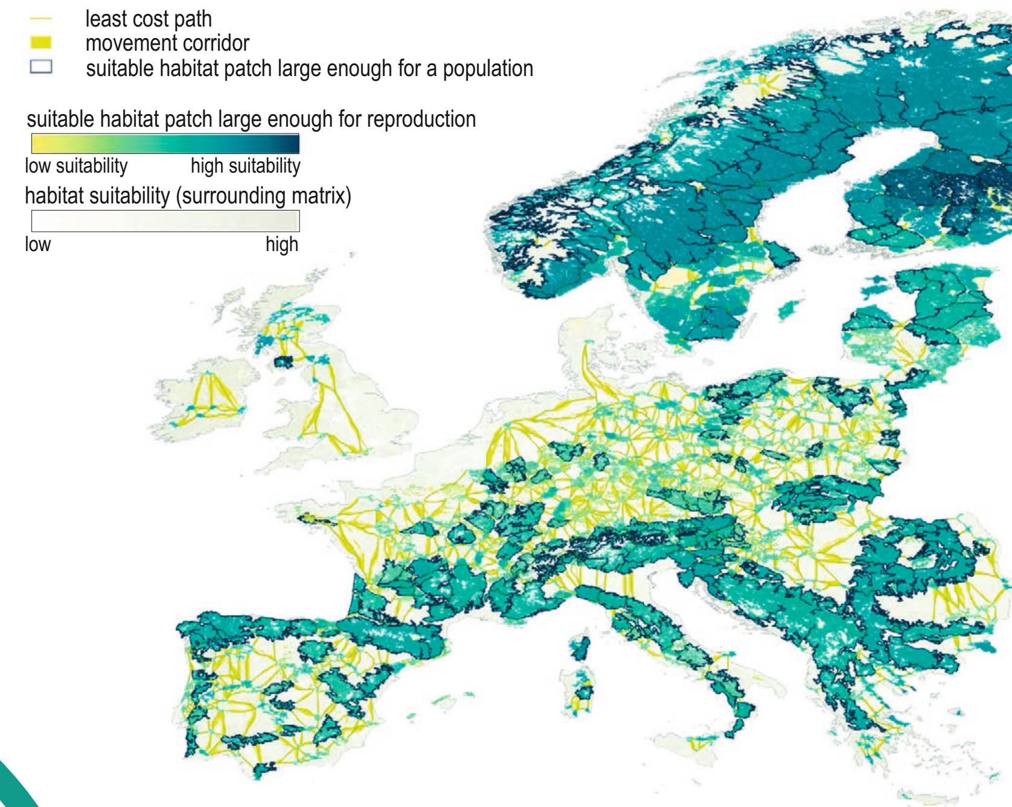


Data sources: Center for International Earth Science Information Network - CIESIN - Columbia University 2016
Data basis for choosing weighting factor and classification: COHEN and NEWMAN 1991; CROOKS 2002; FAHRIG and RYTWINSKI 2009

combination of input layers using
the weighted geometric mean

$$\bar{x} = \left(\prod_{i=1}^{n} x_i^{w_i}\right)^{1/\sum_{i=1}^{n} w_i}$$

suitability model



- ▬ least cost path
- 🟨 movement corridor
- ☐ suitable habitat patch large enough for a population

suitable habitat patch large enough for reproduction
low suitability high suitability
habitat suitability (surrounding matrix)
low high

final model

patch identification and
classification of the
identified patches
according to the suitability