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Human disturbance is the most limiting factor driving habitat selection of a large carnivore throughout Continental Europe

Abstract

Habitat selection is a multi-scale process driven by trade-offs between benefits, such as resource abundance, and disadvantages, such as the avoidance of risk. The latter includes human disturbances, to which large carnivores, with their large spatial requirements, are especially sensitive. We investigated the ecological processes underlying multi-scale habitat selection of a large carnivore, namely Eurasian lynx, across European landscapes characterized by different levels of human modification. Using a unique dataset of 125 lynx from 9 study sites across Europe, we compared used and available locations within landscape and home-range scales using a novel Mixed Effect randomForest approach, while considering environmental predictors as proxies for human disturbances and environmental resources. At the landscape scale, lynx avoided roads and human settlements, while at the home-range scale natural landscape features associated with shelter and prey abundance were more important. The results showed sex was of relatively low variable importance for lynx's general habitat selection behaviour. We found increasingly homogeneous responses across study sites with finer selection scales, suggesting that study site differences determined coarse selection, while utilization of resources at the finer selection scale was broadly universal. Thereby describing lynx’s requirement, if not preference, for heterogeneous forests and shelter from human disturbances and implying that regional differences in coarse-scale selection are driven by availability rather than preference. These results provide crucial information for conserving this species in human-dominated landscapes, as well as for the first time, to our knowledge, generalising habitat selection behaviour of a large carnivore species at a continental scale.

Keywords

Habitat selection, human disturbance, large carnivore, multi-scale, carnivore ecology, landscape cohabitation

Introduction

Habitat selection is commonly considered an adaptive behaviour tuned over evolutionary time to maximize animals' fitness (*Morris, 2003).* Adequate placement, and use, of the home-range is crucial for individuals' reproductive success and survival, as it depends on the resources available within the home-range. Thus, animals will structure their space use balancing the costs and benefits of the available habitats (*Bunnefeld et al., 2006; Basille et al., 2013*). In addition, habitat selection is a hierarchical process in which animals meet diverse requirements by choosing habitats at different ecological scales (*Johnson, 1980*), from the selection of forage resources at the finest scale (*van Beeck Calkoen et al., 2019*) to species distribution at the broadest scale (*Condit et al., 2013*). Furthermore, while habitat selection may covary at different spatial scales in a uniform landscape, it may not be the case in a realistic landscape with spatially heterogeneous distributions of risks and resources (*Boulinier and Lemel, 1996*). For example, *McMahon et al. (2017)* observed that, at coarser scales, pygmy rabbits (*Brachylagus idahoensis*) chose habitats that provided protection from predation, whereas at finer scales the intensity of patch use was driven by forage availability. Moreover, the availability of resources and distribution of risk factors at finer scales depends on the selection at coarser scales. *Rettie and Messier (2000)* proposed that the most limiting factors should drive behaviour at coarser spatial scales and less so at finer spatial scales. This hypothesis implies that, if animals can spatially partition the most limiting factors at home-range selection scale (2nd order), the selection of features within the home-range should be focussed on different risks or resources.

The spatial distribution of most mammalian carnivores is driven by trade-offs between prey abundance, availability of shelters and potential mates, with the avoidance of mortality risks. For instance, grey wolf (*Canis lupus*) density was shown to be positively correlated with moose presence but simultaneously their territory size was altered to balance territorial defence costs and resource acquisition efficiency (*Kittle et al., 2015*). Similarly, *Dellinger et al. (2019)* found that mountain lions (*Puma concolor*) in California selected steep slopes at the home-range scale to facilitate hunting efficiency, while showing decreased preference for this feature within the home-range due to seasonality of prey occurrence.

Interspecific interactions are a risk component that can play a determining role in shaping spatial territories (*Rostro-García et al., 2015; Balme et al., 2017*; *Newsome et al., 2017*). In particular, the effects of humans and human-related disturbances on apex predators have received special attention in recent years (*Suraci et al., 2019; Ordiz et al., 2021*). As a response to human disturbance, tigers (*Panthera tigris*) in India locate their den sites in areas with low anthropogenic pressure (*Majumder et al., 2012*) and cheetah (*Acinonyx jubatus*) in the Maasai Mara were found to avoid humans, which apparently represented higher risks than competitors (*Klaassen and Broekhuis 2018*). Similarly, leopard (*Panthera pardus*) density in Tanzania correlated positively with the distance to the boundaries of a national park, a proxy for decreasing anthropogenic disturbances, showing avoidance of high human activity levels (*Havmøller et al., 2019*).

Studying how human disturbances shape large carnivore distribution is therefore of paramount importance for their conservation and of special interest in human-dominated landscapes such as Europe. In fact, most large carnivores were locally extinct throughout Europe by the mid-20th century (*Chapron et al., 2014*). Nowadays, Eurasian lynx (*Lynx lynx,* hereafter: lynx) distribution in continental Europe is characterized by small and isolated populations (*Linnell et al., 2008*). According to the Natura 2000 Habitats Directive, lynx's conservation status in Europe is 'favourable' in the boreal biogeographical region, with most continental areas 'unfavourable-bad' or 'unfavourable-inadequate' (*European Environment Agency, 2012*). However, lynx's favourable public image, compared to other large carnivores (*Trajçe et al., 2019*), combined with its apparent ability to persist in human-dominated landscapes, make it a model large carnivore species regarding conservation and landscape cohabitation (*Carter and Linnell, 2016*).

Given their large spatial requirements, large carnivores must cross human-dominated landscapes to integrate enough appropriate habitats, likely leading to an increase in mortality risk

(*Fahrig 2007; Kowalczyk et al. 2015*). Indeed, human activities represent the major threat for lynx individuals due to accidental killings, e.g. vehicle collisions and "bycatch" with snares targeting ungulates (*Kowalczyk et al. 2015*), poaching (*Heurich et al., 2018; Arlettaz et al., 2021*) motivated by competition with hunters (*Basille et al., 2009; Červený et al. 2019*), and in some countries legal harvest (management strategy) (*Sunde et al., 1998a*). Nevertheless, lynx populations have distributions in highly fragmented areas characterized by relatively high anthropogenic pressure (**Figure 1**). At broad scales, lynx's distribution has been attributed to availability of prey, forested landcover, and avoidance of highly fragmented anthropogenic landscapes (*Schadt et al., 2002a; Schadt et al., 2002b; Niedziałkowska et al., 2006; May et al., 2008; Müller et al., 2014*), although their distribution in Europe still leaves many suitable patches unoccupied (*Magg et al., 2016*). Studies of lynx's habitat selection at finer scales also reported avoidance of human risk factors. For example, in the Bohemian Forest Ecosystem lynx were shown to avoid trails and roads during daytime (*Filla et al., 2017*) and rest in locations far from recreational activity (*Belotti et al., 2018*). Similarly, in Southern Norway resting sites were in areas of lower human modification than kill sites (*Bouyer et al., 2015*). However, behavioural plasticity allows lynx to take advantage of these areas. For example, lynx have been observed to reduce time spent at kill sites located in more human-frequented areas (*Belotti et al., 2018*) and increase their speed to reduce the chance of encountering people (*Gehr et al., 2017*). Further, microhabitat selection of lynx has been shown to include complex structured heterogeneous habitats for stalking prey and low visibility, as well as rugged sites for resting (*Podgórski et al., 2008; Hočevar et al., 2021*). However, all these studies were regionally limited, restricting inferences to their sites.

Considering the cause-specific mortality of lynx, mentioned previously, it is expected that avoidance of human disturbances should be an important limiting factor that drives lynx spatial distribution at the coarsest scale (*Rettie and Messier, 2000*). This situation is complicated when we consider the role of sex, which could potentially influence trade-offs. *Bunnefeld et al. (2006)* found female lynx would approach human settlements more closely to hunt in high foraging efficiency areas or seek more secure refuges, depending on the age and presence of accompanying dependent young. Contrastingly, the larger home-ranges of males might imply lower selectivity for risk avoidance and bold, explorative behaviour. For large carnivore management it is crucial to understand how space use, and consequently habitat use, of these species are constrained by intrinsic, such as sex, and extrinsic factors, such as environmental and human-related factors (*Kowalczyk et al. 2015, Lopéz-Bao et al., 2019*). Such information is essential to support the planning of large-scale management actions (*Boitani et al., 2015*). However, to our knowledge there has been no multiregional investigation of the habitat selection patterns of lynx that embraces gradients of habitat and anthropogenic pressure that may occur across a large geographical extent.

In this study we took advantage of a pan-European radiotracking dataset to analyse the multi-scale (home-range and within home-range) habitat selection of lynx exposed to a diverse array of habitats and human influences. Assuming animals select their home-ranges for their landscape characteristics (*Thomas and Taylor, 2006*), we investigated lynx's sex-specific home-range and within home-range habitat selection with the following predictions: i) lynx select habitats with lower human disturbance, especially at large spatial scales (2nd order) according to the "limiting factor avoidance hypothesis", ii) lynx select habitats associated with shelter and prey at 3rd order (*Podgórski et al. 2008*), and finally iii) we predict a sex-dependent selection process, regarding responses to both habitat and human disturbance. Specifically, we expect males to be less selective than females, as they use larger areas (*Herfindal et al., 2005*), while females often prioritize refuges and food availability to rear offspring (*Oliveira et al., 2018*). Overall, we aimed to generalize basic species knowledge beyond the limits of single study sites. We were able to achieve this and highlight the most limiting factors for Eurasian lynx.

Materials and methods

Study area and data collection

Our study area covers the European subcontinent, extending from the French Jura Mountains in the southwest to Estonia in the northeast (**Figure 1**). VHF and GPS data were collected from nine study sites distributed across this area between 1988 and 2021 (**Table 1**). A total of 125 adult individuals (63 males, 62 females) were captured and equipped with tracking-collars (*Schmidt et al., 2008; Podgórski et al. 2013*). Locations of VHF collared animals (*n=84*) were obtained via triangulation of signals and in-situ tracking (*Breitenmoser et al., 1993*; *Schmidt et al., 1997*), resulting in one location per day on average with a precision of at least 1 km^2. GPS collars (*n=44*) obtained between 1 and 30 locations daily. The study sites represent a cross-section of the biogeographical regions and habitats in Europe (**S1**).

Home range estimation

We subsampled telemetry locations to a maximum of one location per individual per day and of one location per individual per night/crepuscular (chosen at random), thereby reducing autocorrelation of higher frequency fixes (*Bouyer et al., 2014*) and harmonizing GPS and VHF data. We did not consider individuals with <30 days with locations in the reduced dataset for analysis (*Lendrum et al., 2014*). Most VHF data was collected during daytime when lynx rest and are easier to localize. We did not use VHF locations explicitly as "used" in analyses (see 'Habitat selection analysis'), hence their temporal imbalance could be neglected. GPS locations were relatively balanced: 43% day and 57% night or crepuscular (**S1**). We inspected incremental plots (time vs cumulative home-range area) to check for range shifts before including individuals in the analysis. We limited the investigation to resident adult individuals (≥2 years old; *Linnell et al., 2001*) to exclude dispersal behaviour. Tracking periods with range shifts were split to remove the non-residential behaviour and any remaining residential periods were treated as above **(S1**). We estimated the home-ranges from the reduced dataset using Kernel Density Estimation (KDE) from the R package "adehabitatHR" (*Calenge 2006*) with 0.8*reference bandwidth (*Aronsson et al., 2016)* and delineated the home-range boundaries at 95% and 50% vertices.

Habitat selection analysis

We performed habitat analyses at second and third orders, which are the selection of a home-range within the geographical area (2nd order) and the selection of habitat components within the home-range (3rd order) *(Meyer and Thuiller, 2006; Mayor et al., 2009).* At home-range level (2nd order), we compared two randomly sampled sets of points ("used" and "available") for each individual and their respective study sites. Based on the number of locations in each individual's reduced dataset *n*, "used" (i.e. selected by individuals) points were filtered by sampling *n**0.95 and *n**0.5 locations within the home-range and home-range core, respectively. We computed "available" points by sampling an equal number of points as the corresponding used points within the 'available landscape' (*Fattebert et al., 2015*). We defined the available landscape by aggregating the individual home-ranges for each study site with an additional buffer equal to the mean home-range (95% KDE) radius ($\sqrt{\mathrm{home}-\mathrm{range\ area}/\pi}$) of the individuals in that study site (*Oliveira et al., 2018*). Within the home-range (3rd order selection), we compared "used", in this case the actual telemetry locations, and "available" locations within the home-range (*Filla et al., 2017*). We computed available points by sampling an equal number of points as used points within the home-range or home-range core. We assessed the 3rd order selection using only GPS data (*Kie et al., 2010*).

Environmental predictors

We included a range of environmental predictors as proxies for human disturbances, shelter locations, prey abundance, and topography (**Table 2**). Their values were extracted at the used/available locations for use in model fitting. Our study sites all resided in countries with stable land use models (*Gómez et al., 2018*), as such we assumed landscape variables did not vary greatly among tracking periods, and therefore chose temporally median or mean predictors to characterize the landscapes (further details, S1). The predictors were: distance to forests, distance to settlements, distance to roads, road density, slope, roughness, tree cover density, mean NDVI, and sd NDVI. Human disturbances can be separated into human presence and human development (e.g. *Suraci et al., 2021*). The predictors distance to roads and distance to settlements are derived from the latter and, with road density, were used as proxies of human disturbance in the landscape. NDVI is closely related to photosynthetic activity and used in this study as a proxy for prey abundance (*Basille et al., 2009*). A few locations from two transboundary sites (4,7) fell in Belarus or Ukraine and supplementary geospatial data were required (**S1, Table 2**). We maintained the highest resolution of the predictors possible and calculated road density at 1km^2 to respect the spatial scale of lynx home-ranges (km^2). Violin plots of environmental predictor distributions by study sites, see **S1**.

Model fitting and validation

We investigated how explanatory variables affected habitat selection using Mixed Effect randomForest (MErf) (*Ngufor et al., 2019*). This represents a novel application of a mixed modelling approach developed for machine learning algorithms. MErf combines the flexibility of "randomForest" (*Breiman, 2001*) for habitat modelling (*Cushman and Wasserman, 2018*), with the advantages of Generalized Linear Mixed Models (GLMM) for structured data. MErf iterates between randomForest, to fit fixed effects (environmental predictors, sex, study site), and GLMM to fit random effects with individual ID nested within the study site (1|study site/individuum). randomForest automatically fits any fixed effect interactions. We used balanced samples of used and available points for best randomForest performance (*Barbet-Massin et al., 2012*) and the reduced dataset (at 3rd order) improves compliance with the RF assumption that bagging is independent (*Cushman, 2010)*. We confirmed that explanatory variables were not multicollinear (QR-matrix decomposition p<1e-07), using R package "rfUtilities" (*Evans and Murphy, 2014*). To account for regional and temporal differences, we also included "study site" as a fixed effect. We assessed fixed effects' Out-Of-Bag errors and conducted k-fold cross-validation (k=5) to compute accuracy, sensitivity, specificity and 'area under the curve'. We used permutation variable importance (*n=100*) to determine the parameters relative impacts, using the R package "vip" (*Greenwell et al., 2018*). We visualized variables using 'Accumulated Local Effects' plots (*Apley, 2020*), with a "loess" smoother. Further details, **S2.**

We conducted our analyses with the software R (R 5.3.2) (*R Core Team, 2018*). In particular, the packages "rgeos" (*Bivand and Rundel, 2018),* "sp" (*Bivand et al., 2013*), "raster" (*Hijmans 2019*), "RRF" (*Deng, 2013*)*,* "lme4" (*Bates et al., 2015*), and "ggplot2" (*Wickham, 2016*).

Results

At 2nd order habitat selection, the variable importance (Figure 2) of 'study site' and 'distance to settlements' were highest ranked in both home-range and home-range core models (≈15%). The relative importance of study site for the 3rd order models was much lower (<10%). In contrast, the most important variable in the 3rd order models was 'tree cover density' (home-range≈20, core≈30%). After these, 'NDVI', 'distance to roads' and 'distance to settlements' ranked highly in all models (10-15%), especially relative to the remaining variables. The variable 'sex' and 'individuum' were ranked lowest in all models.

We visualised the 'Accumulated Local Effects' (responses) for the highest ranked variables (importance≥10 in either 2nd or 3rd order): distance to roads, distance to settlements, NDVI mean and tree cover density (remaining variables, see **S3**). At 2nd order habitat selection (**Figure 3**), we observed that lynx tend to avoid human settlements, particularly at the home-range level, shown by the avoidance of distances <2km. We found an avoidance of roads (<1km), with avoidance more evident in the home-range core and generally a selection of distances >1km. Distance to settlements and roads both plateaued after 2.5-3km. There was also a selection of NDVI values >0.6 (higher productivity) and a strong avoidance of lower values. There was a weak avoidance of the highest and lowest 'tree cover density' values, <25% and >85% for both sexes and a slight selection of values around 70-80%. Finally, at this order, sexes exhibited virtually uniform responses.

At 3rd order habitat selection (**Figure 4**) male and female lynx again showed equal preferences. Lynx selected distances of 1km from roads, with an avoidance of closer distances in both home-range and home-range core. Similarly, there was a strong avoidance of close distances to human settlements (<1 km), and moreover a similar selection of distances approx. 2 km to settlements. NDVI values around 0.7 were preferred, and the highest values were avoided in the home-range core. In addition, there was a strong bimodal selection for the highest and medium (25-70%) values of tree cover density within the home-range and home-range core.

The predictors' interactions with study site revealed more variability at 2nd order than at 3rd order (**S3**) and coincident with the differing distributions of predictors variables available at each site (**S1**). The differences between study sites (*n=9*) at the 2nd order were most apparent in distance to roads and distance to settlements at home-range level. Here, distance to settlements showed fair agreement but with differing intercepts among sites, apart from the Dinaric and Baltic (PO) sites that also selected close distances. For distance to roads, despite disparity in greater distance, in most study sites lynx exhibited similar patterns of avoidance of roads, while in the Alpine (CH) there was selection near roads. The responses at 2nd order home-range core broadly agreed. At 3rd order, there was high conformity across sites (*n=6*) increasing from home-range to the home-range core (**S3**).

Among the distance variables, responses beyond ≈3km plateaued, suggesting the variables provide inference up to this level and could be associated with landscape artefacts above this. Finally, for all models, we obtained out of bag errors <4% (fixed effects), cross-validation accuracy was >64%, specificity and sensitivity >63%, and 'area under the curve' >0.71 (**S2**).

Discussion

Our analysis revealed strong evidence of human-driven habitat selection for lynx. As predicted, i) lynx generally avoided roads and anthropogenic landscape features, shown by their preference for higher distances from human settlements and roads, with a higher importance at 2nd order. Consistent with prediction ii), we found a preference for landscape features characteristic of shelter and hunting opportunities, which were of higher importance within the home-range (3rd order). Contrary to prediction iii), we found homogeneous responses between sexes. To our knowledge, this is the first study to reveal habitat selection behaviour of lynx at 2nd and 3rd order on a pan-European scale. Our results indicate relatively homogeneous utilization of resources within the home-range, with larger differences between sites found in home-range selection. This suggests 2nd order selection is driven by availability and resources utilized at 3rd order tend to be more universal.

We found a general pattern that lynx selected areas for home-range placement away from roads and human settlements. These results are consistent with local, single site, studies on felid's home-range selection, for example: home-range selection and occupancy of lynx in Poland revealed avoidance of human settlements, transportation infrastructure and activity (*Niedziałkowska et al. 2006*; *Bubnicki et al. 2019*), and lynx home-range placement in the Jura Mountains avoided urbanized areas (*Schadt et al., 2002b*). Various other felid species have shown avoidance of humans in cohabited landscapes (*Wilmers et al., 2013*; *Klar et al., 2008; Klaassen and Broekhuis, 2018).* Given the importance of human-caused mortality for lynx in Europe, such as illegal and legal killing, wildlife vehicle collisions (*Arlettaz et al., 2021; Heurich et al., 2018; Basille et al., 2009; Breitenmoser-Würsten et al., 2007; Kowalczyk et al. 2015; Sunde et al., 1998a*), this coarse-scale avoidance of human structures implies consistency with the limiting factor avoidance hypothesis that states the negative factor that most affects species should be avoided most at coarser ecological scales (*Rettie and Messier, 2000*). Our results therefore implicate human factors as most limiting for lynx. This is consistent with studies exploring processes besides resource selection. For example, in Białowieża Forest and the Bohemian Forest Ecosystem human-dominated areas outside protected areas were found to act as population sinks (*Kowalczyk et al. 2015; Heurich et al., 2018*). In our results, these two study sites and the Dinaric exhibited selection at distances close to settlements in home-range selection, contrasting to the clearer avoidance found generally. This is likely due to the landscape similarities between the study areas (BBA, Baltic (PO), Dinaric). Namely, where the predominantly forested available landscapes contained relatively few human settlements and therefore lynx seem to select closer to settlements when near the forest perimeter. The importance of distance to human infrastructures was lower within the home-range, though there was a similar avoidance of the closest distances (<1 km) to settlements that was largely uniform among sites. Although we found a general avoidance of roads by lynx, in the Alpine (CH) study area this was not the case in home-range selection. Given the rugged terrain in this region, we suggest the 2-D distance to roads might belie the perceived security afforded by altitudinal separation. This assertion is consistent with the greater avoidance for home-range core selection we found. In this analysis we did not consider forestry tracks. It was previously shown that lynx utilize such forestry tracks for movement or marking (*Vogt et al., 2014*; *Allen et al., 2017; Krofel et al., 2017*). However, forestry tracks cannot be considered the same mortality threat for lynx as ordinary roads. Considering both selection orders, it is justified that lynx consider humans a threat and try to avoid the closest proximity.

We found that lynx tended to establish home-ranges (2nd order) in productive forested areas, which is likely due to lower human disturbance, higher prey densities and featureful hunting grounds, and avoided unforested areas. However, selection across different tree cover densities was close to availability, probably because all sites can be broadly defined as forested. Prior analyses found lynx in the Jura Mountains (*Schadt et al., 2002b*) and Poland (*Niedziałkowska et al., 2006*) placed home-ranges in areas with ≈53% and 68% forest cover respectively, with the latter describing a lower threshold of 40% for occupation. We found the Alpine (CH) study site occupied an area of just 46% forest cover (S1). That said, lynx is capable of surviving in areas with almost no forest (*Linnell et al., 2021*). Beyond this, we observed avoidance of purely forested (>90% forest cover) locations in home-range selection, demonstrating requirements for complex landscape features by selecting less homogeneously forested or unforested areas than was available. The 2nd order analysis had a slight bias towards resting locations given the VHF data. However, at this order used locations were randomly distributed in the home-range, not empirical locations themselves, thereby limiting any effect. Within the home-range and home-range core (3rd order) we found lynx selected high and medium tree cover. This is consistent with studies that have shown resting sites correlated positively with high coverage and habitat characteristics that imply low human accessibility, necessary for lynx's perception of safety (*Podgórski et al., 2008; Belotti et al., 2018; Signer et al., 2019).* In the 3rd order analysis, day and night locations were relatively balanced, therefore the behaviour we observed is general or a mix of temporal behaviours (*Filla et al., 2017*).

In addition to shelter, we predicted an affinity to landscapes that provide food resources. Habitat selection within the home-range (3rd order) showed that lynx also selected habitats characterized by medium tree cover density (25-70%). These could be land-cover types, ranging from meadows interspersed with woodland to forests with openings and edge features, which offer good cover opportunities for prey detection, stalking and ambushing (*Podgórski et al., 2008; Belotti et al. 2015*) and are characterised by higher roe deer (main lynx prey) densities (*Melis et al., 2010*). Further, we used NDVI as a proxy for prey abundance (*Melis et al., 2010*) and found a preference for medium values at 3rd and high values at 2nd orders, respectively. This describes home-range placement that maximizes the productivity, or prey abundance, within the home-range, even though the highest NDVI was in general not preferred within the home-range. This disparity could be explained by lynx's preference for low visibility and ruggedness in many situations (*Podgórski et al., 2008; Belotti et al., 2018)*, which correlates with heterogeneous landcover of reduced photosynthetic density (lower NDVI) than productive forest or meadows (*Gamon et al., 1995*). In general, combining the NDVI response with preference for landscapes around 1-2km from settlements, it seems lynx utilize productive mosaic landscapes surrounding settlements. This could follow the distribution of lynx's main prey (*Basille et al., 2009; Müller et al., 2014*), roe deer, whose densities decline with increasing forest cover (*Melis et al., 2010*) and preferentially forage at ecotone and meadows (*Dupke et al., 2016*) and often appear in higher numbers in human-altered habitats (*Lopéz-Bao et al., 2019*), such as crops and artificial feeding sites (*Ossi et al., 2017*). This seems to be consistent with a trade-off in lynx's habitat selection, whereby the avoidance of human-related risks must be balanced with the preference for landscapes with high prey densities, which can often be found close to human disturbances. Our study sites exhibit diverse landscapes and management practices, for which vegetation indices could have diverse correlates. Despite this there was largely uniform responses, although in two sites (Baltic (ET), Carpathian (PO)) showed contrasting avoidance of high NDVI in home-range core at 2nd order. This differing selection could indicate the necessity to diversify hunting grounds, which are less prevalent and not strictly within the forest, or depending on seasonal prey distributions (*Borowik et al., 2013*). NDVI constitutes an indirect index of prey abundance, it has been connected to lynx's prey via performance measures (*Pettorelli et al., 2006*) and habitat selection (*Gaudry et al., 2015*), and remains a fair proxy pending availability of Europe-wide prey or floor-level biomass mapping.

Our results show sex had relatively low importance for habitat selection in lynx. We could not detect higher selectivity in females than males at either order, likely because we did not consider seasonality. We expected males to be driven principally by access to mates, rather than the distribution of food resources (*Sandell 1989, Schmidt et al., 1997*). *Bunnefeld et al. (2006)* showed that female lynx could tolerate more, or less, risk depending on the reproductive cycle (i.e.

presence, vulnerability, and energetic costs of rearing offspring). Sex-specific behaviours have also been reported in other felids, e.g.: pumas, where females were less cautious of developed areas than males (*Wilmers et al., 2013*), and conversely European wildcats (*Felis silvestris*) where females avoided anthropogenic structures more than males (*Oliveira et al., 2018*). In contrast, our results suggest that any sex-differences are temporally restricted phenomena (i.e. mating or maternal behaviours) and not general behaviour. We considered year-round selection, thereby diluting seasonal preferences, which ultimately highlights the intrinsically similar preferences of sexes. Such simplification is necessary for contextualizing habitat selection of large carnivores at a pan-European scale.

Habitat availability is ubiquitous in habitat selection since a home-range's attributes are inherently determined by food and cover availability. For example, home-range size increases with decreasing productivity as animals exploit larger areas to gain sufficient resources (*Herfindal et al., 2005; Walton et al., 2017*) or decreases with higher conspecific densities (*Morris, 2003*), which implies an impact on selection. This was reflected by the importance of 'study site' in our analyses, which was higher in the 2nd order, thereby, suggesting a greater impact on home-range placement in the available landscapes compared to use of resources within the chosen home-ranges. Expressly, differences between study sites might constrain coarse selection, but it implies fine-scale selection was more homogenous and desirable resources were universal. Our sites included alpine, boreal, and continental biogeographical regions, differing landscape management, and natural and socio-political conditions. These seem to be partitioned favourably by home-range selection, providing the preconditions for uniform responses across study sites at 3rd order. This could be interpreted as a coherent signal, from lynx, indicating preferred conditions, or conservatively, conditions that offer enough security and resources given the risks in Europe. More pessimistically, this could be a large carnivore squeezed into diverse landscapes with only limited niche availability. Nevertheless, the requirements (utilization at 3rd order) appear to include some areas away from human infrastructure (≈1-2km) and diverse landscape structures (forests, meadows). Lynx can take advantage of prey in multi-use landscapes, provided they have also heterogenous forests that include medium tree cover (25-70%) and high tree cover (>90%), supplying adequate cover while hunting and moving, as well as areas for shelter. Together these factors help lynx cohabit human landscapes.

Our study considered distance to human developments (roads and settlements) as disturbance proxies, however different types of disturbance can have disparate effects (*Suraci et al., 2021*). Human presence and activities are ephemeral disturbances that can drive spatiotemporally varying habitat selection (*Richter et al., 2020*). Although human presence and activity types have not been explicitly proven to affect lynx, the avoidance of developments we, and others (e.g. *Belotti et al., 2018; Niedziałkowska et al., 2006*), have found are convincing. Further, the crepuscular nature of lynx (*Heurich et al., 2014*) likely already minimises the effect of human ingression of natural landscapes by precluding temporal overlaps, which only underlines the importance of protecting refuge habitats necessary for large carnivores to rest during times of heightened human activity. Detailed studies of spatiotemporal human-carnivore interactions under different human activity modes (e.g. recreation, hunting) would be an important step for conservation biology.

This study cannot speculate on habitat-specific behaviours that preclude selection (i.e. internal state) and therefore, despite apparently similar processes, there are likely population differences. Lynx have been known to exhibit plastic behaviour dependent on local conditions (*Gehr et al., 2017*). However, to date, there has been no study of multi-population habitat selection of lynx that can propose generalization for Europe. Further, lynx's spatial-social system is based on territoriality, with low tolerance between same-sex adults and high home-range overlaps between opposite-sexes (*Breitenmoser et al., 1993; Breitenmoser-Würsten et al., 2007*; *Schmidt et al., 1997*). Consequently, the distribution of conspecifics influences selection. In fact, "good" habitat for males could imply access to females. This might blur habitat preferences but is necessary to capture the essence of a dynamic process at a higher population level and increase our knowledge when discussing the species' pan-European conservation. Furthermore, this is best considered when all individuals in a region are radio-tracked simultaneously, which is rarely realized.

We could not consider interspecific competition in this framework because the combinations of competitors (**S1**) were not adequately repeated in our dataset to distinguish their effects from other inter-site differences. Prior studies suggested a low impact of wolves on lynx space use (*Schmidt et al., 2009; Wikenros et al., 2010*). However, segregation is a way to coexist (*Milleret et al., 2018*), for example kleptoparasitism of bears resulted in spatiotemporal avoidance of bear feeding sites by lynx (*Krofel and Jerina, 2016*). Therefore, behavioural adjustments help balance risks and resources. Here, site differences, including human-related ones such as traffic intensity or agricultural practices, were aggregated into one variable that cannot resolve these complexities. Consequently, effects of competitive interactions on lynx habitat selection remains for future work. Despite limitations, we believe the strength of our analysis lies exactly in the general findings across a large geographical scale.

Lynx have been the focus of numerous reintroduction projects since the 1970s, and these have mostly been successful in colonising certain target patches. However, the threats faced decades ago have not changed completely. Foremost, lynx populations in Europe are still restricted to certain patches that are largely isolated from one another. Our results showed that lynx avoid human disturbance features like settlements and roads. Therefore, measures should be engendered that prevent or minimise the expansion of settlements and road networks in core population areas. Protecting these vital habitat patches is important to maintain healthy lynx populations, and to provide offspring that might populate neighbouring habitat patches (*Palmero et al., 2021*). Isolation can lead to genetic drift and potentially inbreeding effects (*Bull et al., 2016*), so it is important that habitat is not degraded further. European Union (EU) member states are obligated to protect certain sites, such as Natura 2000. However, populations extend outside explicitly protected areas. Therefore, restrictions on development should be imposed in strategic roadless patches (*Psaralexi et al., 2017*). Under the EU's common agricultural policy (CAP), the goals for improving ecological and environmental conditions within forestry, including afforestation, are supported with subsidies (*European Commission, 2019*). These should help protect the integrity of large patches with low human disturbances. Under the CAP, EU farmers must set aside at least 5% of their land for ‘ecological focus areas’ (EFAs) to promote biodiversity and other environmental goals (European Commission, 2017). However, typically farmers choose the cheapest and most productive in terms of agricultural output (Zinngrebe et al., 2017). Therefore, policy should do more to prioritise EFAs that encourage biodiversity (Pe’Er et al., 2019). This could make multi-use landscapes around core areas more amenable for lynx and, in conjunction with large suitable patches, might foster more widespread cohabitation in the future. Although not considered in this analysis, such measures might also improve the situation for dispersing individuals and help connect populations.

Conclusions

An awareness of common biological conditions and habitat requirements is an important foundation to facilitate coordinated management actions on large scales (*Kaczensky et al., 2013*). Here we presented, to our knowledge, the first multi-scale habitat selection analysis of a large carnivore on a continental scale that contributes to filling these gaps. This approach allowed us to provide a more universal picture of lynx behaviour than isolated local studies. Lynx avoided human disturbances, especially at coarser spatial scales, which, in combination with their prime mortality factors, is consistent with the limiting factor avoidance hypothesis. Landscape features associated with shelter and hunting opportunities were more critical for habitat selection within the home-range, highlighting the hierarchical nature of selection processes. By partitioning the available landscapes at 2nd order, lynx could utilize habitats with sufficient security for shelter sites and take advantage of prey resources in human-modified landscapes, for which heterogeneous tree cover is imperative. Lynx's habitat use was therefore driven by unavoidable landscape cohabitation and consistent with a trade-off between prey resources and mortality risk associated with humans. Thus, our results help delineate in a broad European context that lynx seem able to tolerate human disturbance, provided there are enough refuges available (*Sunde et al., 1998b*). Considering the relatively homogenous responses across sites at the home-range scale and sexes, and the low importance of study site, especially within the home-range core, we receive a message from lynx describing the feasible, if not preferred, landscape features for their main activities. Together with the high importance of study site for 2nd order selection, this also implies that differences in coarse-scale selection are rather driven by regional differences in availability than differences in preference. However, the versatility of lynx should not be overestimated, since their preferred resources seem homogeneous, caution should be taken wherever possible not to erode the habitat they currently occupy and further determine thresholds that limit home-range occupation such as minimum breeding habitat patches.

Some complexities were outside the scope of this study (e.g.: intraspecific/interspecific competition, temporality, forest structure, and lynx-harvest) and require dedicated study. Our results put the landscape requirements of lynx into a broad context, revealing trends that transcend population boundaries. Finally, we advocate research considering multiple populations of any species studied. This will improve the understanding of fundamental processes that cannot be extrapolated from single population studies.

Abbreviations

CAP – Common Agricultural Policy
EFA – Ecological Focus Area
KDE - Kernel Density Estimation
MErf – Mixed Effect random forest
NDVI - Normalized Difference Vegetation Index

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Human disturbance is the most limiting factor driving habitat selection of a large carnivore throughout Continental Europe

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Figures and tables

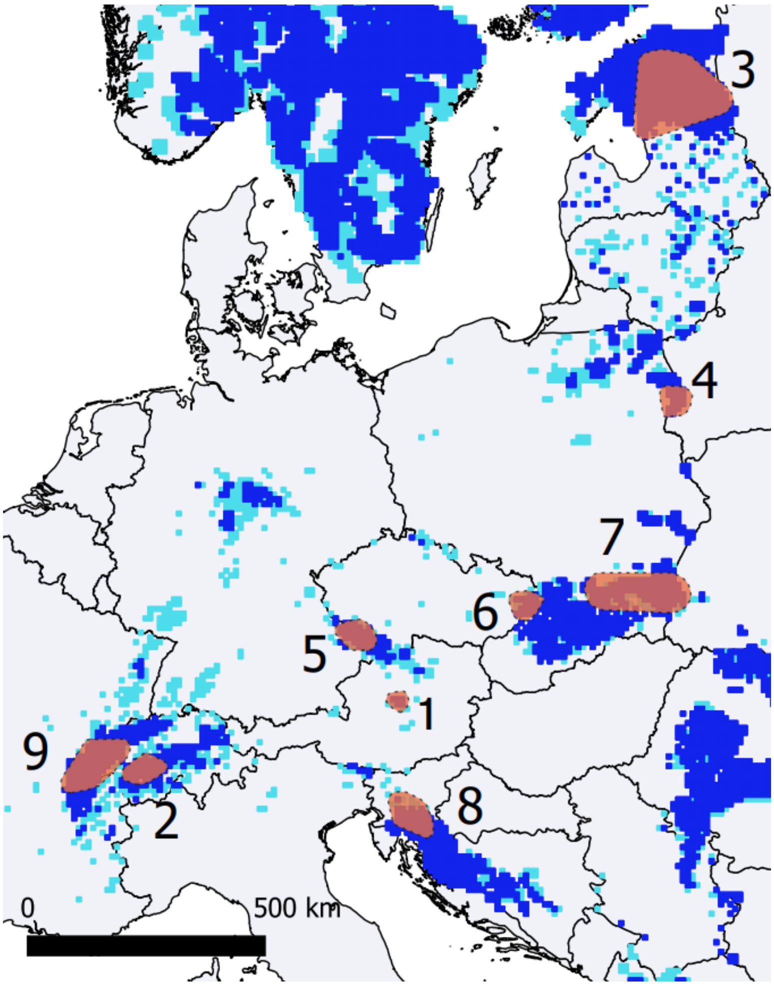

Figure 1*- Locations of the 9 study sites plotted in red (convex hulls) across 7 lynx populations (12 countries). Namely: 1, Alpine (Austria); 2, Alpine (Switzerland); 3, Baltic (Estonia); 4, Baltic (Poland, Belarus); 5, Bohemian-Bavarian-Austrian; 6, Carpathian (Czechia, Slovakia); 7, Carpathian (Poland, Slovakia, Ukraine); 8, Dinaric (Slovenia, Croatia); 9, Jura (France, Switzerland); Lynx distribution across Europe is plotted in dark (permanent presence) and light (sporadic presence) blue (Kaczensky et al., 2021). See also* ***S1****.*

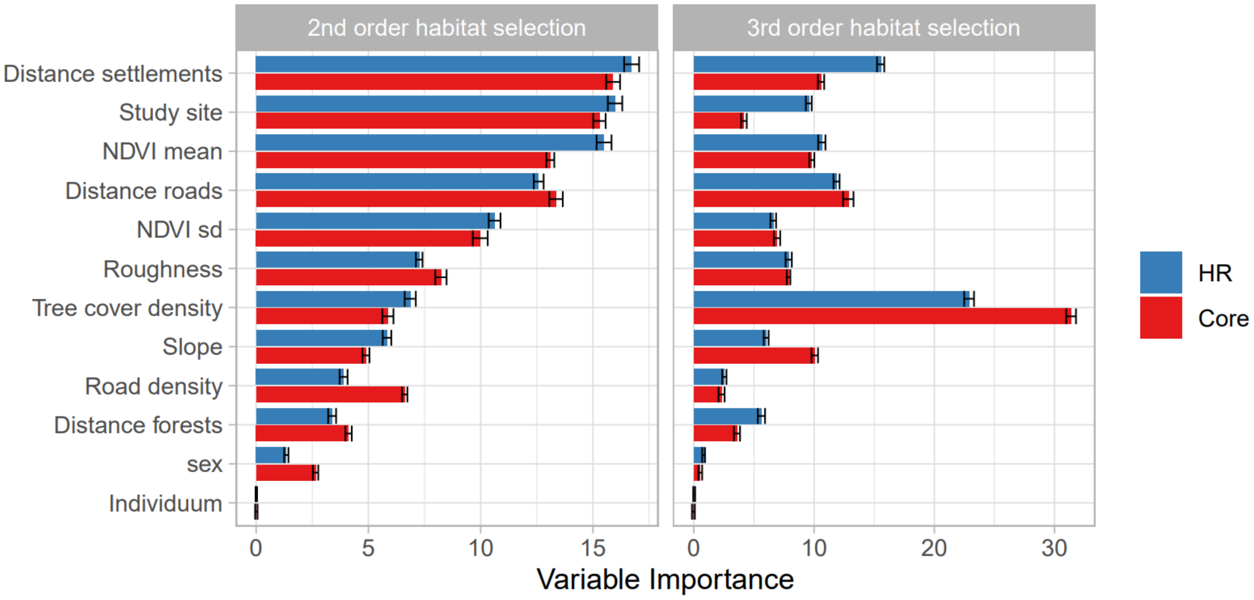

***Figure 2** - Variable importance of explanatory variables in 2^{nd} (home-range) and 3^{rd} (within home-range) order habitat selection at full home-range (95%) and home-range core (50%) levels, with SE. Calculated using a model-agnostic permutation (n=100) method and ordered by decreasing importance in 2nd order home-range selection.*

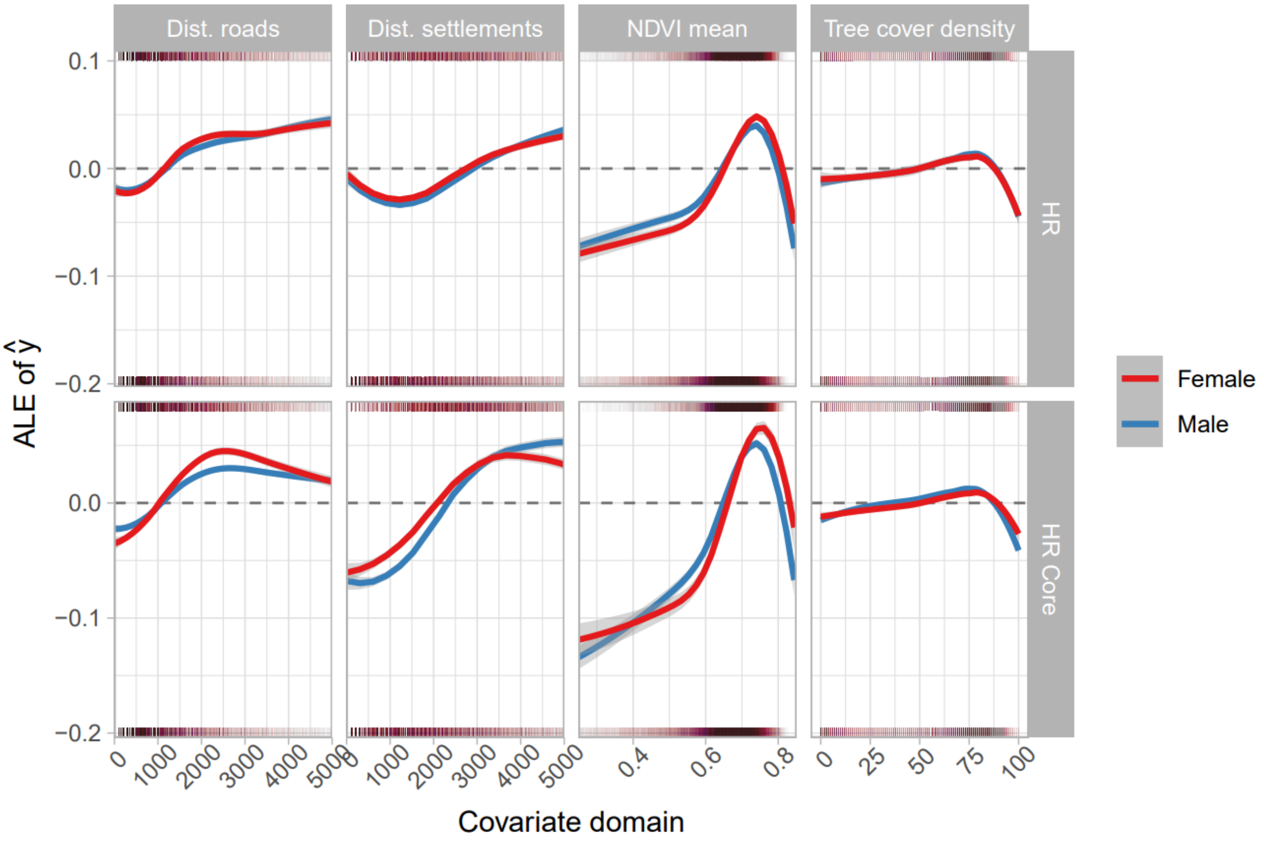

***Figure 3** - Predicted probabilities of 2^{nd} order home-range (95%) and home-range core (50%) habitat selection by Eurasian lynx in Europe for variables with importance≥10 in either 2^{nd} order 3^{rd} order (other variables, see S3). Estimated with 'Accumulated Local Effects' (positive $\hat{y}$ indicates selection, and negative $\hat{y}$ signifies avoidance) for males (blue) and females (red). Rug plots indicate the frequency distribution of the used (upper) and available (lower) data. Confidence interval shows SE of loess smoother.*

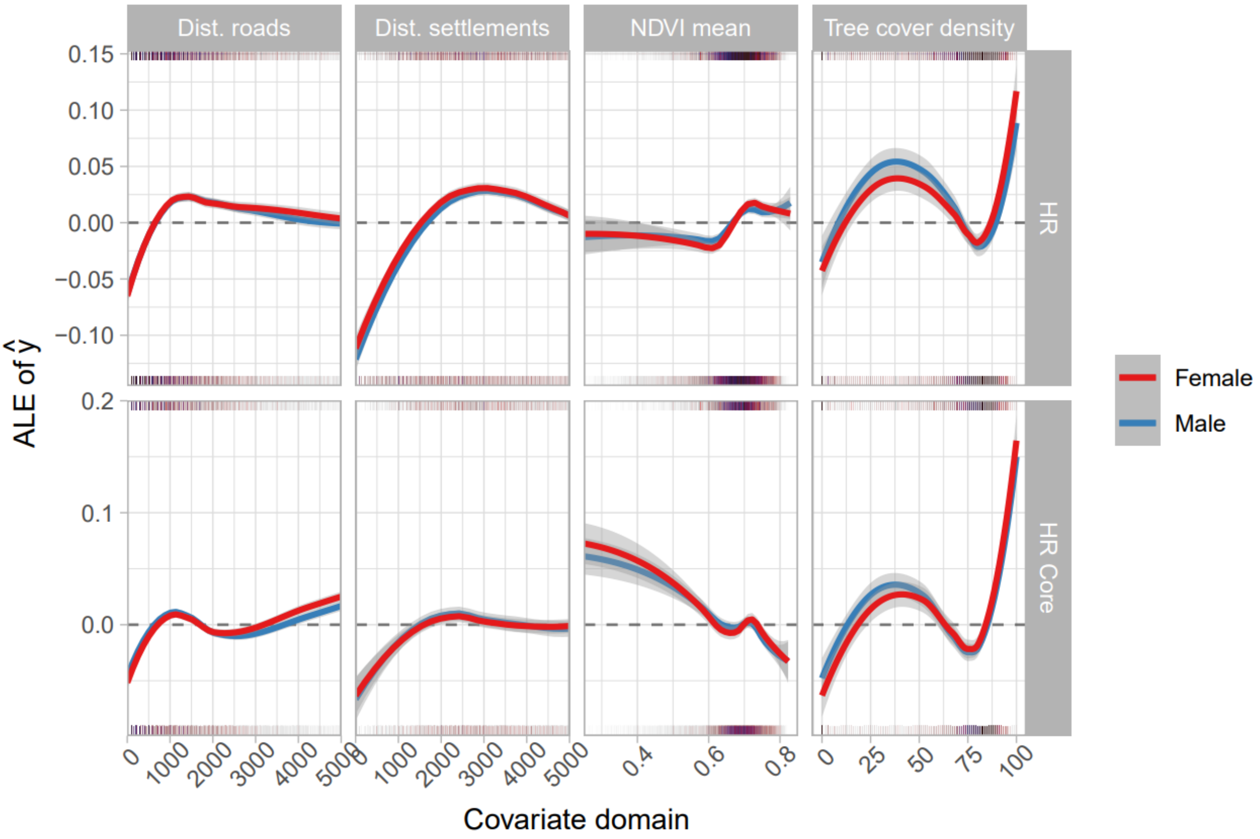

Figure 4 *- Predicted probabilities of 3rd order within home-range (95%) and within home-range core (50%) habitat selection by Eurasian lynx in Europe for variables with importance≥10 in either 2nd order 3rd order (other variables, see S3). Estimated with 'Accumulated Local Effects' (positive $\hat{y}$ indicates selection, and negative $\hat{y}$ signifies avoidance) for males (blue) and females (red). Rug plots indicate the frequency distribution of the used (upper) and available (lower) data. Confidence interval shows SE of loess smoother.*

Table 1 *- Summary table of the individuals from each population and site used in the analyses, and average home range (home-range) size (km²) by KDE 95% (see 'Home range estimation'). With reintroduced populations °. The mean home-range area (95% KDE) of males (443.36±283.14 km²) was significantly larger than females (191.92±116.34 km²) across all study sites (Welch's t-test t(93.649)=6.8178, p=8.917e-10).*

Population/Study site	**Number of GPS [m/f]**	**Number of VHF [m/f]**	**Average male home-range size (±SD)**	**Average female home-range size (±SD)**	**Locations Day/Night**	**Tracking period**

Alpine°	1-Austria	1/3	0	390.70	181.97(108.97)	989/1114	2011-2015
	2-Switzerland	0	10/14	309.41(208.73)	112.09(53.71)	3263/313	1997-2001
Baltic	3-Estonia	14/4	0	574.27(359.45)	337.77(262.08)	3433/3673	2004-2018
	4-Poland, Belarus	3/1	10/5	342.75(171.17)	194.93(81.84)	3557/1948	1991-2012
Bohemian-Bavarian-Austrian°	5-Czechia, Germany	5/5	5/4	480.95(231.83)	235.75(122.96)	4419/3960	1997-2013
Carpathian	6-Czechia, Slovakia	3/1	0	301.17(284.41)	93.11	421/1180	2012-2015
	7-Poland, Slovakia, Ukraine	0	2/2	194.38(51.44)	169.40(48.68)	448/226	1999-2004
Dinaric°	8-Slovenia, Croatia	2/4	0	644.93(412.83)	106.50(14.75)	483/1388	2006-2012
Jura°	9-France, Switzerland	0	8/15	551.17(346.51)	231.52(97.47)	9096/936	1988-1999

Table 2 *– Target variables and their corresponding proxies used as predictors in habitat selection models, as well as their ecological importance for inclusion (see also introduction), method of calculation, value ranges (used locations), spatial resolution after harmonization, and data sources.* ▲ *refers to data sources and methods for locations in Belarus/Ukraine (further details and predictor distributions, see* ***S1****).*

Target variable	**Proxy variable**	**Ecological importance**	**Method**	**Range**	**Resolution**	**Data sources**
Human disturbances	Distance to settlements	As proxy for disturbance in the landscape due to settlements. Risk factor due to human mortality causes (*Kowalczyk et al., 2015*) and prey correlate (*Bunnefeld et al., 2006*).	Euclidean distance to closest settlement (aggregating Corine's "artificial" landcovers).	0 – 17,395 m	100m (min. areal mapping unit 25ha)	*Copernicus Land Monitoring Service;* © *OpenStreetMap*▲.
	Distance to roads	As proxy for disturbance in the landscape due to roads. One of the largest mortality causes of lynx (*Breitenmoser-Würsten et al., 2007*).	Euclidean distance to closest road (aggregating highways, primary, secondary, tertiary and trunk).	0 – 10,327 m	100m	© *OpenStreetMap*
	Road density	Broad scale indicator of roads in the landscape, see also 'distance to roads'.	Sum road lengths in each cell of a 1 km^2 grid (road classes as above).	0 – 12.79 km/km^2	1000m	© *OpenStreetMap*
Shelter and hunting sites	Distance to forests	Proxy for availability of shelter and hunting sites in the landscape (*Podgórski et al., 2008*).	Euclidean distance to closest forest edge. ▲*forest assumed where tree cover >50% per pixel.*	0 – 4,427 m	100m (min. areal mapping unit 25ha)	*Copernicus Land Monitoring Service; Global forest Watch (Hansen et al., 2013)* ▲.
	Tree cover density	Describes the gradient of habitat in terms of potential cover features for refugia and hunting, see also 'distance to forests',		0 – 100	100m	*Copernicus Land Monitoring Service; Global forest Watch (Hansen et al., 2013)* ▲.

Environmental productivity	Normalized Difference Vegetation Index (NDVI)	Proxy describes plant productivity as an indicator of prey density (*Melis et al., 2010).*	Mean and SD of summer (June-September) NDVI from 2000-2020.	-0.74 – 0.83 (0.01 – 0.39)	250m	*16-day MODIS data (Didan, 2015).*
Topography	Roughness	Proxy describes terrain characteristics important for hunting and resting sites *(Belotti et al., 2018; Hočevar et al., 2021).*	The max. difference between a pixel and its 8 nearest neighbours. *(Wilson et al., 2007),*	0 – 547 m	90m	*'Shuttle Radar Topography Mission' elevation model (Farr et al., 2007)*
	Slope	See ‘roughness’.	Terrain steepness. (*Wilson et al., 2007*).	0 – 74.4°	90m	*'Shuttle Radar Topography Mission' elevation model (Farr et al., 2007)*