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RESEARCH ARTICLE

Prerequisites for coexistence: human pressure and refuge habitat availability shape continental-scale habitat use patterns of a large carnivore

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Abstract
Context Adjustments in habitat use by large carnivores can be a key factor facilitating their coexistence with people in shared landscapes. Landscape composition might be a key factor determining how large carnivores can adapt to occurring alongside humans, yet broad-scale analyses investigating adjustments of habitat use across large gradients of human pressure and landscape composition are lacking.
Objectives Here, we investigate adjustments in habitat use by Eurasian lynx (*Lynx lynx*) in response to varying availability of refuge habitats (i.e., forests and rugged terrain) and human landscape modification.
Methods Using a large tracking dataset including 434 individuals from seven populations, we assess functional responses in lynx habitat use across two spatial scales, testing for variation by sex, daytime, and season.

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Results We found that lynx use refuge habitats more intensively with increasing landscape modification across spatial scales, selecting forests most strongly in otherwise open landscapes and rugged terrain in mountainous regions. Moreover, higher forest availability enabled lynx to place their home ranges in more human-modified landscapes. Human pressure and refuge habitat availability also shaped temporal patterns of lynx habitat use, with lynx increasing refuge habitat use and reducing their use of human-modified areas during periods of high exposure (daytime) or high vulnerability (postnatal period) to human pressure.

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Conclusions Our findings suggest a remarkable adaptive capacity of lynx towards human pressure and underline the importance of refuge habitats across scales for enabling coexistence between large carnivores and people. More broadly, we highlight that the composition of landscapes determines how large carnivores can adapt to human pressure and thus play an important role shaping large carnivore habitat use and distributions.

Keywords Animal tracking · Adjustment · Eurasian lynx · Functional response · Habitat availability · *Lynx lynx*

Introduction

Human activities pose manifold threats to wildlife, including habitat loss and modification, as well as anthropogenic mortality, making human pressure a key factor shaping wildlife behavior (Gaynor et al. 2018; Tucker et al. 2018). Large carnivores are particularly susceptible to human pressure, because of their large home ranges, naturally small population sizes, frequent conflicts with humans, as well as a lack of evolutionary adaptation to predation pressure (Ripple et al. 2014). Given an increasing awareness of the important roles that large carnivores play in ecosystems (Atkins et al. 2019), as well as an ongoing expansion of the global human footprint into large carnivore habitats (Wolf and Ripple 2017), how to foster coexistence of large carnivores and humans has emerged as a key conservation challenge of our time (Carter and Linnell 2016).

An important mechanism allowing large carnivores to co-occur and potentially to co-exist with humans are adjustments in habitat use. For example, pumas (*Puma concolor*) in California select smaller prey when living close to human settlements (Smith et al. 2016), African lions (*Panthera leo*) exploit human-modified areas during times of low human activity to access prey (Suraci et al. 2019), and numerous carnivore species shift their temporal activity patterns in response to human pressures, typically becoming more nocturnal (Gaynor et al. 2018; Lamb et al. 2020). Available studies have mostly highlighted specific adaptations within single populations, yet broad-scale patterns of large carnivore habitat use might also be shaped in major ways by varying human pressure (Muhly et al. 2019; Thompson et al. 2021). However, variations in large carnivore habitat use across multiple populations and gradients of human pressure have rarely been analyzed (Dellinger et al. 2020; Cimatti et al. 2021). In addition, responses by large carnivores to human pressures also might vary across spatial scales of habitat use (e.g., establishment of home ranges in the wider landscape vs. use of areas within a home range; Mayor et al. 2009). For example, several studies have found carnivores to avoid human-caused mortality risks primarily at broader scales, while selecting mainly for higher resource availability at finer scales (Ripari et al. 2022; Thorsen et al. 2022). A better understanding of how human pressure shapes large carnivore habitat use across scales could provide important insights into their adaptive capacity and reveal opportunities and limitations for *landscapes of coexistence* where large carnivores and people co-occur sustainably (Oriol-Cotterill et al. 2015).

In addition to human pressure itself, a second factor likely influencing broad-scale patterns of habitat use are variations in the environmental context that large carnivores experience, that is, different landscape compositions in terms of land cover, topography, or climate (hereafter: landscape composition). The landscape features available to an animal define its option space for adjustments in habitat use and thus should also influence how large carnivores can adapt to human pressures (Bouyer et al. 2015; Muhly et al. 2019). A growing body of research has highlighted the strong dependence of wildlife habitat use on habitat availability (Aarts et al. 2013). A key concept in this context are so-called *functional responses* in habitat use (Mysterud and Ims 1998; Northrup et al. 2022). Functional responses describe how an animal adjusts the use of a habitat feature with changes in its availability (e.g., changes in forest use with changing forest cover in the landscape), thereby providing insights into the plasticity of habitat use across environmental gradients.

Refuge habitats are likely particularly important to allow large carnivores to adapt to human pressures. Refuge habitats refer to landscape features that are characterized by overall low human presence and provide cover for large carnivores to avoid human encounters, such as forests or rugged terrain.

Although such landscape features are also important to large carnivores for other reasons, such as hosting prey species as well as providing cover for resting, denning, and hunting (Podgórski et al. 2008; May et al. 2008), large carnivores could additionally depend on these features to reduce human-induced mortality (Oriol-Cotterill et al. 2015). Several studies have documented fine-scale adjustments resulting in an increased use of cover by large carnivores near humans (Schuette et al. 2013; Gehr et al. 2017). At such finer scales, the importance of refuge habitats should also vary temporally, since carnivores' dependence on refuge habitats should increase during phases of higher exposure to human pressure (e.g., during day vs. night) or higher vulnerability (e.g., during the postnatal period). Although it has been suggested that broad-scale distribution patterns of large carnivores, showing a strong association with forests and rugged terrain, are, at least partly, a result of human influence (May et al. 2008; Martínez-Abraín et al. 2020), studies investigating the connection between large carnivores' dependence on refuge habitats and gradients of human pressure across spatial scales and over time are missing.

Understanding how large carnivore habitat use varies across gradients of human pressures and different landscape compositions requires datasets spanning multiple populations. While such datasets have traditionally been missing, the ongoing proliferation of animal tracking data, along with efforts to share and integrate datasets in harmonized databases through the establishment of collaborative networks opens new opportunities in this regard (Urbano et al. 2021; Thompson et al. 2021). Methodologically, such analyses require disentangling how habitat use varies in response to changes in multiple variables simultaneously (e.g., human pressure *and* refuge habitat availability). However, functional responses so far have commonly been studied by regressing the use of a single habitat feature against its availability (Holbrook et al. 2019), thus neglecting the potential synergistic effects of multiple habitat factors (Northrup et al. 2022).

Europe represents an interesting case for studying how large carnivore habitat use varies along gradients of human pressure and landscape composition. After the widespread extirpation of large carnivores in Europe during the last centuries, several species have recently expanded their ranges through reintroductions and natural recolonizations (Chapron et al. 2014). Yet, the high degree of human pressure in many parts of Europe makes coexistence between large carnivores and humans challenging. Despite a recent population recovery and range expansion, partly driven by several reintroductions, many European populations of Eurasian lynx (*Lynx lynx*; hereafter lynx) remain highly fragmented, endangering their long-term survival (Schmidt et al. 2011). In addition to lynx' dispersal ability (Zimmermann et al. 2007), their capacity to adjust to human pressure is therefore likely key for determining whether lynx can persist in Europe's human-dominated areas and therefore, to what extent currently isolated populations can be connected into viable metapopulations (Bonn Lynx Expert Group 2021). Several recent studies have highlighted that human pressure is a central driver of lynx habitat selection in Europe (Ripari et al. 2022; Thorsen et al. 2022), but how lynx adapt their habitat use in relation to human pressure and landscape composition at broad scales remains unclear.

Here, we make use of a large collection of telemetry data encompassing seven lynx populations across Europe to investigate functional responses by lynx across gradients of refuge habitat availability and human landscape modification at two scales of habitat use (establishment of home ranges in the wider landscape and use of areas within home ranges), also analyzing variation of habitat use relating to sex, daytime, and season. Specifically, we test the following research hypotheses:

H1: Lynx use refuge habitats (forests and rugged terrain) more intensively at higher levels of human pressure at both spatial scales of habitat use.

H2: Lynx avoid human pressures more strongly at broader scales than at finer scales.

H3: At finer scales, lynx' use of refuge habitats is higher, and their use of human-modified areas lower during daytime and for females during the postnatal period.

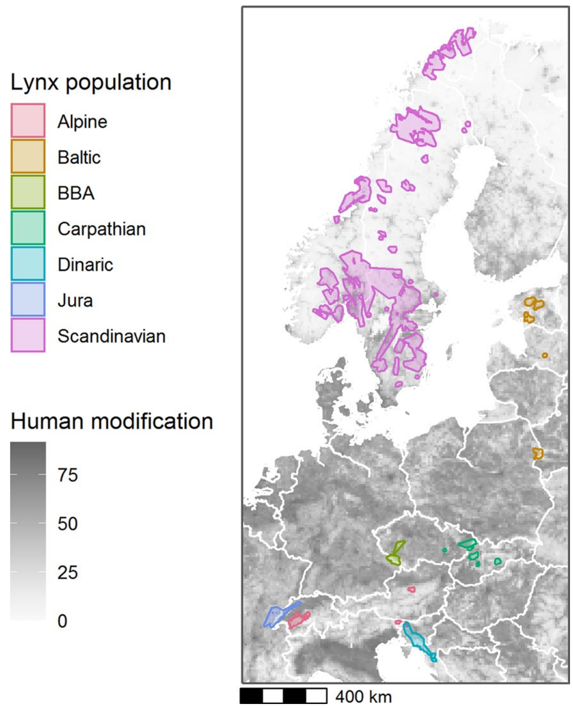

Fig. 1 Extent of lynx telemetry data. Polygons correspond to the extent of lynx home ranges per lynx population in our dataset (*BBA* Bohemian-Bavarian-Austrian). Background raster shows the degree of landscape modification [human modification index; (Kennedy et al. 2019)] in grey colors at a 10 km resolution

Materials and methods

Animal tracking data

We used GPS and VHF telemetry datasets collected in 13 countries, covering seven lynx populations from across Europe (Kaczensky et al. 2021); Fig. 1). Prior to all analyses, tracking datasets were harmonized through a standardized procedure of quality checks (Urbano et al. 2021).

We filtered lynx individuals, discarding animals with fewer than 50 telemetry locations to ensure a robust estimation of lynx home ranges (Seaman et al. 1999). Moreover, we removed dispersing individuals, which often differ in their habitat use compared to resident animals (Hemmingmoore et al. 2020). To reduce potential issues of spatiotemporal autocorrelation, we standardized the sampling frequency of our tracking data to one location per two hours. Our final dataset contained ca. 417,000 unique telemetry locations from 434 lynx individuals (230 females/204 males; see Table S1 in Online Resource 1 for a full overview), featuring a median monitoring length of 480 days per individual.

In addition to filtering data, we classified locations into day- and night-time locations (day-time: 07:01–21:00; night-time 21:01–07:00). Although actual daylight lengths are varying across seasons and latitudes, we used fixed time windows since our goal was to characterize varying levels of human activity during day vs. night with this variable. We further assigned locations to two seasons within the year (postnatal period vs. the rest of the year) to allow testing whether females adapted their habitat use during the first months of kitten rearing. Due to the lack of consistent information on the breeding status of females, we defined the postnatal period as the first 100 days after the beginning of the parturition season, irrespective of breeding status (most female lynx are reproducing each year; López-Bao et al. 2019). Based on data from a recent study on the distribution of parturition dates of lynx across Europe (Mattisson et al. 2022), we defined the beginning of the parturition season as 145th day of the year for datasets north of 65° latitude (May 25th in non-leap years), and as the 130th day of the year for all other locations (May 10th).

Environmental variables

To characterize gradients of human pressure and landscape composition, we compiled environmental rasters from several sources. As a proxy for human pressure, we used the human modification index (Kennedy et al. 2019). The human modification index is derived by integrating remotely-sensed data and ground-based inventories on the extent and intensity of several anthropogenic stressors globally at a 1 km^2 resolution and was available for the years 1990, 2000, 2010, 2015 and 2017. The underlying datasets include continuous variables on human population density, built-up areas, agriculture (cropland extent and livestock density), transportation infrastructure (density of roads and railways), energy production and mining, which are combined into a cumulative score of landscape modification by calculating a fuzzy sum (Kennedy et al. 2019). The index thus provides an aggregate indicator of the overall degree of human pressure potentially affecting wildlife. Similar aggregate measures of human modification have previously shown promise in explaining patterns of habitat use and population dynamics for large carnivores (Lamb et al. 2020).

As variables characterizing the availability of habitat features offering protection for lynx from human pressures, we used data on the distribution of two refuge habitats: forest cover and terrain ruggedness. Both variables have been identified as key habitat features for lynx, particularly in the context of providing cover for resting and for escaping from human disturbance (Podgórski et al. 2008; Filla et al. 2017; Hočevar et al. 2021). We obtained the distribution of forest cover from a recent global land cover map created at 100 m resolution (Buchhorn et al. 2020) and the terrain ruggedness index from a suite of topographic variables derived from a 90 m digital elevation model (Amatulli et al. 2018). Overall, our tracking dataset covered large gradients in refuge habitat availability and human modification (see Fig. S1 in Online Resource 1 for an overview of variable distributions across the seven studied populations).

Characterizing habitat use and availability

To reflect the hierarchical, multi-scale nature of habitat selection (Mayor et al. 2009), we assessed functional responses of lynx at two spatial scales: the placement of home ranges in the wider landscape (hereafter *landscape scale*, also referred to as second-order habitat selection; Johnson 1980), and the use of locations within home ranges (hereafter *home range scale*; also referred to as third-order habitat selection). We derived home ranges for each lynx individual using 95% minimum convex polygons (MCPs). We chose 95% MCPs over more advanced techniques such as kernel density estimation or local convex hulls since our goal was to define approximate ranging areas that allow for a comprehensive sample of available habitats at the home range scale (Holbrook et al. 2017; Fattebert et al. 2018). We derived summaries of habitat use and availability for each lynx individual, randomly sampling 10 potentially available locations for each used location at both scales, also transferring other attributes such as sex and observation time to available locations. At the landscape scale, we defined used locations by sampling random points within lynx home ranges equal to the number of tracking locations available for an animal and characterized availability by sampling random points within 100 pseudo-home ranges that we created by shifting individuals' home ranges in random XY-directions at distances of 1–80 km, corresponding to likely dispersal distances by lynx (Zimmermann et al. 2007; Samelius et al. 2012). At the home range scale, we used the telemetry locations as used points and sampled available locations randomly within lynx home ranges.

Assessing functional responses

Functional responses can be analyzed either at the level of *habitat use* or *habitat selection* (Holbrook et al. 2019). A functional response in habitat use describes how the values of an environmental variable vary at locations used by an animal dependent on habitat availability (i.e., average values of environmental variables across the wider landscape). A functional response in habitat selection, describes how the ratio of habitat use to availability varies along a gradient of availability (Holbrook et al. 2019). We here focus on the former, since our goal was to understand general patterns of lynx' association with different habitat factors throughout its European range. Most commonly, functional responses are assessed in two-stage approaches (Northrup et al. 2022) [although see e.g., Matthiopoulos et al. (2011) for a single-stage approach using interaction effects in resource selection functions]. First, habitat selection or use are characterized by either deriving selection coefficients for each individual animal through resource selection functions or by calculating average variable values at used tracking locations (Holbrook et al. 2019). Then, in a second step, selection coefficients or average values are regressed against habitat availability to assess how use/selection changes with availability (hereafter referred to as functional response models), with a regression slope of $\beta = 1$ indicating proportional increases with availability (Mysterud and Ims 1998).

In our analysis, we summarized habitat use as mean values at used and available locations for each individual, calculating separate means based on the date and time of locations. At the landscape scale, we calculated means per individual and season (postnatal period vs. rest of year; $n = 768$ samples). At the home range scale, we calculated means per individual, season, and daytime (day vs. night; n = 1252). While functional response models have typically been univariate, that is, regressing the use/selection of a single habitat feature against the availability of that feature (Northrup et al. 2022), we here use a multivariate approach allowing to assess the influence of multiple variables concurrently. To that end, we fitted multiple linear regression models including the availability (i.e., mean values) of all environmental variables (i.e., forest cover, rugged terrain, and human modification) as well as their two-way interactions as predictors (correlations between all variables were below 0.45; see Fig. S2 in Online Resource 1). We built separate functional response models for each variable at the two spatial scales (landscape and home range scale), resulting in a total of six models.

We additionally tested for variation in habitat use by season (postnatal period vs. rest of year), sex (male vs. female), and, at the level of home range use, variation by daytime (day vs. night). To that end, we tested adding binary factor variables for season, sex and daytime (for models of home range use), as well as their interaction effects with all other terms to our models. We tested models with increasing levels of complexity, including one (daytime/sex/season), two (daytime and sex/season and sex) or all three factor variables and their interactions at a time and then compared the support for model setups using the Akaike Information Criterion (AIC). To visualize functional responses, we derived marginal model effects using the *ggeffects* package (Lüdecke 2018). To assess variation in habitat use by sex, season and daytime, we calculated contrasts between regression coefficients using the *contrast* package (O'Callaghan et al. 2021).

Results

Lynx increased their use of refuge habitats with increasing human pressure. Specifically, lynx increased their use of forests at both scales of habitat use (landscape and home-range -scale use) as an adjustment to increasing human modification. This adjustment was particularly strong in open landscapes with low forest cover (Fig. 2a, c), whereas this pattern was not observable when forest availability was high. Lynx also increased their use of rugged terrain in response to increasing human modification at both scales, but only in landscapes offering relatively high levels of available rugged terrain (Fig. 2b, d). The effect of human modification on altering lynx' use of rugged terrain, however, was considerably smaller than the effect of human modification on forest use. Based on AIC values, there was support for sex differences in lynx' use of forest cover at the landscape scale (see Fig. S3 in Online Resource 1 for an overview of AIC values for all model setups and Table S2 in Online Resource 1 for an overview of model coefficients of all selected models). Specifically, female lynx tended to place their home ranges so that they include more forest cover particularly at low levels of human modification and high forest availability in the landscape (see Fig. S4 in Online Resource 1).

At the home range scale, lynx tended to use both types of refuge habitat (forest and rugged terrain) more during daytime than nighttime (models including interaction effects with daytime were supported based on AIC). Day-night differences were stronger in open landscapes (low forest availability; Fig. 3, left panel) and rugged landscapes (high availability of rugged terrain; Fig. 3, middle panel). Moreover, in open landscapes, lynx increased their daytime use of forests as human modification of the landscape increased (Fig. 3, left panel). While a similar trend was discernible for the use of rugged terrain, differences between different levels of human modification were less clear than for forest cover (overlapping confidence intervals; Fig. 3, middle panel). In highly human-modified landscapes, lynx used more modified areas less during daytime compared to nighttime (Fig. 3, right panel).

In addition to human modification affecting the use of refuge habitats, the availability of refuge habitats also affected lynx' association with human modification. Lynx established home ranges in more human-modified landscapes when more forest cover was available (Fig. 4a). Conversely, at the home range scale, lynx occurring in highly modified landscapes (i.e., high levels of human modification within their home ranges) used locations with lower human modification when forest availability was at intermediate to high levels (Fig. 4b). In contrast to forest availability, availability of rugged terrain did not have clear effects on lynx' association with human modification (see Fig. S5 in Online Resource 1).

We also found an indication for seasonal variation in habitat use (postnatal period vs. rest of year), as

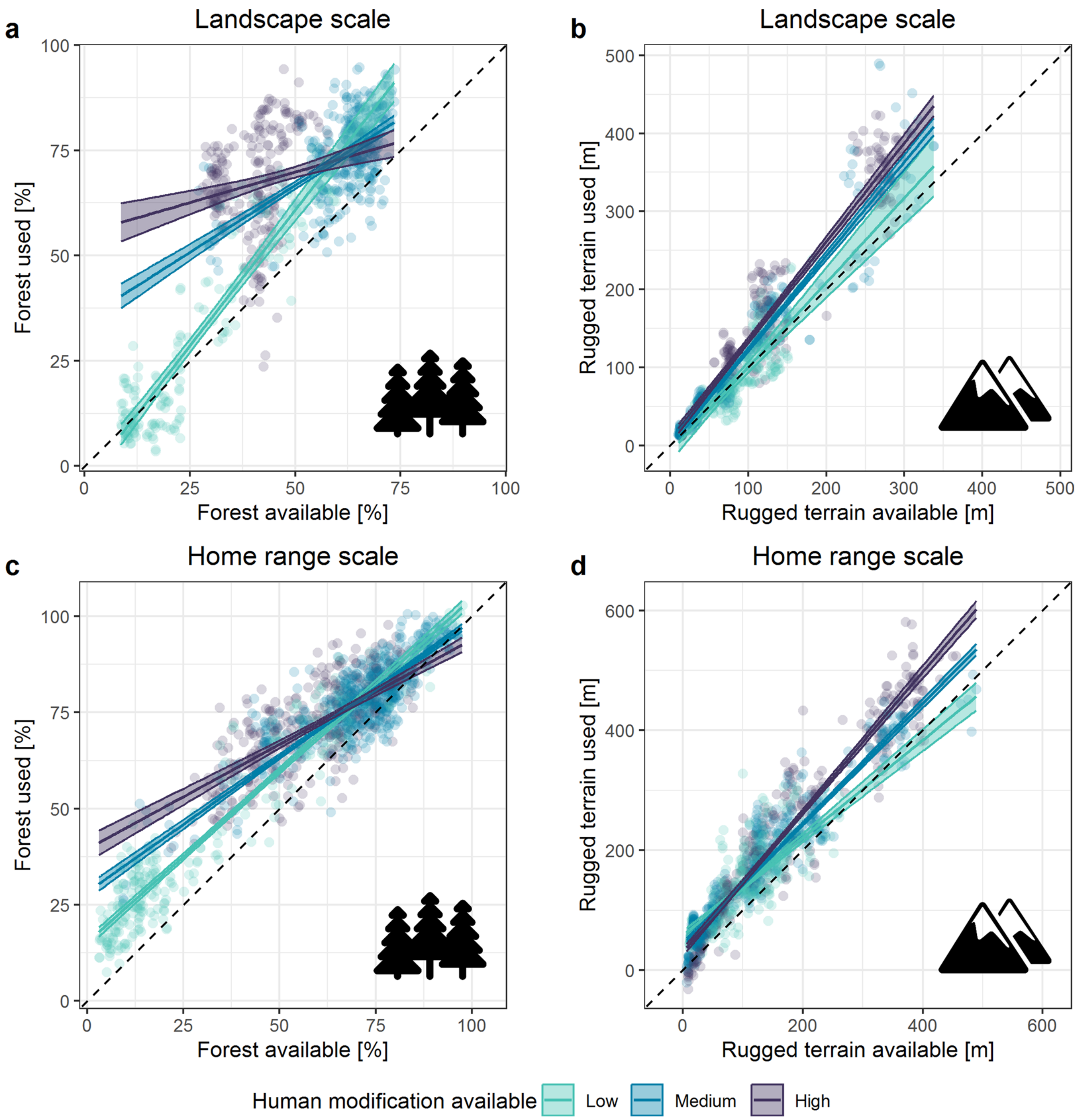

Fig. 2 Lynx' use of refuge habitats (forest cover and rugged terrain) with varying human modification at two scales of habitat use. Plots show functional responses in habitat use (i.e., use in dependence on availability), with dashed diagonal lines indicating proportional use. Marginal model effects with 95% confidence intervals and partial residuals for low, medium, and high levels of human modification (10th, 50th and 90th percentile in our dataset) are highlighted in different colors. Other variables are kept at their mean values for computing marginal effects

models of lynx' use of human modification including interaction effects with the season variable were favored based on AIC. In strongly human-modified landscapes, lynx increased their use of refuge habitats during the postnatal period. While the effects of human modification on forest use were similar between sexes, females showed a stronger increase in rugged terrain use than males (Fig. 5, left and middle panel). Conversely, the use of human-modified

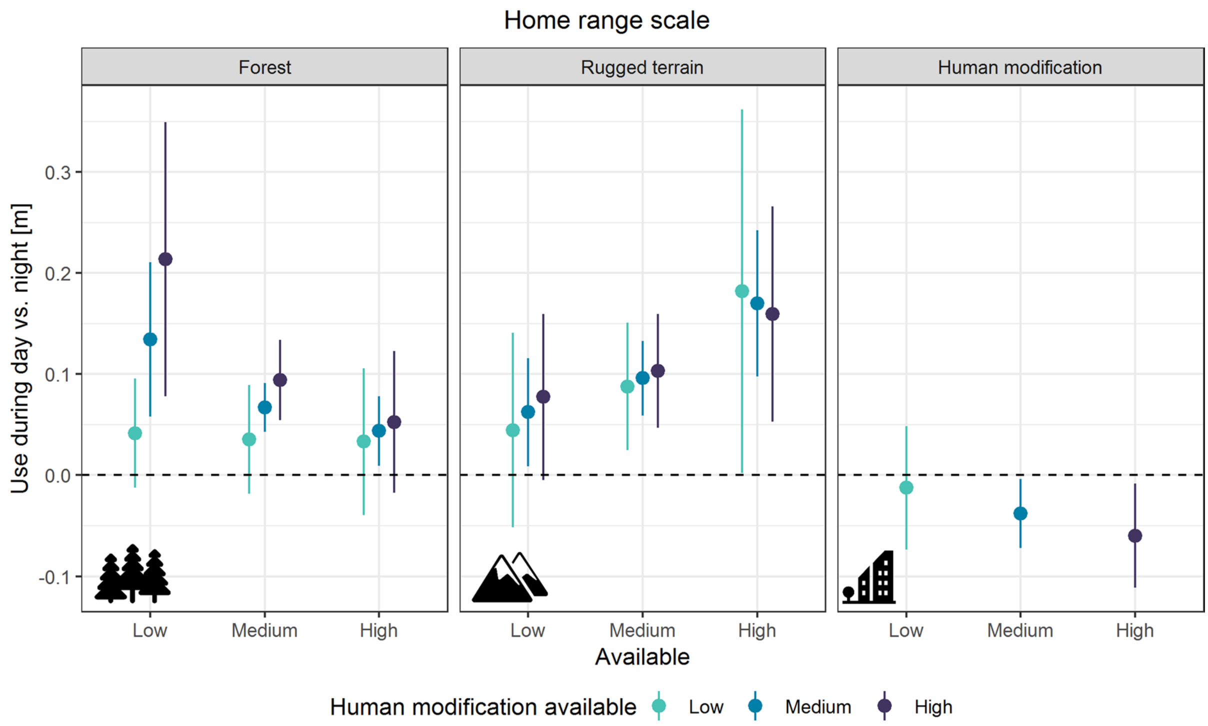

Fig. 3 Difference between daytime and nighttime use of refuge habitats (forest cover and rugged terrain) and human modification at the home range scale, depending on the level of human modification within home ranges. Values above zero indicate higher use of the respective habitat type during daytime than nighttime. Low, medium, and high values of human modification correspond to 10th, 50th and 90th percentile in our dataset. Coefficients were standardized to ensure comparability between variables

areas by lynx tended to be lower during the postnatal period, particularly for females (Fig. 5, right panel).

Discussion

Large carnivore's capacity to adapt to humans is a key factor determining whether or not they can coexist with people in shared landscapes (Carter and Linnell 2016). We here assessed, for the first time, functional responses in habitat use for a large carnivore at a continental scale and across spatial scales. Our study yielded three main findings. First, lynx' use of refuge habitats (i.e., forests and rugged terrain) was influenced by human pressure gradients across the continent, with lynx increasing their use of refuge habitats with a higher level of human modification at both scales of habitat use. Second, while lynx avoided human pressure particularly at broad scales, a higher availability of forest cover allowed lynx to occur (i.e., place home ranges) in more human-modified landscapes, further underscoring the importance of refuge habitat availability for human-carnivore coexistence. Finally, we found that human pressure and landscape composition shaped differences in temporal habitat use of lynx, influencing both the diurnal use of refuge habitats as well as lynx' seasonal association with human landscape modification. More generally, our study highlights that it is the interaction of human pressure and refuge habitat availability, not human pressure alone, that determines whether large carnivores can recover and persist in human-dominated landscapes, having implications for efforts to conserve and restore large carnivore populations.

We found that lynx used refuge habitats more intensively with increasing human modification at both scales of habitat use. This supports our first hypothesis and demonstrates that refuge habitats are important in allowing carnivores to adjust to human pressures across scales. Several studies have

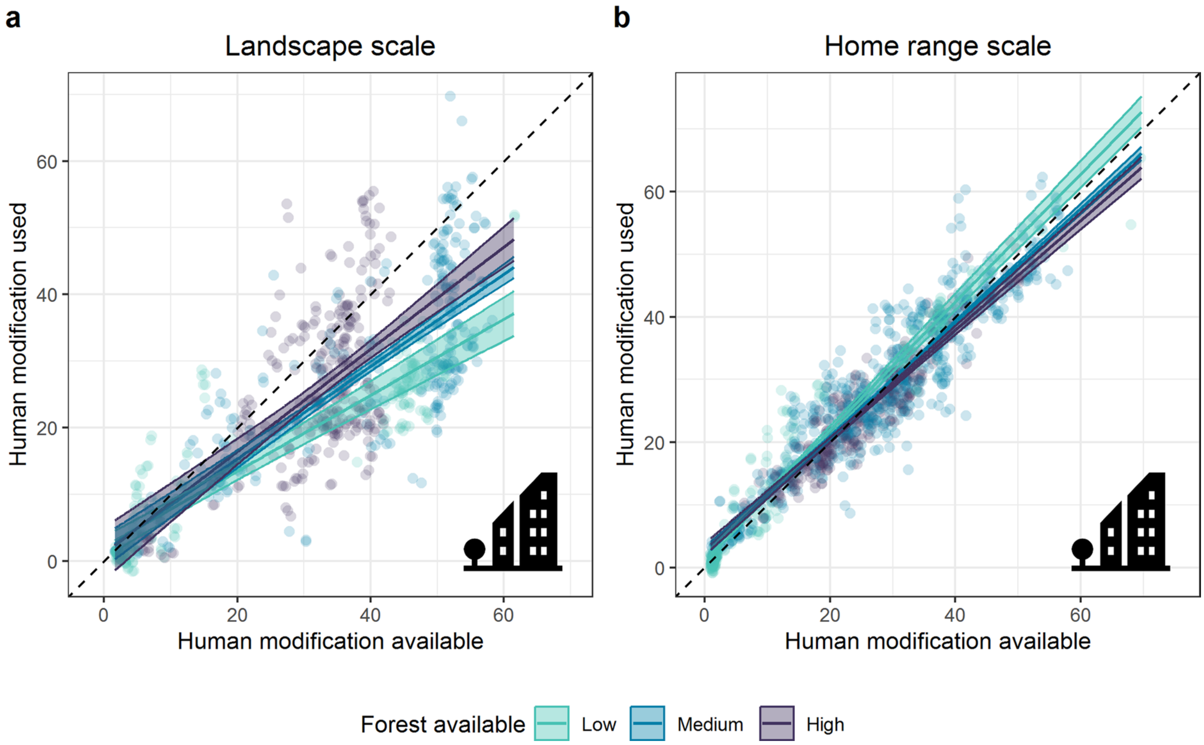

Fig. 4 Habitat use of human-modified areas by lynx for varying levels of available forest cover at two scales of habitat use. Plots show functional responses in habitat use (i.e., use in dependence on availability), with dashed diagonal lines indicating proportional use. Marginal model effects with 95% confidence intervals and partial residuals for low, medium, and high levels of forest cover (10th, 50th and 90th percentile in our dataset) are highlighted in different colors. Other variables are kept at their mean values for computing marginal effects

shown similar adjustments by large carnivores at fine scales, with carnivores increasing their use of cover habitats when being close to humans, for example lynx in Switzerland and lions in southern Kenya (Schuette et al. 2013; Gehr et al. 2017). Here, we provide the first continental-scale perspective showing that broad-scale patterns of refuge habitat use are strongly shaped by gradients of human pressure. Adjustments of refuge habitat use by lynx were particularly strong in open landscapes with low levels of forest availability as well as in landscapes with high levels of rugged terrain. Both are plausible results: large carnivores are most vulnerable to anthropogenic impacts in open landscapes (Suraci et al. 2019) and more rugged topography allows carnivores to avoid people more effectively (Grilo et al. 2019). The stronger use of forests at the landscape scale and of rugged terrain at the home range scale might relate to the different ways in which lynx use these habitats to avoid human pressures. While continuous forest areas allow lynx to generally live away from human pressure, rugged terrain allows them to avoid humans at fine scales and hence co-occur with people in shared landscapes. Collectively, our results highlight the outstanding importance of refuge habitats in human-dominated landscapes for enabling human–carnivore coexistence.

At the same time, our results also imply that lynx are indeed able to persist in relatively open landscapes if levels of human pressure are low. For example, lynx in northern Norway occur at very low levels of forest cover (ca. 25% forest cover within home ranges; Linnell et al. 2021), likely also enabled by the low anthropogenic influences in these regions. Similarly, other large carnivores commonly associated with forest habitats can persist in savannas and steppes provided sufficient protection and low levels of human disturbance, such as wolves in Central Asian steppes or North American prairies (Riley et al. 2004; Tiralla et al. 2021), but these habitats have often been the

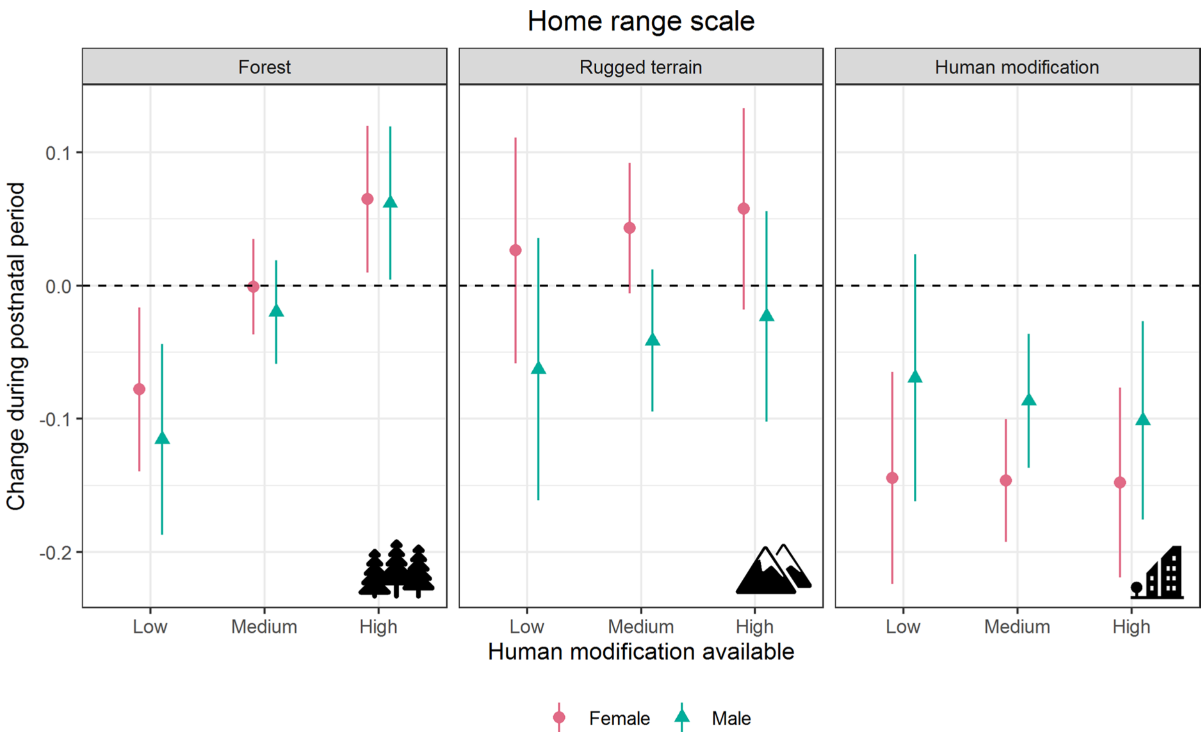

Fig. 5 Changes in lynx' use of refuge habitats (forest cover and rugged terrain) and human modification during the postnatal period, grouped by sex and different levels of human modification. Values below zero indicate lower use during the postnatal period compared to the rest of the year. Low, medium, and high values of human modification correspond to 10th, 50th and 90th percentile in our dataset. Coefficients were standardized to ensure comparability between variables

first to lose large carnivores once human pressure increased (Laliberte and Ripple 2004). More broadly, our findings thus support the hypothesis that the strong association of carnivore distributions with refuge habitats that today is observable in many large carnivores is largely driven by human pressure (May et al. 2008; Martínez-Abraín et al. 2020).

Our analyses suggest that the availability of refuge habitat influences whether large carnivores can occur in human-dominated landscapes. Lynx commonly face a trade-off between accessing prey and avoiding negative anthropogenic impacts, since important prey species, particularly roe deer (*Capreolus capreolus*), occur at higher densities in mixed-use landscapes characterized by higher levels of human modification (Basille et al. 2009; Gehr et al. 2017). In line with our second hypothesis and with previous research (Ripari et al. 2022; Thorsen et al. 2022), we found that lynx avoided human pressures particularly at broad scales (i.e., placement of home ranges), supporting the notion of a hierarchical selection process in which the most important limiting factors (i.e., human-caused mortality risk in our case) are determining broad-scale selection patterns, while fine-scale selection is more strongly influenced by resource acquisition (Rettie and Messier 2000; Ripari et al. 2022). We here extend these findings by highlighting that the availability of refuge habitats is an additional mediating factor in lynx's use of human-modified landscapes. Lynx could establish home ranges in landscapes with relatively high levels of human modification if these landscapes featured intermediate or high forest availability. In such situations, however, lynx compensated for the higher baseline-level of human pressure by avoiding human modified areas more strongly at finer scales. Our findings of a varying response to human pressure across scales are in line with regional-scale studies on lynx habitat use in Norway (Basille et al. 2013; Thorsen et al. 2022) and are underlining the importance of assessing habitat use at multiple scales for understanding wildlife responses to human pressure.

Several previous studies have highlighted temporal variation in large carnivore habitat use as an adaptation to human pressure, particularly increased nocturnality (Gaynor et al. 2018; Lamb et al. 2020). While the generally higher use of refuge habitats by lynx during daytime also reflects natural circadian activity patterns of a crepuscular and nocturnal hunter (Heurich et al. 2014; Hočevar et al. 2021), we also found a clear influence of human pressure on diurnal patterns of refuge habitat use (Thorsen et al. 2022). In both open landscapes providing little cover for avoiding humans, as well as in rugged landscapes offering effective cover for co-occurring near humans, lynx depended more strongly on refuge habitats during daytime (i.e., phases of high levels of human activity). Moreover, we also observed a direct effect of human modification on diurnal refuge habitat use under some conditions, as in open landscapes, lynx increased their use of forest cover with increasing human modification, thus partly confirming our third hypothesis. A strong dependence on refuge habitats for resting during daytime has been documented for other large carnivores occurring in open or human-dominated landscapes, such as lions in the African savannah (Suraci et al. 2019) or wolves in northwestern Iberia (Llaneza et al. 2016). In sum, we thus highlight that not only overall activity patterns, but also diurnal patterns of refuge habitat use are shaped by human pressure.

Further confirming our third hypothesis, we found an increase in refuge habitat use as well as a reduced use of human-modified areas by female lynx during the first months after kittens are born, when their movements are strongly constrained by proximity to the natal den (Breitenmoser et al. 1993; Jędrzejewski et al. 2002). This corroborates previous findings by Bunnefeld et al. (2006), who observed female lynx selecting for locations further from human activity when having newborn kittens. The increased use of refuge habitats and lower use of human-modified habitats during the postnatal period by males in our dataset might be caused by generally higher risks associated with human-modified habitats during summer due to increased recreational activity by humans (Ordiz et al. 2011), indicating that this factor might have influenced our results and thus might represent an additional driver of adjustments in lynx habitat use. Yet, given the sex-specific differences we observed (Fig. 5), our results indicate that the postnatal period represents a time of high sensitivity particularly for female lynx. The availability of suitable natal den sites thus might be an important limiting factor for the persistence of lynx in human-dominated landscapes (White et al. 2015).

Combining tracking datasets collected across several Eurasian lynx populations at a continental scale allowed us to provide new insights into how lynx adjust their habitat use in response to human pressure and refuge habitat availability. Such ‘big’ tracking datasets, enabled by large-scale collaborations and initiatives for harmonizing and sharing tracking datasets (Kranstauber et al. 2011; Urbano et al. 2021) are particularly valuable for large carnivore research as they allow understanding the adaptive capacity of species under different environment contexts and overcome the often small sample sizes of local studies, thereby providing important information to transboundary conservation efforts needed to safeguard many large carnivores (Thompson et al. 2021). Methodologically, our analysis demonstrates that using functional response models offers a simple, yet effective approach for understanding how the availability of multiple factors interactively shape patterns of wildlife habitat use. While functional response models have highlighted the context-dependence of habitat use in relation to habitat availability, they typically have been limited to univariate analyses (Northrup et al. 2022). We here show that functional responses themselves can be context dependent. The interactive effects of human pressure and refuge habitat availability on lynx habitat use we found, as well as the considerable temporal and sex-specific variation we observed underline the importance of considering complexity when assessing functional responses. As a limitation of our study, we were not able to include information on prey availability in our models, which represents another important factor potentially driving variation in habitat use by carnivores. Given the generally high levels of prey species abundance across our study sites, prey availability should have a limited influence on variation in lynx habitat use in our case. Another limitation of our analysis is that particularly at finer scales, other factors not included in our models might influence the use of forests and rugged terrain by lynx. Although prey availability tends to be higher in human-modified landscapes, in addition to risk avoidance, lynx might use forests and rugged terrain because of their suitability as hunting habitat. Moreover, other factors might influence the quality of forests and rugged terrain as refuges, such as the presence of roads (Filla et al. 2017), forest type (Cristescu et al. 2019), or the availability of other non-forest refuge habitats, such as shrublands (Milanesi et al. 2022). Despite these limitations, our study exemplifies how better data availability and improved methodologies enable a more nuanced understanding of complex patterns of wildlife habitat use at broad scales (Cagnacci et al. 2010).

Although our findings suggest considerable flexibility of lynx in adapting to human pressure through adjusting their habitat use, it remains unclear which fitness costs are associated with these adaptations. Studies on large carnivore demography have commonly shown higher mortality in human-dominated landscapes (Moss et al. 2016; Morales-González et al. 2020; Lamb et al. 2020). Thus, while lynx seem able to adjust to living in landscapes characterized by high levels of human pressure, the long-term viability of populations occurring in human-dominated landscapes remains unclear, as co-occurrence does not necessarily imply coexistence. Directly linking data on variation in habitat use to demographic data can help determining under which conditions actual coexistence between large carnivores and people is taking place or where carnivores' adjustments might create population sinks or ecological traps (Nisi et al. 2022). While studies from Scandinavia have found no clear effect of habitat characteristics on lynx reproduction and survival (López-Bao et al. 2019; Andrén et al. 2022), it is unclear whether these findings also hold for more human-dominated landscapes such as Central Europe.

The ongoing comeback of large carnivores in Europe and other parts of the world provides unique possibilities for protecting these species and for restoring the ecological functions they provide. However, carnivore comebacks pose considerable challenges given increasing human–wildlife conflicts where carnivores and people co-occur (Carter and Linnell 2016). Landscapes of coexistence require areas large carnivores perceive as 'safe enough' (i.e., that are not avoided due to fear of human-caused mortality) and where actual mortality levels remain low enough not to create population sinks (Oriol-Cotterill et al. 2015). Given the striking adaptive capacity of large carnivores highlighted in this study and elsewhere (Suraci et al. 2019; Kautz et al. 2021), human-caused mortality (e.g., from poaching, legal hunting and vehicle collisions) typically will remain the most limiting factor determining where coexistence between carnivores and people can take place (Lamb et al. 2020). Yet, our work highlights the critical role of refuge habitats as prerequisites for coexistence, allowing large carnivores to persist even at high levels of human pressure. Maintaining such refuges in human-dominated landscapes, particularly also beyond protected areas (e.g., military training grounds; Reinhardt et al. 2019) thus should be a key goal for large carnivore conservation and restoration efforts.

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