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Research Article

Habitat complexity and prey composition shape an apex predator's habitat use across contrasting landscapes

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The spatial ecology of stalk-and-ambush predators like the Eurasian lynx *Lynx lynx* depends on prey availability and environmental features, yet the relative roles of these factors remain unclear at large spatial scales. In this study, we analysed lynx habitat use across central and southern Finland using snow-track data from the Wildlife Triangle Scheme (2016–2020) and a joint species distribution modelling framework (HMSC) to assess both environmental drivers and spatial predator–prey associations. The Finnish lynx population offers a unique opportunity to study a contiguous population with stark regional differences in prey availability, enabling inferences about environmental and prey effects on space use. Across the study area, lynx habitat use was primarily associated with structurally complex forests and terrain, as expected for a stalk-and-ambush predator. Overall, environmental conditions explained habitat use patterns to a greater degree in the central region than in the south, which we posit is due to differences between the regions in prey species. In the central region, habitat use by lynx and its prey, the mountain hare *Lepus timidus*, was similar, in contrast to the southern region, where lynx were spatially associated with roe deer *Capreolus capreolus* and white-tailed deer *Odocoileus virginianus*, both of which showed habitat use patterns differing from those of lynx. These results indicate that lynx adjust their space use according to prey availability, while still retaining a core preference for complex habitat, as expected for a stalk-and-ambush predator. Our results are a clear demonstration of how the interplay between environmental conditions and community composition of prey shapes a generalist predator's habitat use and how this can contribute to overall resilience at the population level. Our study captures insights into habitat use at the landscape scale across contrasting ecological contexts, with implications for the management and conservation of large carnivores in human-modified environments.

Keywords: ambush predator, apex predator, habitat complexity, habitat use, hierarchical modelling, prey abundance



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Introduction

After decades of intense persecution, large carnivores have made a remarkable recovery across Europe (Chapron et al. 2014). This recovery has occurred largely in human-dominated landscapes, shifting the focus from preventing extinction to understanding how these species can coexist with human populations (Lute et al. 2018). In this context, a key ecological strategy facilitating coexistence is behavioural flexibility, particularly in the use of space. Understanding the ecological conditions that support these adaptive spatial behaviours is therefore crucial for designing species-specific and sustainable long-term conservation strategies (Boitani and Linnell 2015).

The Eurasian lynx *Lynx lynx* serves as an ideal model for investigating the mechanisms of coexistence in modern landscapes. At broad geographic scales, its distribution is fundamentally constrained by the availability of extensive forest ecosystems (Niedziałkowska et al. 2006, Basille et al. 2008, Rozyłowicz et al. 2010). Within these suitable forest regions, lynx exhibit considerable flexibility in their local distribution, occupying both pristine and human-modified environments. This flexibility in space use is heavily modulated by gradients of human presence and by specific environmental features. Across Europe, lynx tend to select habitats with intermediate levels of anthropogenic disturbance, where human activity is often associated with increased prey availability (Lone et al. 2014, Bouyer et al. 2015, Gehr et al. 2017). In such landscapes, lynx may mitigate potential risks through temporal avoidance, using open or human-modified areas mainly at night while selecting dense, undisturbed habitats for daytime resting (Bouyer et al. 2015, Filla et al. 2017).

Beyond spatial behaviour, lynx display marked trophic flexibility, adjusting their diet to locally available prey (Khorozyan and Heurich 2023). In central and eastern Europe, the Eurasian lynx primarily functions as a specialist predator of medium- and large-sized ungulates, switching to smaller mammals when ungulates are scarce (Jędrzejewski et al. 1993, Khorozyan and Heurich 2023). In contrast, Asian populations tend to specialise on lagomorphs, resembling the foraging ecology of the Canada lynx *Lynx canadensis* and the Iberian lynx *Lynx pardinus* (Mengülluğlu et al. 2018). Still, trophic flexibility in lynx can be constrained by their hunting strategy. As a stalk-and-ambush predator (Holmes and Laundré 2006, Balme et al. 2007), lynx depend strongly on habitat structural complexity to hunt successfully (Podgórski et al. 2008, Belotti et al. 2013, Schmidt et al. 2023, Čonč et al. 2024). Higher structural complexity typically arises from multi-layered vegetation, dense understory, irregular topography, and the presence of elements such as shrubs and fallen logs, which limit prey visibility and mobility, thereby increasing the prey vulnerability to ambush (Savino and Stein 1982, James and Heck 1994, Bartholomew et al. 2000).

While structurally complex habitats can enhance stalk-and-ambush success, lynx must also follow prey abundance, which may be highest in more open or human-modified

areas. As a result, habitats that maximise hunting efficiency do not always coincide with areas of highest prey availability, forcing lynx to navigate a spatial mismatch between cover and prey encounter rates (Hopcraft et al. 2005, Smith et al. 2020). In human-modified environments, lynx habitat use therefore emerges from the combined influence of habitat structure, prey communities, and spatial context. Capturing this joint influence remains challenging, particularly in large-scale, human-modified landscapes where habitat structure, prey availability, and spatial processes are often decoupled by anthropogenic activities and are difficult to represent within conventional analytical frameworks.

Observational studies of predator–prey dynamics commonly rely on single-species distribution models in which predators are analysed independently of their prey, or in which prey species are included as fixed predictors of predator occurrence (Araújo and Luoto 2007). Alternative approaches such as conditional Bayesian networks (Staniczenko et al. 2017) or structural equation models (Poggiato et al. 2025), have also been used to represent predator–prey relationships, but require explicit assumptions about the direction and structure of species interactions. While these approaches have provided valuable insights, they typically examine environmental conditions, prey availability, and spatial structure separately or across different scales, making it difficult to disentangle their relative contributions to predator habitat-use strategies. As a result, integrated inference is limited, which can hamper the development of cohesive, large-scale forest and land management strategies aimed at ensuring the long-term persistence of large carnivore populations.

The emergence of joint species distribution models provides an alternative framework to address these challenges, as they allow the simultaneous modelling of multiple species, the separation of shared environmental responses from residual species associations, and the explicit incorporation of spatial structure through random effects (Norberg et al. 2019). For example, hierarchical modelling of species communities (HMSC; Ovaskainen et al. 2017, Tikhonov et al. 2020), a Bayesian joint species distribution model, jointly estimates species–environment relationships while accounting for spatially structured variability via hierarchical random effects, without imposing a priori assumptions about species interactions. Instead, it partitions co-occurrence patterns into shared responses to environmental gradients and residual associations, allowing us to assess whether predator–prey co-occurrence patterns are more consistent with common habitat responses or with spatial associations beyond those explained by the environment.

Our study examines how lynx habitat use emerges from the joint influence of environmental conditions and prey availability. We focus on the Eurasian lynx in Finland, where the population is continuously distributed, stable and increasing, with an estimated size of 2400–2600 individuals in 2021 (Ministry of Agriculture and Forestry of Finland 2021). Forest structural conditions relevant to lynx habitat use in Finland are shaped by intensive forest management, leading to widespread simplification characterised

by even-aged monocultures, loss of old-growth forests, and reduced volumes of dead wood (Kuuluvainen and Gauthier 2018, Mönkkönen et al. 2022). Prey distributions in Finland vary regionally. In the south, prey availability is heavily influenced by human activity through the introduction of white-tailed deer *Odocoileus virginianus* and the presence of species that thrive in cultural landscapes, such as roe deer *Capreolus capreolus* and European hare *Lepus europaeus*. In contrast, the mountain hare *Lepus timidus* remains the dominant prey for lynx in northern regions (Pulliainen et al. 1995).

This context provides a rare opportunity to examine lynx habitat use across contrasting environmental conditions and prey communities within a single, contiguous population, thereby minimising confounding effects of population fragmentation, dispersal limitation, or regional differences in population history. It allows variation in habitat structure and prey distribution to be evaluated against a common demographic and biogeographic background. Understanding how lynx respond to such variation helps clarify predator-prey relationships in boreal ecosystems and informs forest management and conservation planning in human-modified landscapes where habitat structure and prey availability are jointly shaped by human activities.

Within this framework, we pursue two objectives. First, we identify the environmental variables that influence lynx habitat use in managed forest landscape. Second, we assess how regional variation in prey community composition is reflected in lynx habitat use. We hypothesize that lynx occurrence is positively associated with structurally complex habitats, consistent with its stalking-and-ambush hunting strategy, and that patterns of habitat use differ among regions in relation to prey availability, particularly the relative abundance of mountain hares and ungulates.

Material and methods

Study area

The study area covers approximately two-thirds of Finland, excluding the reindeer husbandry region, which encompasses all of Lapland and parts of northern Ostrobothnia and Kainuu (Fig. 1). In these northern regions, Eurasian lynx is rare, having been nearly extirpated due to hunting permits issued to protect semi-domesticated reindeer *Rangifer tarandus*. Our analyses therefore focus on the central and southern parts of the country, where lynx populations occur naturally and face lower hunting pressure.

The region lies within the boreal forest zone, characterised by a mosaic of coniferous and deciduous forests, agricultural land, wetlands, and numerous lakes. Forests are dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, interspersed with silver birch *Betula pendula*, downy birch *Betula pubescens*, and occasional aspen *Populus tremula*. While the majority of state-owned forests occur in the north, in the central and southern regions, are mostly privately owned. The landscape also contains small settlements and an agricultural matrix, which becomes more extensive towards the west and around southern population centres. Snow cover lasts for approximately six months per year. Human population density ranges from 3.9 inhabitants km² in the north to 170.4 inhabitants km² in the most densely populated southern areas. Mean July temperatures range from 18°C in the south to 13°C in the north, and mean February temperatures from -5 to -13°C. Annual precipitation averages 700–750 mm in the southwest and 450–500 mm in the northeast (1981–2010).

To account for environmental variation in prey composition and abundance, we divided the study area into two

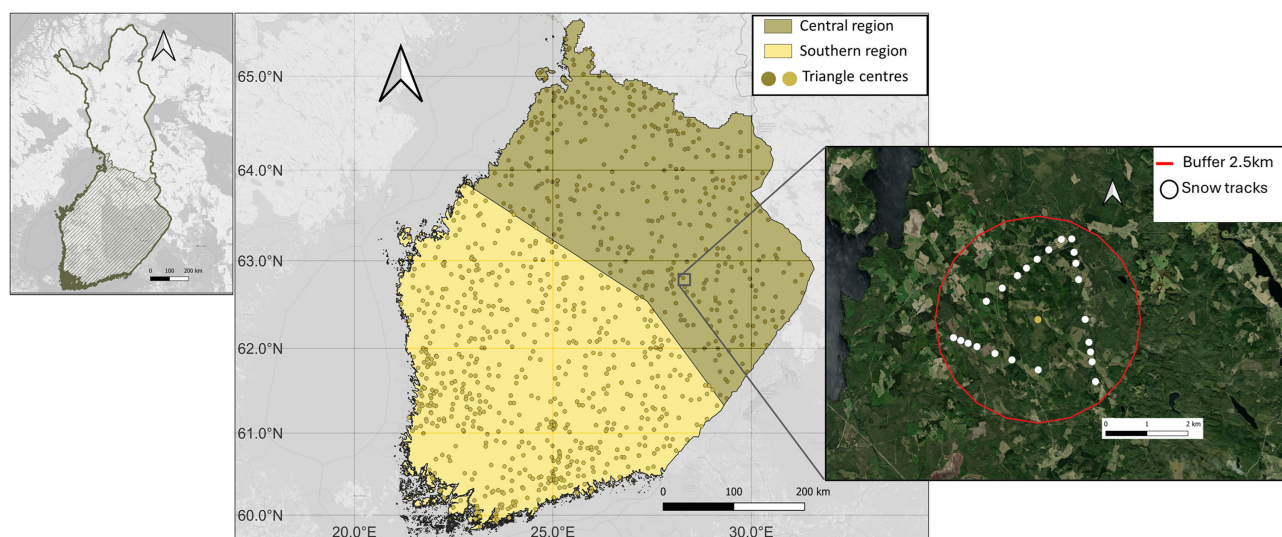


Figure 1. Study area divided into two macro-regions based on latitude: the central region (green) and the southern region (yellow). Dots indicate the centres of wildlife monitoring triangles. The inset at the bottom right illustrates a 2.5 km radius buffer (red circle) around a triangle centre (yellow dot), with locations of surveyed snow tracks of various mammal species represented in white.

macro-regions: 1) central Finland, where mountain hare is more abundant prey species, and 2) southern Finland, where white-tailed deer, roe deer and brown hare are more abundant (Fig. 1). This division follows the prey distribution described by Pulliainen et al. (1995), but with the boundary shifted north-eastward to follow the expansion of white-tailed deer indicated by our data (Kukko and Pusenius 2020).

Mammal survey data

We used data from the Wildlife Triangle Scheme, a national monitoring program coordinated by the Natural Resources Institute Finland – Luke (Pellikka et al. 2005). This program provides standardized long-term data on wildlife abundance across Finland. It is based on a network of permanently positioned triangle-shaped transects, surveyed annually by trained volunteers, primarily hunters, who record mammal tracks in the snow within a single day. Only tracks intersecting with the predefined survey line are counted. To distinguish fresh tracks from older ones, the survey is conducted after a known number of elapsed days since previous snowfall. Alternatively, an initial pre-count is conducted to mark existing tracks before the actual survey, again providing a known length of the potential timespan (number of days) during which new snow-tracks have accumulated.

Snow-track data include two types of fixed survey routes, both shaped as equilateral triangles: 1) Forest triangles, consisting of three 4 km sides (12 km total), are primarily located in relatively homogeneous forest habitats and were established in 1989. 2) Field triangles, established in 1999, have three 2 km sides (6 km total) and are situated in agricultural landscapes mixed with forests, predominantly along the coast. Forest triangles are surveyed between 15 January and 29 February (extending to 15 March in the north), during a period of typically stable snow cover. Field triangles are surveyed from 1 January to 5 March to accommodate the more variable and ephemeral snow conditions in southern agricultural areas, allowing greater flexibility in timing. To ensure representative sampling across the diverse Finnish landscape, both triangle types were included, allowing for a more accurate assessment of lynx habitat use across different ecological contexts.

For this study, we analysed data from 967 unique triangular transects surveyed between 2016 and 2020. These included 759 wildlife triangles (located in forested areas) and 208 field triangles (located in agricultural areas). Of the total transects, 375 were located in the central region and 592 in the southern region. The central region comprised 363 wildlife triangles and 12 field triangles, while the southern region included 396 wildlife triangles and 196 field triangles. A total of 265 transects located in the reindeer husbandry region and Lapland were excluded from the analysis.

Study species

The study area includes a set of species that interact with lynx as prey or potential competitors and were included as response variables in our analyses. Key mammal prey species of the lynx include mountain hare, brown hare and roe deer

(Levänen et al. 2019, Linnell et al. 2020, Tasser et al. 2023). Additionally, white-tailed deer, introduced by humans in 1934 from North America, has expanded rapidly in Finland, particularly in southern regions where its population continues to grow (Poutanen et al. 2023). Other ungulates present in the study area include moose *Alces alces* and wild forest reindeer *Rangifer tarandus fennicus*. Species potentially associated with lynx through shared prey or space use include sympatric large carnivores such as the wolf *Canis lupus*, particularly in relation to larger ungulates, as well as smaller carnivores, such as the red fox *Vulpes vulpes*, which may overlap with the lynx in the use of smaller prey.

Our analysis incorporated all species listed above to represent the broader ecological context in which lynx habitat use occurs. However, because our primary interest lies in lynx-prey associations, we centered the presentation of results on the Eurasian lynx and its key prey species, while other taxa are included to characterize the biotic context contributing to the habitat use of the lynx in Finland.

Environmental covariates

We calculated the environmental covariates as averages within a 2.5 km buffer radius (area approx. 19.6 km²) from the georeferenced center of each wildlife triangle by using QGIS ver. 3.32. This buffer was selected as minimum size to cover the immediate landscape surrounding each triangle while capturing spatial variation in land cover, topography, and human influence (Helle and Nikula 1996). All spatial data were set to the EPSG:3067 – ETRS89/TM35FIN (E, N) coordinate reference system, with units in meters, ensuring consistency across datasets.

Habitat complexity

Habitat complexity was assessed using dead wood potential (DWP) and terrain ruggedness. DWP was used as an indicator of forest structural complexity, as higher values are associated with forest conditions such as the presence of old trees, decaying wood, and greater vertical heterogeneity (Acker et al. 1998, Wikstrom and Eriksson 2000, McElhinny et al. 2005, De Meo et al. 2024). To facilitate the interpretation of this metric, we provide example photographs illustrating forest structural conditions across a range of DWP values at locations included in the lynx snow-track dataset (Supporting information).

DWP was derived from the high biodiversity value forests 2018 dataset provided by the Finnish Environment Institute (2018) using the raster version ‘NAT2’ (96 m resolution; Mikkonen et al. 2023). This index estimates dead wood potential based on forest inventory data adjusted for forestry impacts on biodiversity and integrates information on forest fertility, tree species composition, mean diameter at breast height (DBH), and total tree volume. Tree species composition was assessed for seven common Finnish taxa: black alder *Alnus glutinosa*, silver birch, downy birch, Norway spruce, Scots pine, European aspen, and other broad-leaved species. Higher DWP values correspond to forests with limited management, large trees and greater structural diversity,

whereas lower values reflect intensively managed stands with smaller wood volumes and reduced dead wood availability (Mikkonen et al. 2020, 2023).

In addition to DWP, we included terrain ruggedness to represent the topographic complexity, capturing local variation in elevation associated with rocky and irregular landscapes within the study area. Terrain ruggedness was quantified as the standard deviation of elevation within each buffer, using the digital elevation model (DEM) dataset (2 m resolution; EuroGeographics 2023).

Landscape composition

We quantified key aspects of landscape composition within the triangle buffers by measuring forest and peatland cover and stream networks. Forest cover was calculated as the proportion of forested pixels relative to the total number of pixels within each buffer, using the Finnish multi-source national forest inventory canopy cover dataset (16 m resolution; Luke MS-NFI 2019). In addition to forests, we assessed the proportion of peatbogs, representing the extent of open and sparsely forested wetlands within each buffer. Peatbog extent was derived by selecting pixels classified as open bog, sparsely forested bog, and forested bog from land cover in peatlands and wetlands dataset (16 m resolution; Finnish Environment Institute 2020a). As with forest cover, the proportion of peatbogs was calculated as the number of peatbog pixels relative to the total number of pixels within the buffer.

Water availability was characterized through the distance to the nearest stream and the total stream length within the buffer. Distance to the nearest stream was calculated as the shortest distance in meters from the buffer edge to the closest mapped stream or river. Total stream length was computed as the total length in meters of all stream segments within each buffer. Both variables were derived from water bodies according to Water Framework Directive dataset (linear features only; Finnish Environment Institute 2016).

Human influence

To account for anthropogenic pressures on the landscape, we measured proximity to roads and residential areas. Road network data were derived from the road network dataset (Finnish Transport Infrastructure Agency 2021), which includes connecting roads, regional roads, highways, and main roads. Similarly, the distance to the nearest residential area was calculated as the shortest distance in meters from the buffer edge to the closest residential area. Residential area data were derived from the sparsely and densely built settlements dataset (Finnish Environment Institute 2020b).

Climatic conditions

To assess the influence of winter conditions on wildlife, we included average snow depth as a spatial climate variable in our models. Snow depth data were obtained from gridded daily observations (1 km resolution; Finnish Meteorological Institute 2016). For each year, we calculated the mean snow depth over the winter period (1 November–4 April) and then averaged these seasonal means across 2016–2020 to represent

the study period. For each year, we calculated the mean snow depth over the winter period (1 November–4 April) and then averaged these seasonal means across 2016–2020 to represent the study period.

Statistical analysis

We analysed snow-track data for nine mammal species across Finland using the hierarchical modelling of species communities (HMSC) framework. The multivariate response consisted of annual snow-track counts for each of the study species recorded in wildlife triangles from 2016 to 2020. Each observation corresponded to a wildlife triangle-year combination, and each response variable represented a different species. Predictor variables included habitat structural complexity (dead wood potential and terrain ruggedness), land cover (forest cover and peatbogs), topographic variation, human influence (distance to residential areas and roads), hydrological features (distance to streams) and sampling effort.

Species abundances were modelled using a log-linear Poisson distribution and a log-link function. We applied a $\log(1+x)$ transformation to distance to residence, roads, streams, and to terrain ruggedness. Variables expressed as proportion (i.e. forest cover and peatbogs) were transformed using the arcsine-square root function. All continuous variables were standardized to a mean of zero and scaling by their standard deviation to ensure comparability of effect sizes and prevents numerical stability during parameter estimation.

Within the HMSC framework, species-specific responses to environmental covariates were estimated in a hierarchical structure that allows partial pooling across species. In addition, residual species-to-species associations were quantified to capture shared responses to unmeasured environmental factors or spatial associations consistent with ecological interactions, such as predator–prey relationships. We fitted one model to the entire study area and two additional models restricted to the central and southern regions to examine potential regional differences in species environment relationships and predator–prey spatial associations.

To account for variation in sampling effort among survey sites, we included the natural logarithm of sampling effort as an additional covariate in the model. For each triangle and year, sampling effort (prior to log-transformation) was calculated as the product of the surveyed distance (in 10 km) and the number of days since snowfall or track marking. Because the monitoring method targets fresh tracks and to minimise potential detectability biases associated with older tracks, we restricted analyses to surveys with no more than five days of track accumulation.

Prior to model fitting, we assessed multicollinearity among predictors by calculating Pearson correlation coefficients and the variance inflation factor (VIF). Strong correlations were defined as $|r| \geq 0.7$. The distance to streams and stream length correlation was above the threshold ($r = -0.95$) and we kept only the distance to streams as the representative measure of water availability. All VIF values for the retained predictors ranged from 1.03 to 2.33, indicating no problematic multicollinearity (Zuur et al. 2010; Supporting information).

Residual species-to-species associations were inferred from the posterior distributions of the covariance matrix associated with the random effects (Tikhonov et al. 2019). These associations describe patterns of co-occurrence among species after accounting for shared responses to measured environmental covariates and the spatial structure imposed by the sampling design. As such, they do not represent direct interaction strengths but rather indicate whether species tend to co-occur more or less frequently than expected given the environmental predictors included in the model (Poggiato et al. 2021). For each species pair, we summarised residual associations using the posterior mean and credible intervals. Associations were considered supported when at least 80% of the posterior distribution had the same sign, indicating consistent positive or negative co-occurrence across posterior samples.

To account for spatial and temporal dependency, we included three hierarchical random effects at the intercept-level, shared across species. Spatial autocorrelation was modelled at the wildlife triangle level using a nearest neighbour Gaussian process (NNGP), with each triangle connected to its 10 nearest neighbours (Tikhonov et al. 2019). Temporal variation was accounted for by including year-specific random effects, and a regional random effect was included in the full study area model to capture for broad-scale differences between central and southern Finland.

We fitted the models using Markov chain Monte Carlo (MCMC) sampling. For each model, we ran 10 parallel MCMC chains, each with a total of 150 000 iterations, discarding the first 50 000 iterations as burn-in and applying a thinning interval of 100. This resulted in 1000 posterior samples per chain and a total of 10 000 posterior samples used for inference. Model convergence was assessed by examining the effective sample size (ESS) and the potential scale reduction factor (PSRF), with PSRF values below 1.1 indicating satisfactory convergence (Gelman and Rubin 1992; Supporting information). Trace plots and posterior density plots for selected parameters confirmed adequate mixing across chains (Supporting information).

Model explanatory power was evaluated using SR^2 , calculated as the squared Spearman correlation between observed

and predicted values. We also computed conditional SR^2 ($C.SR^2$), which assesses predictive performance conditional on species presence, and Tjur's R^2 to evaluate discrimination for presence-absence predictions derived from count data. R code for the fitted model and all figures are provided in the Supporting information.

Results

Across the entire study area, the full model explained, on average, 54% of the variation in track counts for all species included in the analysis. Among the random effects, the spatial variation among wildlife triangles accounted for the largest share of variance (32.9%) and was the strongest predictor for half of the species included in the model, indicating a relevant spatial structuring in species distribution, whereas differences among regions (3.8%) and years (1.8%) contributed more modestly. These results highlight the dominant role of spatial heterogeneity relative to temporal or broad regional variation in shaping mammal track distributions at the scale of the study area.

Focusing on the Eurasian lynx, the full model explained 15.5% of the variation in track counts (SR^2), of which 11.9% was attributable to the occurrence component (presence-absence predictions) and 2.7% to the abundance component conditional on occurrence. Variance partitioning of the predictors showed that dead wood potential was the most influential variable, accounting for 17.3% of the explained variance and showing a positive association ($\beta = 0.29$; 80% CI: 0.23–0.37), about six times stronger than its mean importance across all species (2.9%). Snow depth was the second most important variable, accounting for 9.8% of the variance ($\beta = 0.18$; 80% CI: 0.06–0.30), followed by terrain ruggedness which accounted for 7.9% of the explained variance ($\beta = 0.21$; 80% CI: 0.13–0.28). The remaining predictors showed smaller contributions to the explained variance (Fig. 2). Across species, the direction and relative support of these environmental effects varied, but habitat complexity variables showed consistently positive associations for lynx

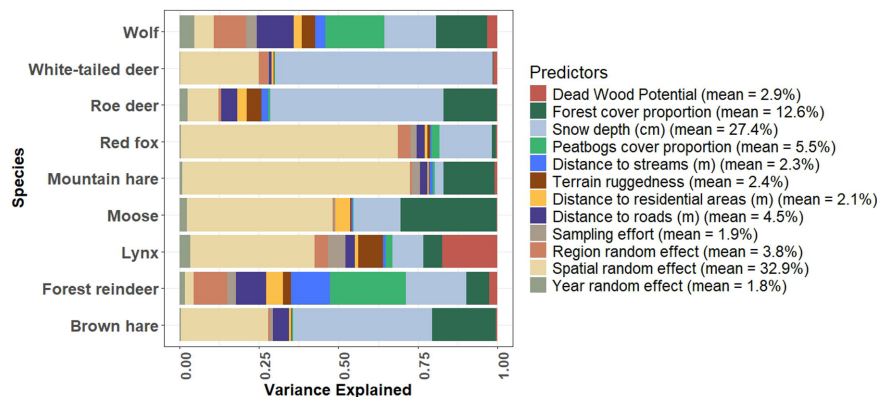


Figure 2. Variance partitioning across species. Bars represent species, and colours indicate the proportion of variance explained by each predictor. The legend shows the average variance explained per predictor across all species.

compared with several prey species and potential competitors (Fig. 3). Analyses conducted separately for central and southern regions revealed consistent patterns, with habitat complexity variables remaining dominant predictors in both regions (Supporting information).

The HMSC model captured substantially more variation in lynx habitat use in the central region (19.1%) than in the southern region (8.0%). Environmental predictors also accounted for a larger share of the explained variance in the central region (10.0%) than in the south (4.9%). In both regions, most of the explanatory power arose from the occurrence component, whereas abundance conditional on occurrence contributed comparatively little to overall model performance. Specifically, the occurrence component explained 12.7% of the variance in the central region and 6.7% in the southern region, while conditional abundance accounted for only 3.1 and 0.9%, respectively.

Spatial residual associations revealed a clear regional shift in the direction of lynx associations with prey species (Fig. 4). In the central region, lynx tracks were associated with lagomorph prey, showing a positive association with mountain hare (mean = 0.71, 80% CI: 0.55–0.85) and a negative association with brown hare (mean = -0.40, 80% CI: -0.69 to -0.13), while associations with ungulate prey were unsupported. In contrast, in the southern region, lynx associations shifted towards ungulate prey, with positively supported associations with white-tailed deer (mean = 0.86, 80% CI: 0.61–0.99) and roe deer (mean = 0.72, 80% CI: 0.30–0.99), whereas associations with lagomorphs were unsupported. Lynx also showed supported positive spatial associations with other ungulates, including moose in both regions and forest reindeer in the southern region only. Residual association with potential competitors also varied regionally, including a negative association with red fox (mean = -0.28, 80% CI: -0.49 to -0.08) and positive

with wolf (mean = 0.46, 80% CI: 0.14–0.79) in the central region, whereas in the southern region only a positive association with red fox was supported.

Discussion

We show that Eurasian lynx habitat use across Finland is shaped by a consistent association with structurally complex habitats, while spatial associations with prey species shift across regions. Predator and prey habitat use was more similar in the central region than southern region, suggesting that despite lynx's reliance on complex habitats, they adjust their space use to take advantage of prey availability. Together, our findings highlight how trophic flexibility in lynx is expressed through region-specific spatial associations with prey, while remaining constrained by consistent habitat requirements linked to its hunting strategy. The strong spatial structuring observed in our models suggests that additional processes operating at different spatial scales, such as movement behavior, territoriality, or fine-scale landscape features, may further shape lynx occurrence beyond the factors captured here.

Environmental drivers, prey associations and lynx habitat use

Our findings support the importance of habitat structure in shaping lynx habitat use across the study area. Both dead wood potential and terrain ruggedness were disproportionately important for lynx. These variables captured complementary aspects of habitat complexity with dead wood potential reflecting forest structure and terrain ruggedness representing topographic heterogeneity. Although our study design does not allow direct inference about predatory behaviour, the association between lynx occurrence and structurally complex habitats is consistent with a stalk-and-ambush

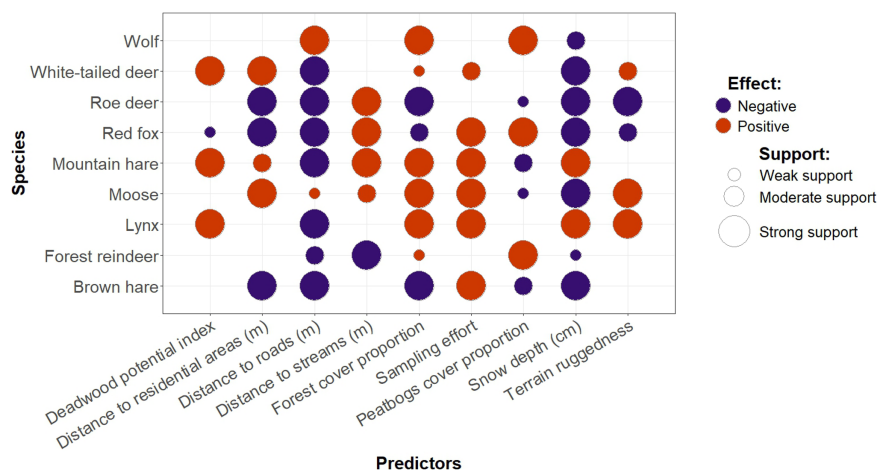


Figure 3. Posterior beta coefficient plot illustrating the beta relationship between predictors (x-axis) and each species (y-axis) in the full model. Dot colour indicates the sign of the relationship (positive or negative), while dot size represents the support level, defined as the posterior probability that the coefficient has the estimated sign. Support level is categorized into three main levels: weak support (support value between 0.8 and 0.9); moderate support (support value between 0.9 and 0.95); strong support (support value ≥ 0.95). The unsupported level (< 0.8) is shown as blank.

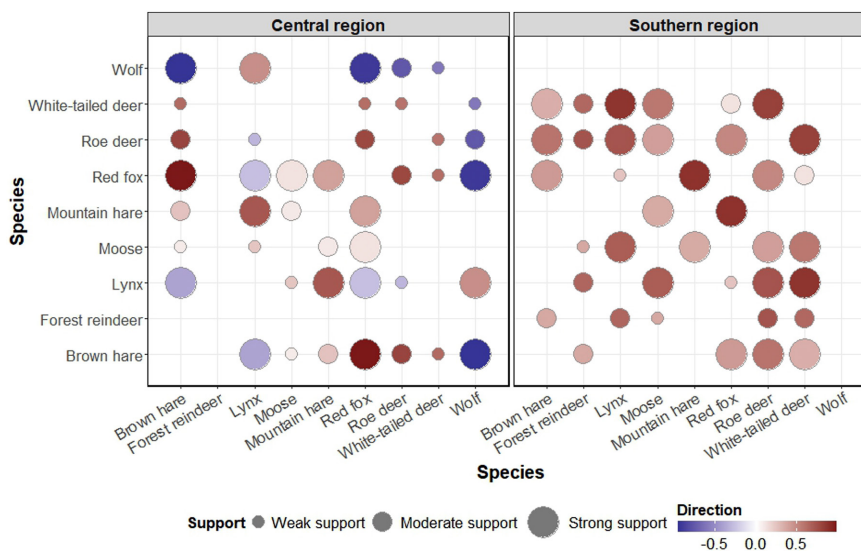


Figure 4. Residual species-to-species associations within the wildlife triangles. Positive associations are shown in red and negative associations in blue. The support value represents the posterior probability that the association has the estimated sign. Support levels are classified as weak (0.8–0.9), moderate (0.9–0.95), and strong (≥ 0.95). The unsupported level (< 0.8) is shown as blank.

hunting strategy (Murray et al. 1995), which distinguishes lynx from the other species considered here.

Structurally complex environments may support lynx not only by facilitating hunting, but also by providing refuge areas in landscapes increasingly shaped by human activities (Palomares 2001, Bouyer et al. 2015, Filla et al. 2017). In contrast, direct measures of human presence, such as distance to roads and residential areas, contributed little to explaining lynx habitat use in our models. While dispersing lynx in Finland have been shown to avoid settlements and infrastructure (Herrero et al. 2020), our results suggest that habitat used within established home ranges is shaped less by direct avoidance of human features and more by forest structural conditions. Notably, forest cover itself had limited explanatory power, whereas dead wood potential was consistently important, indicating that lynx respond to forest structure rather than forest extent per se. This interpretation aligns with studies showing that lynx habitat use is better explained by specific forest conditions that provide cover and hunting opportunities, rather than by forest presence alone (Holbrook et al. 2017).

Snow depth also emerged as an important predictor of lynx habitat use, reflecting the role of winter conditions in shaping predator–prey interactions rather than direct habitat selection by lynx. Snow conditions are known to alter the relative movement costs and vulnerability of prey and predators, sometimes conferring a hunting advantage to lynx and at other times acting as a barrier (Stenseth et al. 2004). In our analysis, snow depth was not consistently more influential for lynx than for other species, particularly ungulates, suggesting that its effects on lynx are largely indirect, mediated through changes in prey distribution and accessibility (Lang and Gates 1985, Mysterud and Østbye 1995, Mysterud et al. 1997). This interpretation is consistent with work showing that predator space use often reflects prey availability more closely than environmental drivers shaping prey habitat

use per se (Keim et al. 2011, Trainor and Schmitz 2014, Trainor et al. 2014).

Further evidence for the interpretation that predators follow their prey comes from the regional differences in lynx–prey spatial associations and the amount of variance explained by all environmental variables, not just snow depth. In the central region, lynx habitat use overlapped consistently with that of its primary prey, the mountain hare. This contrasts with the southern region where the habitat use of lynx clearly contrasted with their primary associated prey, roe deer and white-tailed deer. This trend is presumably reflected in our analysis where we found comparatively higher amounts of variance explained by the environmental covariates for lynx in the central region and lower amounts in the southern region. While these spatial patterns indicate that prey abundance and distribution strongly influence lynx habitat use, predator–prey interactions are inherently reciprocal, and spatial co-distribution may also reflect top-down processes. Our joint modelling framework does not allow us to infer the directionality of these relationships, but previous research (Kauhala and Helle 2000) and a recent hunting moratorium in our study area that resulted in a sharp increase in the lynx population (Herrero et al. 2025), supports a predominantly bottom-up interpretation at the spatial scales considered here. In this broader context, ecological flexibility emerges as a key adaptive strategy for large generalist predators in heterogeneous environments. Comparable patterns have been documented across multiple systems, where felid predators adjust habitat use and foraging strategies in response to local prey availability rather than exerting uniform control over prey populations (Newbury and Hodges 2018, Karandikar et al. 2022). Such behavioural and trophic flexibility likely enables large carnivores to track spatial variation in resources while remaining constrained by species-specific hunting strategies and landscape structure.

Non-primary prey species associations

Patterns of spatial association between lynx and other species can be interpreted in light of prey use and hunting strategy, which may modulate the strength of interspecific interactions across regions. In the central region, the negative association with red fox, for example, is consistent with intraguild predation and partial trophic overlap. Lynx are known to kill foxes opportunistically (Mortensen et al. 2013, Wikenros et al. 2013), and both species were associated with lagomorph prey, although lynx were more closely associated to mountain hare whereas foxes were more closely associated with brown hare. In the southern region, where prey diversity is higher and ungulates represent a larger component of the lynx prey base, the association with red fox occurred in a context of broader resource availability and reduced direct overlap in prey use, consistent with expectations that prey diversity can modulate predator interactions (Elmhagen and Rushton 2007, Jähren et al. 2020).

Associations between lynx and wolves varied across regions and can be interpreted in relation to differences in hunting strategy and prey use. Wolves are cooperative coursing predators, whereas lynx are solitary stalk-and-ambush predators, and these contrasting hunting modes are associated with differences in prey selection, with wolves typically targeting larger prey through group hunting. Such distinctions in hunting behaviour may contribute to reduced spatial overlap and limited direct competition at the scale considered here. Interpretation of these patterns is constrained by the lower prevalence of wolf observed in our data (Supporting information).

Associations between lynx and large herbivores can arise through different processes depending on species. For moose, spatial overlap is not expected to reflect direct predation, as moose are not typical lynx prey, and more plausibly indicates shared responses to environmental features or residual spatial structure that our environmental covariates did not capture. In contrast, associations with forest reindeer reflect ecologically meaningful overlap, as lynx are known to occasionally prey on semi-domesticated reindeer in northern Finland. In this case, spatial co-occurrence could indicate areas of elevated encounter probability rather than shared habitat preferences alone, with potential implications for wild forest reindeer.

Scope of inference and modelling considerations

Our results should be interpreted in light of the scale, observation process, and modelling framework used to analyse lynx habitat use. Although the spatial patterns identified here are consistent with ecological expectations for a large ambush predator with a flexible diet, they do not allow direct inference about causal predator–prey interactions or demographic feedback. Instead, they describe spatial associations that reflect how lynx, prey, and other species co-occur across landscapes under shared environmental and spatial constraints.

A substantial proportion of the explained variation in lynx occurrence was captured by spatial random effects, indicating that processes operating beyond the measured environmental covariates play an important role in shaping lynx space use.

However, it is clear that the environmental variables that were important in our model have also previously been identified as important predictors of lynx distribution (Schmidt and Gorny 2023, Čonč et al. 2024). Overall, this suggests that the prominence of spatial random effects reflects in our model reflects additional processes operating not captured by these known habitat associations. Those missing processes likely include movement behaviour, territoriality, landscape connectivity, and historical distribution patterns, which are difficult to quantify explicitly at broad spatial extents. Wildlife triangles used in this study have a perimeter of approximately 12 km, and telemetry studies show that individual lynx can move distances comparable to, or exceeding, the dimensions of wildlife triangles within short time periods, and that space use varies strongly with sex and reproductive status, indicating that snow-track counts may be influenced by activity patterns in addition to local abundance (Jędrzejewski et al. 1993, Linnell et al. 2007).

These scale-related constraints are further reflected in the modelling results, where explanatory power was driven primarily by presence–absence rather than by variation in track counts conditional on presence. This suggests that the analyses are more informative about where lynx occur than about the intensity of space use within occupied areas. In addition, environmental predictors were averaged within a 2.5 km radius buffer around triangle centres, representing local habitat conditions at the triangle scale, but not the full spatial extent over which individual lynx move or establish home ranges. As a result, these predictors may only partially capture the spatial scales at which lynx respond to habitat features. Unmeasured landscape elements, such as natural movement corridors, spatial clustering of suitable habitats across adjacent triangles, or the distribution of supplemental feeding stations for ungulates, may therefore contribute to residual spatial structure not explained by the covariates included in the models.

The interpretation of species associations is constrained by the fact that spatial co-occurrence does not imply interaction. It has been suggested that explicitly incorporating trophic dependencies into species distribution models can improve inference about predator–prey relationships by accounting for prey availability and interaction pathways (Trainor and Schmitz 2014). Such approaches require the specification of trophic links or assumptions about interaction directionality (Staniczenko et al. 2017). Here, we instead used a joint species distribution modelling framework to examine spatial associations among lynx, prey, and other species while accounting for shared environmental responses and spatial structure, allowing prey–predator associations to vary across regions without imposing a priori interaction pathways. Consequently, the analysis identifies region-specific patterns of spatial co-occurrence, while the direction of predator–prey interactions remain unresolved.

However, even in a case where interactions would have been directly estimated (e.g. sampling kill sites or by using telemetric data), an additional constraint of our modelling framework is that residual species associations are assumed

to be symmetric, and their estimation can be influenced by differences in species prevalence. When species occur at very different frequencies, residual associations are more difficult to interpret as indicators of interaction strength (Zurell et al. 2018). Given the nature of our data, we partially address this by analysing regions separately, reducing heterogeneity in prey communities and prevalence and allowing consistent patterns in the sign of associations to be evaluated within more ecologically coherent contexts. While this does not permit inference about interaction strength or path directionality, it allows assessment of whether associations are consistently positive or negative across regions. Within these bounds, the regional differences observed are consistent with expectations for a predator that adjusts space use in response to prey availability and accessibility under varying environmental conditions. Developing approaches that allow asymmetric residual associations within joint species distribution models has been identified as an important methodological advance for disentangling prey-driven and predator-driven processes in heterogeneous landscapes (Staniczenko et al. 2017, Si-Moussi et al. 2020).

Conclusions

Our findings highlight the remarkable ecological flexibility of the Eurasian lynx, observed within a single Finnish population living in contrasting environmental and trophic conditions. This flexibility, however, does not mean that lynx use all habitats equally. In cases where they adjust space use to prey availability, they still retain a core association for complex habitats. Our results thus contribute to a broader understanding of how large carnivores adjust habitat use to prey availability. This link between environmental heterogeneity, prey patchiness, and flexible habitat use, demonstrated in our study, may generalize to other carnivore systems where, predator foraging decisions are not solely determined by total prey abundance, but critically by the spatial arrangement of habitat types that jointly determine both prey vulnerability and predator search efficiency. Similar trends are likely to be found especially in other generalist predators that are adaptable in their diets and occupy diverse habitats like the Eurasian lynx. In contrast, predators with either very specific habitat requirements or specialist foragers are unlikely to be able to take advantage of environmental heterogeneity in the same way. The application of a joint species distribution model was central to these insights, as it allowed us to evaluate lynx habitat use in relation to multiple prey species simultaneously. This integrative framework not only represents a transferable methodology for generating information directly relevant to conservation planning but also demonstrates how landscape-level analyses can reveal patterns critical for effectively managing large carnivores across heterogeneous ecological settings. Such knowledge can ultimately support assessments of the feasibility of reintroduction or translocation initiatives in areas that vary in ecological conditions and human influence.

Future research should assess the temporal stability of these patterns through multi-year surveys and explore species-specific or multi-scale habitat predictors, particularly for wide-ranging predators and smaller prey species. Such developments will improve our understanding of how ecological processes and human pressures jointly shape predator–prey dynamics, ultimately strengthening the scientific basis for large carnivore conservation.

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Author contributions

Francesca Malcangi: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (lead); Investigation (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Caio Graco Rodrigues Leandro Roza:** Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Validation (lead); Visualization (equal); Writing – review and editing (equal). **Andreas Linden:** Data curation (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Supervision (equal); Writing – review and editing (equal). **Janne Sundell:** Conceptualization (supporting); Funding acquisition (supporting); Investigation (supporting); Supervision (equal); Writing – review and editing (equal). **John Loehr:** Conceptualization (lead); Formal analysis (supporting); Funding acquisition (supporting); Supervision (lead); Validation (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qjq2bvqw3> (Malcangi et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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