

# Dracula's menagerie: A multispecies occupancy analysis of lynx, wildcat, and wolf in the Romanian Carpathians

Marissa Dyck<sup>1</sup>, Ruben Iosif<sup>2</sup>, Barbara Promberger-Fürpass<sup>2</sup>, and Viorel Popescu<sup>1</sup>

<sup>1</sup>Ohio University

<sup>2</sup>Foundation Conservation Carpathia

February 9, 2022

## Abstract

1. The recovery of terrestrial carnivores in Europe is a conservation success story. Initiatives focused on restoring top predators, require information on how resident species may interact with the re-introduced species as their interactions have the potential to alter food webs, yet such data are scarce for Europe. 2. In this study, we assessed patterns of occupancy and interactions between three carnivore species in the Romanian Carpathians. Romania houses one of the few intact carnivore guilds in Europe, making it an ideal system to assess intraguild interactions, and serve as a guide for reintroductions elsewhere. 3. We used camera trap data from two seasons in Transylvanian forests to assess occupancy and co-occurrence of carnivores using multispecies occupancy models. 4. Mean occupancy in the study area was highest for lynx (?winter= 0.76 95% CI: 0.42-0.92; ?autumn= 0.71 CI: 0.38-0.84) and wolf (?winter= 0.60 CI: 0.34-0.78; ?autumn= 0.81 CI: 0.25-0.95) and lowest for wildcat (?winter= 0.40 CI: 0.19-0.63; ?autumn= 0.52 CI: 0.17-0.78) 5. We found that marginal occupancy predictors for carnivores varied between seasons. We also found differences in predictors of co-occupancy between seasons for both lynx-wolf and wildcat-wolf co-occupancy. For both seasons, we found that conditional occupancy probabilities of all three species were higher when another species was present. 6. Our results indicate that while there are seasonal differences in predictors of occupancy and co-occupancy of the three species, co-occurrence in our study area is high, and is dependent on the existence of continuous, relatively undisturbed forests. 7. Terrestrial carnivore recovery efforts are ongoing worldwide. Insights into interspecific relations between carnivore species are critical when considering the depauperate communities they are introduced in. Our work showcases that apex carnivore coexistence is possible, but dependent on protection afforded to forest habitats and their prey base.

## Introduction

Terrestrial carnivores are some of the most imperiled species today due to their large home range requirements, high metabolic demands, sensitivity to habitat fragmentation, and persecution by humans (Crooks, 2002; Palomares & Caro, 1999; W. J. Ripple et al., 2014; Woodroffe & Ginsberg, 1998). Carnivores are also important top-down regulators in ecological communities (Beschta & Ripple, 2009; W. J. Ripple & Beschta, 2006; W. Ripple J. & Beschta, 2012). The loss of key carnivore species can have devastating ecosystem effects (Effiom et al., 2013; W. J. Ripple et al., 2014) and changes in abundance or occurrence of carnivores can trigger trophic cascades (W. Ripple J. & Beschta, 2012). As such, the recovery of apex predators as a conservation tool to restore ecosystem functions (termed trophic rewilding) has become increasingly popular (Jørgensen, 2015; Seddon et al., 2014). Trophic rewilding is an ecological restoration strategy used to promote self-regulating ecosystems (Svenning et al., 2016).

Rewilding efforts in the context of apex predators requires not only an understanding of their ecological interactions within the carnivore guild, but also the broader context of these interactions including sources of anthropogenic impacts. Many apex predators readily reestablish in human-dominated landscapes and exhibit potential coexistence with humans (Chapron et al., 2014; Lamb et al., 2020). Although the effects of apex predator recovery in natural landscapes are relatively well understood, there are significant knowledge

gaps regarding the effects of their recovery in shaping species interactions (both intraguild and across trophic levels) in human-dominated landscapes (Dorresteijn et al., 2015). Interactions between carnivores are complex in nature, but are integral to shaping the ecology and structure of wildlife communities. Therefore, examining such interactions in landscapes that harbor viable carnivore populations may provide important insights into the effects of carnivore recovery on the mesocarnivore communities that often dominate landscapes where apex predators have been eliminated.

Grey wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) are top predators in many temperate ecosystems in Europe and Asia, but their co-occurrence has been severely limited by extirpation of one species (most often wolf). This is particularly the case for most of Western and Central Europe due to a long history of human habitation and persecution of carnivore species. Both wolf and Eurasian lynx are recovering in Europe's landscapes (Chapron et al., 2014; Kaczensky et al., 2013) either through natural range expansion (wolf) or reintroductions and population augmentation (lynx). The wildcat (*Felis silvestris*) is a mesocarnivore that was once common in Europe, has also been extirpated, and currently at the core of reintroduction programs in some European Union states. In this context, the Romanian Carpathians represent one of the few natural areas in Europe that still harbor intact viable populations of all three species and serve as a stronghold for carnivore populations in Europe, despite anthropogenic influences common (hunting, forestry, farming, and livestock production) (Popescu et al., 2016; Salvatori et al., 2002).

While no work has been conducted on understanding the spatial relations and interactions between these three species simultaneously, research exists on pairwise interactions between species, particularly for lynx and wolf. Lynx and wolf are sympatric across most of their range and there is some diet overlap between them. Research addressing coexistence between these species differ in their findings, but recent studies looking at spatial interactions between these species in Europe found that these two apex predators coexist and competition between them is low (Schmidt et al., 2009; Wikenros et al., 2010). In Poland, lynx and wolf territories overlap and researchers concluded that the co-occurrence of these two species was facilitated by heterogeneous habitat and specialization on different prey (Schmidt et al., 2009). These predictors, habitat heterogeneity and diet, are also explaining competitive interactions between canids and felids in North America, with a lack of interference competition in heterogeneous habitat (Dyck et al., 2022). Therefore, we expect to observe similar co-existence (high co-occurrence) and little evidence of interference competition (neutral or positive conditional occupancy values) between lynx and wolf in our study area. Additionally, we expect to observe differences in co-occurrence based on seasonal changes in these species' behaviors. For example, male lynx move further during the mating season (January-March) and female lynx move further during periods of extensive kitten care (May-August) (Jedrzejewski et al., 2002), which could cause increased interactions with wolves. Research on wildcats is scarce, but a study conducted in the Jura Mountains of central Europe found no evidence of avoidance between lynx and wildcat (Zimmermann & Raoul, 2011). No published research examines interactions between wildcats and wolf, however interspecific interactions have been assessed between wildcats and red foxes. A study in Spain found that the two carnivores exhibited active avoidance towards one another and exhibited aggressive behaviors during encounters suggesting interference competition (Ruiz-Villar et al., 2021). Given the size difference between wolf and wildcats and their different diets, it is likely that the relationship between wildcats and wolf will be similar to that of wildcats and lynx.

In this study, we aimed to address these knowledge gaps by studying the intraguild interactions of two apex carnivores, the Eurasian lynx and the grey wolf, and a mesocarnivore, the wildcat in the Romanian Carpathians using multispecies occupancy models (Rota et al., 2016). Unlike traditional occupancy modeling, multispecies occupancy models allow for the estimation of co-occupancy probabilities for more than two species and do not assume asymmetric interactions (i. e., dominant and subordinate species). This is useful for estimating co-occupancy probabilities between species for which there is not a priori knowledge about interspecific relationships or for which there is not an obvious dominant or subordinate species. Multispecies occupancy models also allow for the estimation of marginal occupancy (occupancy of a single species irrelative of other species) and conditional occupancy (occupancy of a single species based on the presence or absence of another species) probabilities in relation to variables of interest (e.g., altitude). This approach has been used effectively to assess habitat use, interspecific interactions of carnivores in a variety of landscapes (Dechner et

al., 2018; Lombardi et al., 2020; Van der Weyde et al., 2018). Previous research on lynx-wolf and lynx-wildcat interactions suggests a high capacity for coexistence, low interspecific competition, and little to no intraguild killing. However, this research is limited and there has been no work on lynx-wolf dynamics or interactions of lynx, wildcat, and wolf in the same region. Additionally, none of the published literature has been conducted in an area with a fully intact carnivore guild. This information is crucial to understanding the effects of apex predators on mesocarnivores and the carnivore guild. By using a multi-species occupancy approach, we can analyze complex intraguild interactions and better understand competition and coexistence patterns. Results can elucidate variables and thresholds important for occurrence and coexistence of elusive species and help inform management or reintroduction efforts. Our specific objectives were: 1) evaluate seasonal predictors for occupancy of each species, 2) characterize the spatial relationships (co-occurrence) of each species in winter and autumn, and 3) identify predictors that facilitate co-occurrence. Specifically, we analyzed the effects of potentially dominant apex carnivores on the occupancy and detection of a mesocarnivore to understand potential impacts reintroductions of apex predators may have on smaller carnivores. We also evaluated seasonal changes in marginal and co-occupancy probabilities to better understand how species persist and interact under different environmental conditions.

## Materials and Methods

### *Study area*

The study was part of research conducted by Foundation conservation Carpathia (FCC) to estimate the density of lynx in the Romanian Carpathians (Iosif et al., 2022). The study area is situated in the Southern Carpathians, Romania, covering 1,200 km<sup>2</sup> in the eastern part of the Făgăraș Mountains, Piatra Craiului, and parts of Leaota Mountains (Figure 1). The altitude of the study area ranges from 600 to 2400 meters. Forests cover most of the area (62%), along with a mosaic of urban-rural landscape and agriculture with significant areas of natural vegetation (22%), and alpine grasslands and subalpine shrubs (16%). Although bisected by a high traffic national road, the area is recognized as a corridor for large carnivore dispersal. The road network is dominated by unpaved forest roads and temporary logging roads. Large carnivore hunting is not allowed in the study area. However, anthropogenic disturbance persists in the form of year-round selective logging, regulated hunting of ungulates, and livestock grazing.

### *Camera trapping and environmental variables*

We divided the study area into a grid of 2.7 km x 2.7 km cells (Figure 1) and removed cells with more than 2/3 of their area exceeding 1800 m altitude and cells more than 1/2 of their area covered by urban landscape features. From the remaining cells, we sampled every other cell, when it was not possible to reach a selected cell, we used an adjacent cell. Each sampled cell contained a trap station, randomly located within the cell. We conducted two seasons of monitoring: (1) December 17<sup>th</sup>, 2018, to March 31<sup>st</sup>, 2019 (winter) and (2) October 9<sup>th</sup>, 2019, to January 15<sup>th</sup>, 2020 (autumn). We installed 64 camera trap stations during winter, and 76 during autumn, with high spatial overlap between seasons (Figure 1). Each trap station had two opposite cameras installed at a height of 40 to 60 cm positioned towards animal paths. We used two camera models per trap station, a CuddeBack C1 Model 1279 with white flash for high quality color pictures in night conditions, and a Bushnell Trophy infrared camera. Camera traps were installed on animal trails along mountain ridges, mid-slopes, upper valleys, and bottom of slopes to detect carnivores at various altitudes/habitats. Camera traps were installed 1-2 weeks prior to the start of monitoring to account for additional anthropogenic disturbance from the camera installation process. At each camera trap location, we recorded the presence or absences of anthropogenic disturbance (i.e., logging or settlements) as a binary variable for species detection and occurrence. We also recorded *altitude* (m) via GPS and extracted *distance to stream* (m), *distance to settlement* (m), and *distance to roads* (m) from the camera trap location using Geographic Information Systems (ArcGIS 10.7, ESRI, Redlands CA). Within a 500-meter buffer around each camera trap location, we calculated the *density of local roads* (km/km<sup>2</sup>), the *proportion of forested area* and *aterrain ruggedness index (TRI)* (Riley et al., n.d.). Full covariate descriptions and summaries are available in Table 1.

## Occupancy modeling

We implemented a multispecies occupancy model of two or more interacting species (Rota et al., 2016) in program R 3.5.1 (R Core Team, 2019) via package *unmarked* (Fiske & Chandler, 2011) to explore how environmental and anthropogenic variables affect the marginal occupancy (occupancy without accounting for interactions with other species), co-occupancy (overlap in marginal occupancy between species), and conditional occupancy (effects of each species presence on other species detection and occupancy) of lynx, wildcat, and wolf in the Romanian Carpathians. Unlike traditional co-occupancy models, multispecies occupancy models do not require *a priori* assumptions of asymmetric interactions, therefore species were not considered dominant or subordinate to one another (Rota et al., 2016). Data from the two seasons were analyzed separately, and sessions were divided into 14-day sampling occasions, with the winter and autumn seasons having eight and seven sampling occasions respectively. Camera trap photos were cataloged by FCC staff and volunteers, and the date, time, location, and species identification were recorded for each animal detection (Iosif et al., 2022). Covariates were checked for correlation using Pearson’s correlation tests and Pearson’s Chi-squared test (for numerical and factors respectively), those with high correlations  $r > 0.7$  were not included in the same models for the same parameter. We first explored combinations of five detection covariates for species-specific detection probabilities (Table 1) by comparing models with the same marginal occupancy parameterization for each species. Detection covariates were kept the same for all three species as we did not have a biological reason to vary them between species. We also included the latent presence/absence of every other species as species-specific detection covariates (e.g., lynx detection predicted by the presence/absence of wildcat and wolf). Although multispecies occupancy models do not assume asymmetric interactions between species, we wanted to explore the possibility that dominant species could exist in our system and affect the presence of other species. Therefore, we also included species-specific detections of lynx as a function of the latent presence/absence of potentially dominant wolf, and wildcat as a function of lynx and wolf.

From these models, we determined a best model for each season based on Akaike Information Criterion (AIC), using R package *MuMIn* (Bartoń, 2020). We included the top detection covariates in the models exploring marginal occupancy and co-occupancy. We then ran a series of models to assess the marginal occupancy of our three species using environmental and anthropogenic variables (Table 1) that were determined *a priori* and we hypothesized would affect the marginal occupancy of each species. The candidate set of marginal occupancy models was similar for both seasons, models were only removed if variation in covariates was not great enough to allow estimation (i.e. models produced NAs or unreasonable estimates and standard errors). We compared the marginal occupancy models for each season using AIC to identify the best covariates explaining occupancy of each individual species. Using the top covariates from the marginal occupancy analysis, we ran a series of additional candidate models that reflected *a priori* hypotheses regarding pairwise co-occupancy between lynx and wildcat, lynx and wolf, and wildcat and wolf, and compared the models using AIC and biological relevance (Table 2). Due to data limitations (small sample size), we did not implement a three-species co-occupancy parameterization.

## Results

Camera trapping yielded 435 occurrences of all three species in winter and 353 occurrences in autumn, with 6459 and 7083 trap nights for winter and autumn, respectively. We obtained a total of 195 and 179 occurrences of lynx, 69 and 66 occurrences of wildcat, and 171 and 108 occurrences of wolf for the winter and autumn seasons, respectively.

### *Marginal occupancy*

Mean occupancy for both seasons was highest for lynx (winter [ $\Psi = 0.76$  95% CI: 0.42-0.92], autumn [ $\Psi = 0.71$  CI: 0.38-0.84]) and wolf (winter [ $\Psi = 0.60$  CI: 0.34-0.78], autumn [ $\Psi = 0.81$  CI: 0.25-0.95]) and lowest for wildcat (winter [ $\Psi = 0.40$  CI: 0.19-0.63], autumn [ $\Psi = 0.52$  CI: 0.17-0.78]) (Figure A1). We found that both marginal and co-occupancy predictors for lynx, wildcat, and wolf varied between seasons. In winter, local road density was negatively associated with marginal occupancy of wolf (Figure 2C) and positively associated with marginal occupancy of lynx (Figure 2A), while wildcats occupancy decreased with increased

altitude (Figure 2B). However, in autumn, marginal occupancy of wolf decreased with terrain ruggedness (Figure 2F), and lynx occupancy increased with forest cover (Figure 3D) while wildcat occupancy decreased with forest cover (Figure 3E).

### *Co-occupancy*

We also found differences in predictors of co-occupancy between seasons for both lynx-wolf and wildcat-wolf co-occupancies. In winter, lynx-wolf and wildcat-wolf co-occupancy were predicted by forest cover (Fig 3 B, C), but in autumn, co-occupancy for both pairs were predicted by terrain ruggedness (Fig 3 E, F). Lynx-wildcat co-occupancy was predicted by terrain ruggedness for both winter and autumn seasons and was positively associated with terrain ruggedness in both winter and autumn (Fig 3 A, D), but in autumn the relationship was less linear (Fig 3D). In contrast, both lynx-wolf and wildcat-wolf co-occupancy were negatively associated with terrain ruggedness in autumn (Fig 3 E, F). In winter, wildcat-wolf co-occupancy was negatively associated with forest cover while lynx-wolf co-occupancy was positively associated with forest cover, but only at >75% forest cover (Fig 3 E, F).

### *Conditional occupancy*

In the winter season, we found that occupancy probabilities of all three species were higher when another species was present, regardless of the species (Fig 4). This suggest that carnivore species may aggregate in certain habitats during winter, potentially driven by prey availability. However, the occupancy probability of wildcat, decreased with increasing forest cover when either lynx or wolf were present (Fig 4), potentially a signal for mesopredator exclusion by apex predators in area of higher suitability. Similarly, in autumn, all species tended to co-occur, but this relationship was dependent on terrain ruggedness. Occupancy probabilities for both felids, lynx and wildcat, increased with terrain ruggedness when the other felid species was present, and decreased when the other species was absent (Fig 5). We observed the inverse relationship for both felids when considering the presence/absences of wolf, such that occupancy probabilities for lynx and wildcat decreased with increased terrain ruggedness when wolf were present and showed a positive relationship with terrain ruggedness when wolf were absent (Fig 5). The presence of lynx and wildcat appeared to have no effect on wolf occupancy.

### *Detection probabilities*

For both seasons, the models that included that latent presence/absence of a potentially dominant species as a detection covariate performed significantly better than those that did not ([?]AIC > 5). The top models for each season did not vary in their detection covariates; both models included distance to stream and the latent presence/absence of all species as species specific detection covariates. For both seasons, lynx, wildcat, and wolf detections were positively associated with the presence of the other two species (Table A1).

## **Discussion**

Our study is the first to assess carnivore intraguild interactions in an intact Eastern European carnivore community. We used a multi-species occupancy modeling approach (Rota et al., 2016) to determine predictors and seasonal differences of occupancy and co-occupancy for lynx, wildcats, and wolf in the Romanian Carpathians. Our results indicate that while there are seasonal differences in predictors of occupancy and co-occupancy of the three species, co-occurrence of the three species in our study area is high, and is dependent on the existence of continuous, relatively undisturbed forest ecosystems.

### *Determinants of occupancy*

In winter, local road density was the most important predictor of occupancy for wolf, with higher road density associated with a lower probability of wolf occupancy (Fig 2C). This corroborates findings from Jedrzejewski et al. (2004) in northern Poland where wolf had higher occupancy in less disturbed or less fragmented forests. In our study area, the proportion of forest was not an important predictor of wolf occupancy in either season, even though multiple studies have found it to be an important habitat characteristic for wolf (Jedrzejewski et al., 2004; Zlatanova & Popova, 2013) This may be due to the characteristics of our study

area which is heavily forested (mean proportion forest = 0.78 and 0.75 for winter and autumn monitoring sessions, respectively), thus forest cover is not a limitation to wolf occurrence. In autumn, terrain ruggedness was the most important predictor of wolf occupancy; when terrain ruggedness index was  $>200$  (moderately to highly rugged areas the probability of wolf occupancy declined steeply (Figure 2F). This can be explained by the fact that wolf's main prey source in Romania, wild boar ((Promberger–Fürpass, 2004; Sin et al., 2019) was documented to prefer less fragmented areas with large beech forest stands in autumn and early winter (Fonseca, 2008). Additionally, red and roe deer, which are also important prey for wolves, are known to move after the rut season (November - December) to more marginal, less topographically-fragmented areas that provide connectivity to the lower winter grounds (Zweifel-Schielly et al., 2009). Proportion of forest was a positive predictor of lynx occupancy in autumn, which corroborates other studies that found that lynx occurrence in the Carpathians decreased at low levels of forest cover (Rozyłowicz et al., 2010). Local road density was also an important predictor of lynx occupancy in winter, with lynx occupancy positively associated with road density (Figure 2A). While not heavily documented within the *Lynx* genus, other felid species have been known to use roads as travel corridors and for hunting and movement within their home range (Bailey, 1993; Bragin, 1986; Gordon & Stewart, 2007; Kerley et al., 2002; Matyushkin, 1977; Rabinowitz et al., 1987). Our results suggest that, in winter, Eurasian lynx are more likely to occupy areas with higher densities of local logging roads; these roads, which in our area are mostly unpaved, dirt roads, may provide easier access to resources within lynx home ranges due to decreased complexity of terrain and decreased snow depth/harder snowpack from vehicle travel. We did not observe this relationship with wildcat, however. Rather, there was a slightly negative relationship between density of local roads and wildcat occupancy in autumn (Figure 2E) which could be an artifact of body size; most documented examples of felids utilizing roads for movement within their home ranges was with larger bodied species ( $>11$  kg). We also did not observe this relationship in winter however, this is likely an outcome of the importance of altitude for wildcat occupancy, which has a strong negative relationship (Figure 2B). Higher altitudes are associated with greater snow depth, and while lynx are well adapted to move in deep snow and altitude was not important for lynx occupancy, wildcats have physical limitations that make travel through deep snow more difficult. A study in Switzerland had similar findings whereby wildcats moved to areas free of snow in winter and spring and moved back to high elevations in summer (Mermod & Liberek, 2002). Similarly, in North America, the relationship between Canadian lynx (*Lynx canadensis*) and bobcat (*Lynx rufus*), is mediated by snowpack, with the distribution of the smaller-bodied species, the bobcat, being limited by snow depth at the northern edge of its range (Morin et al., 2020; Reed et al., 2017). Our results for marginal occupancy of lynx, wildcats, and wolf provide insights into both habitat selection and spatial relations for these elusive carnivores in Romania. Our results suggest lynx may use roads for movement and hunting, a practice common for other felids of similar body size, but not described in this species. Additionally, we provide further support for previous findings on habitat selection and occupancy for these three European terrestrial predators.

### *Determinants of co-occupancy*

In both winter and autumn, co-occupancy for lynx and wolf was relatively high indicating that both species have similar habitat requirements. In winter there was a weak effect of forest cover on the co-occupancy of lynx and wolf; co-occupancy increased slightly with proportion of forest cover  $>0.75$ . Increased forest cover may result in an increase in prey availability, which would yield higher co-occupancy between lynx and wolf which share some prey items (primarily roe deer, red deer calves), and the main prey species for wolf, the wild boar (*Sus scrofa*) (Sin et al., 2019) shares similar habitat with red and roe deer. In autumn, terrain ruggedness was a negative predictor of co-occupancy for lynx and wolf, such that predicted co-occupancy was  $\sim 0$  for the highest values of terrain ruggedness. This relationship is driven by the negative relationship between marginal occupancy for wolf and terrain ruggedness, which is also related to prey availability (see above) (Figure 2C). Because marginal occupancy for wolf is  $\sim 0$  at high terrain ruggedness, co-occupancy for lynx and wolf is low as well. Additionally, co-occupancy between wolf and wildcat decreased with terrain ruggedness in autumn (Fig 3F) due to the low marginal occupancy for wolf at high terrain ruggedness. In winter however, co-occupancy of wolf and wildcat was predicted by proportion of forest such that increasing

forest cover resulted in lower co-occupancy (Fig 3C). In both seasons, the co-occupancy of lynx and wildcat increased with terrain ruggedness, but the relationship was stronger in winter (Fig 3A, D). This relationship also provides further evidence that the negative relationship observed for lynx and wolf co-occupancy and terrain ruggedness was driven by wolf marginal occupancy.

### *Management and conservation implications*

The positive effect of wolf and lynx presences on detection of one another, high levels of co-occupancy in winter, and high levels of conditional occupancy in both seasons (higher occupancy probability when other species is present), for lynx and wolf provide little evidence of interference competition between these apex predators. This corroborates findings from other studies assessing interactions between co-occurring felids and canids that overlap in resource use. For example, Wikenros et al. (2010) assessed the effects of a recolonizing wolf population on resident lynx in Sweden and found that lynx demographics were unaffected by the presence of wolf. A greater body of literature focuses on the interactions between two similar species, the sympatric bobcat (*Lynx rufus*) and coyote (*Canis latrans*), in North America. A review of literature on this topic reveals a similar story to that of lynx and wolf in the Carpathians, whereby bobcats and coyotes coexist and exhibit little interference competition in most of their range likely due to specialization on different prey and mediation via use of heterogeneous habitats (Dyck et al., 2022). Efforts to reintroduce or augment Eurasian lynx populations also exist in Europe (e.g., Slovenia, Croatia; <https://www.lifelynx.eu/>). In this context, resident wolf populations should not affect the introduction efforts given that prey base can support both species, and releases occur in highly forested but less topographically fragmented areas. Additionally, our findings also suggest that apex predators have little negative effects on the mesocarnivore, wildcat. This information is useful for management given that wolves are recolonizing their former range in Europe (Chapron et al., 2014). Our findings suggest that wolf would not have negative impacts on wildcat given enough suitable habitat is available, due to low overlap in diet. In summary, studying intraguild interactions in an intact system has enabled us to observe and quantify intraspecific interactions among carnivores where they have co-existed and co-evolved for centuries. This provides insight into their potential long-term dynamics for areas where they are recovering naturally or recovering through rewilding efforts. While our study did not include the summer season, our results from two separate and partially overlapping autumn and winter seasons suggest that competition between lynx, wildcat and wolf is low. However, additional information on the richness and abundance of the prey base, and the spatial and temporal relations between predators and their prey can augment these findings and provide additional management insights in the context of rewilding.

### **Authorship**

MD, VP, RI, and BPF conceived the ideas and designed methodology; RI collected the data; MD analyzed the data; MD and VP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### **Acknowledgements**

We thank Piatra Craiului National Park Administration and the Hunting Associations Bârsa, Jderul, and GTS Muntenia, for permissions to undertake field work. We thank Liviu Ungureanu, Călin Șerban, and rangers of the Foundation Conservation Carpathia for help with camera deployment and checking. Field work was funded by the OAK Foundation grant number OCAY-11-136 and by the European Commission through the Operational Programme 'Environment', grant number SMIS 102086. VDP was partially supported by a grant from the Romanian National Authority for Scientific Research (PN-III-P1-1.1-TE-2019-0835). Travel for MD to Romania was provided by the Ohio University College of Arts and Sciences. Authors have no conflict of interest to declare.

### **References**

Bailey, T. N. (1993). The African Leopard: Ecology and Behavior of a Solitary Felid. In *The African Leopard*. Columbia University Press. <https://doi.org/10.7312/bail90198>

- Bartoń, K. (2020). *MuMIn: Multi-Model Inference* [R package version 1.43.17]. <https://CRAN.R-project.org/package=MuMIn>
- Beschta, R. L., & Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* , 142 (11), 2401–2414. <https://doi.org/10.1016/j.biocon.2009.06.015>
- Bragin, A. P. (1986). *Population characteristics and social-spatial patterns of the tiger on the eastern macro-slope of the Sikhote-Alin mountain range, U.S.S.R.* [Master Thesis]. Pacific Institute of Geography.
- Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedř, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., . . . Boitani, L. (2014). Recovery of large carnivores in Europe’s modern human-dominated landscapes. *Science* , 346 (6216), 1517–1519. <https://doi.org/10.1126/science.1257553>
- Crooks, K. R. (2002). Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation. *Conservation Biology* , 16 (2), 488–502. JSTOR.
- Dechner, A., Flesher, K. M., Lindell, C., Oliveira, T. V. de, & Maurer, B. A. (2018). Determining carnivore habitat use in a rubber/forest landscape in Brazil using multispecies occupancy models. *PLOS ONE* , 13 (4), e0195311. <https://doi.org/10.1371/journal.pone.0195311>
- Dorresteijn, I., Schultner, J., Nimmo, D. G., Fischer, J., Hanspach, J., Kuemmerle, T., Kehoe, L., & Ritchie, E. G. (2015). Incorporating anthropogenic effects into trophic ecology: Predator–prey interactions in a human-dominated landscape. *Proceedings of the Royal Society* ,282 , 8.
- Dyck, M. A., Wyza, E., & Popescu, V. D. (2022). When carnivores collide: A review of studies exploring the competitive interactions between bobcats *Lynx rufus* and coyotes *Canis latrans*. *Mammal Review* , 52 (1), 52–66. <https://doi.org/10.1111/mam.12260>
- Effiom, E. O., Nuñez-Iturri, G., Smith, H. G., Ottosson, U., & Olsson, O. (2013). Bushmeat hunting changes regeneration of African rainforests. *Proceedings of the Royal Society B: Biological Sciences* ,280 (1759), 20130246. <https://doi.org/10.1098/rspb.2013.0246>
- Fiske, I., & Chandler, R. (2011). Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software* ,43 (10). <https://doi.org/10.18637/jss.v043.i10>
- Fonseca, C. (2008). Winter habitat selection by wild boar *Sus scrofa* in southeastern Poland. *European Journal of Wildlife Research* ,54 , 361–366. <https://doi.org/10.1007/s10344-007-0144-9>
- Gordon, C. H., & Stewart, A. E. (2007). Use of Logging Roads by Clouded Leopards. *Cat News* , 47 , 12–13.
- Iosif, R., Popescu, V. D., Ungureanu, L., Șerban, C., Dyck, M. A., & Promberger-Fürpass, B. (2022). Eurasian lynx density and habitat use in one of Europe’s strongholds, the Romanian Carpathians. *Journal of Mammalogy* , gyab157. <https://doi.org/10.1093/jmammal/gyab157>
- Jedrzejewski, W., Niedzialkowska, M., Nowak, S., & Jedrzejewska, B. (2004). Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland. *Diversity & Distributions* , 10 (3), 225–233. <https://doi.org/10.1111/j.1366-9516.2004.00073.x>
- Jedrzejewski, W., Schmidt, K., Okarma, H., & Kowalczyk, R. (2002). Movement pattern and home range use by the Eurasian lynx in Białowieża, Primeval Forest (Poland). *Annales Zoologici Fennici* , 39 , 29–41.
- Jørgensen, D. (2015). Rethinking rewilding. *Geoforum* , 65 , 482–488. <https://doi.org/10.1016/j.geoforum.2014.11.016>
- Kaczensky, P., Chapron, G., Von Arx, M., Huber, D., Andrén, H., & Linnell, J. (2013). *Status, management and distribution of large carnivores-bear, lynx, wolf & wolverine-in Europe* . Verlag nicht ermittelbar.

- Kerley, L. L., Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Quigley, H. B., & Hornocker, M. G. (2002). Effects of Roads and Human Disturbance on Amur Tigers. *Conservation Biology* , 16 (1), 97–108. <https://doi.org/10.1046/j.1523-1739.2002.99290.x>
- Lamb, C. T., Ford, A. T., McLellan, B. N., Proctor, M. F., Mowat, G., Ciarniello, L., Nielsen, S. E., & Boutin, S. (2020). The ecology of human–carnivore coexistence. *Proceedings of the National Academy of Sciences* , 201922097. <https://doi.org/10.1073/pnas.1922097117>
- Lombardi, J. V., MacKenzie, D. I., Tewes, M. E., Perotto-Baldivieso, H. L., Mata, J. M., & Campbell, T. M. (2020). Co-occurrence of bobcats, coyotes, and ocelots in Texas. *Ecology and Evolution* , 10 (11), 4903–4917.
- Matyushkin, E. N. (1977). The choice of route and territory used by the Amur tiger (according to winter tracking data). *Voprosy Teriologii M: (In Russian)* , 146–178.
- Mermod, C. Ph., & Liberek, M. (2002). The role of snowcover for European wildcat in Switzerland. *Zeitschrift Fur Jagdwissenschaft* , 48 (1), 17–24. <https://doi.org/10.1007/BF02192388>
- Morin, S. J., Bowman, J., Marrotte, R. R., & Fortin, M.-J. (2020). Fine-scale habitat selection by sympatric Canada lynx and bobcat. *Ecology and Evolution* , 10 (17), 9396–9409. <https://doi.org/10.1002/ece3.6626>
- Palomares, F., & Caro, T. M. (1999). Interspecific Killing among Mammalian Carnivores. *The American Naturalist* , 153 (5), 492–508. <https://doi.org/10.1086/303189>
- Popescu, V. D., Artelle, K. A., Pop, M. I., Manolache, S., & Rozyłowicz, L. (2016). Assessing biological realism of wildlife population estimates in data-poor systems. *Journal of Applied Ecology* , 53 (4), 1248–1259. <https://doi.org/10.1111/1365-2664.12660>
- Rabinowitz, A., Andau, P., & Chai, P. P. K. (1987). The clouded leopard in Malaysian Borneo. *Oryx* , 21 (2), 107–111. <https://doi.org/10.1017/S0030605300026648>
- Reed, G. C., Litvaitis, J. A., Ellingwood, M., Tate, P., Broman, D. J. A., Siren, A. P. K., & Carroll, R. P. (2017). Describing habitat suitability of bobcats (*Lynx rufus*) using several sources of information obtained at multiple spatial scales. *Mammalian Biology* , 82 (1), 17–26. <https://doi.org/10.1016/j.mambio.2016.10.002>
- Riley, S. J., DeGloaria, S. J., & Elliot, R. (n.d.). Index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* , 5 (1–4), 23–27.
- Ripple, W. J., & Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation* , 133 (4), 397–408. <https://doi.org/10.1016/j.biocon.2006.07.002>
- Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation* , 145 (1), 205–213. <https://doi.org/10.1016/j.biocon.2011.11.005>
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and Ecological Effects of the World’s Largest Carnivores. *Science* , 343 (6167), 1241484–1241484. <https://doi.org/10.1126/science.1241484>
- Rota, C. T., Ferreira, M. A. R., Kays, R. W., Forrester, T. D., Kalies, E. L., McShea, W. J., Parsons, A. W., & Millsbaugh, J. J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution* , 7 (10), 1164–1173. <https://doi.org/10.1111/2041-210X.12587>
- Rozyłowicz, L., Chiriac, S., Sandu, R., & Manolache, S. (2010). The habitat selection of a female lynx (*Lynx lynx*) in the northwestern part of the Vrancea Mountains, Romania. *North-Western Journal of Zoology* , 6 , 122–127.
- Ruiz-Villar, H., Jubete, F., Revilla, E., Roman, J., Urrea, F., Lopez-Bao, J. V., & Palomares, F. (2021). Like cat and fox: Diurnal interactions between two sympatric carnivores in pastoral landscapes of NW Spain.

*European Journal of Wildlife Research* , 67 (1), 16. <https://doi.org/10.1007/s10344-021-01469-3>

Salvatori, V., Okarma, H., Ionescu, O., Dovhanych, Y., Find'o, S., & Boitani, L. (2002). Hunting legislation in the Carpathian Mountains: Implications for the conservation and management of large carnivores. *Wildlife Biology* , 8 (1), 3–10. <https://doi.org/10.2981/wlb.2002.002>

Schmidt, K., Jedrzejewski, W., Okarma, H., & Kowalczyk, R. (2009). Spatial interactions between grey wolves and Eurasian lynx in Białowieża Primeval Forest, Poland. *Ecological Research* , 24 (1), 207–214.

Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world | Science. *Science* , 345 (6195), 406–412.

Sin, T., Gazzola, A., Chiriac, S., & Rîşnoveanu, G. (2019). Wolf diet and prey selection in the South-Eastern Carpathian Mountains, Romania. *PLOS ONE* , 14 (11), e0225424. <https://doi.org/10.1371/journal.pone.0225424>

Svenning, J.-C., Pedersen, P. B. M., Donlan, C. J., Ejrnæs, R., Faurby, S., Galetti, M., Hansen, D. M., Sandel, B., Sandom, C. J., Terborgh, J. W., & Vera, F. W. M. (2016). Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences* , 113 (4), 898–906. <https://doi.org/10.1073/pnas.1502556112>

Van der Weyde, L. K., Mbisana, C., & Klein, R. (2018). Multi-species occupancy modelling of a carnivore guild in wildlife management areas in the Kalahari. *Biological Conservation* , 220 , 21–28. <https://doi.org/10.1016/j.biocon.2018.01.033>

Wikenros, C., Liberg, O., Sand, H., & Andrén, H. (2010). Competition between recolonizing wolves and resident lynx in Sweden. *Canadian Journal of Zoology* , 88 (3), 271–279. <https://doi.org/10.1139/Z09-143>

Woodroffe, R., & Ginsberg, J. R. (1998). Edge Effects and the Extinction of Populations Inside Protected Areas. *Science* , 280 (5372), 2126–2128. <https://doi.org/10.1126/science.280.5372.2126>

Zimmermann, F., & Raoul, F. (2011). *Spatio-temporal interactions between sympatric felids in the Swiss Jura Mountains* (p. 22).

Zlatanova, D., & Popova, E. (2013). Habitat variables associated with wolf (*Canis lupus* l.) distribution and abundance in Bulgaria. *Bulgarian Journal of Agricultural Science* , 19 (2), 262–266.

Zweifel-Schielly, B., Kreuzer, M., Ewald, K. C., & Suter, W. (2009). Habitat Selection by an Alpine Ungulate: The Significance of Forage Characteristics Varies with Scale and Season. *Ecography* , 32 (1), 103–113.

Table 1. Names and descriptions of detection and occupancy covariates used in multispecies occupancy modeling for Eurasian lynx (*Lynx lynx* ), wildcat (*Felis silvestris* ), and grey wolf (*Canis lupus* ) in the Romanian Carpathians, 2018-2020.

	Name	Description	Type	Summary Data
<i>Detection Covariates</i>	Distance to stream	Distance from camera to the nearest permanent stream recorded in meters (extracted using GIS)	Numeric variable ranging from 0-1,140m (winter) and 0-1,300m (autumn)	Mean: winter = 237m autumn = 284m
	Distance to settlement	Distance from camera to the nearest village recorded in meters (extracted using GIS)	Numeric variable ranging from 224-17,058m (winter) and 0-17,786m (autumn)	Mean: winter = 5,413m autumn = 5,155m

	Name	Description	Type	Summary Data
<i>Occupancy Covariates</i>	Distance to road	Distance from camera to the nearest paved road recorded in meters (extracted using GIS)	Numeric variable ranging from 0-1,302 (winter) and 0- 3,059m (autumn)	Mean: winter = 974m autumn = 1,077m
	Impact	Anthropogenic impact in the immediate vicinity of the camera (recorded by personnel in the field)	Binary variable where 0 = no visible disturbance and 1 = isolated buildings, logging, or villages	winter: 0=55, 1=9 autumn: 0=63, 1=13
	Position	Camera position on the landscape (recorded by personnel in the field)	Categorical variable with four levels: ridge, mid-slope, bottom, valley	winter: ridge (23), midslope (24), bottom (5), valley (12) autumn: ridge (29), midslope (29), bottom (10), valley (8)
	Aspect	Exposure of camera trap location (recorded by personnel in the field)	Categorical variable with four levels: north, south, east, west	winter: north (15), south (25), east (16), west (8) autumn: north (21), south (19), east (20), west (16)
	Local road density	Density of roads (km/km <sup>2</sup> ) at the grid cell level	Numeric variable ranging from 0.21-0.34 km/km <sup>2</sup> (winter) and 0.22-0.34 (autumn)	Mean: winter = 0.27 autumn = 0.27
	Terrain Ruggedness Index (TRI)	TRI calculated in R via package ‘ <i>spatialEco</i> ’ using a digital elevation model with resolution 80x80 m and two moving window sizes: 5 cells (covering an area of 0.16 km <sup>2</sup> )	Numeric variable ranging from 84-494 (winter) and (autumn); with recommended classification ranges 81-116 - nearly level surface. 117-161 - slightly rugged surface. 162-239 - intermediately rugged surface. 240-497 - moderately rugged surface.	Mean: winter = 223.5 autumn = 217.8

Name	Description	Type	Summary Data
Proportion forest	Proportion of forest at the grid cell level (extracted from Corine Land Cover 2016 dataset [100x100 m resolution] using GIS)	Numeric variable ranging from 0.1-1.0 for both winter and autumn	Mean: winter = 0.78 autumn = 0.75
Altitude	Altitude of the camera location recorded in meters using GPS by field personnel	Numeric variable ranging from 663-1,600m (winter) and 788-1,617m (autumn)	Mean: winter = 1,153m autumn = 1,182m

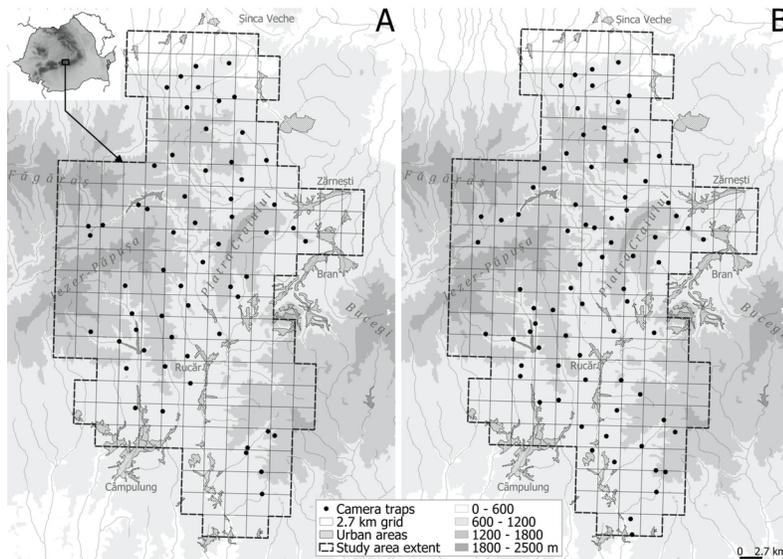


Figure 1. Study area for winter (A) and autumn (B) sessions and the locations of 64 (winter) and 76 (autumn) camera trap stations in Romanian Carpathians, Romania used for camera trap surveys. Sessions lasted from December 17<sup>th</sup>, 2018, to March 31<sup>st</sup>, 2019 (winter) and October 9<sup>th</sup>, 2019 to January 15<sup>th</sup>, 2020 (autumn).

### Hosted file

image2.emf available at <https://authorea.com/users/459659/articles/555863-dracula-s-menagerie-a-multispecies-occupancy-analysis-of-lynx-wildcat-and-wolf-in-the-romanian-carpathians>

Figure 2. Marginal occupancy probabilities for Eurasian lynx (*Lynx lynx*), European wildcat (*Felis silvestris*), and grey wolf (*Canis lupus*) predicted by the top model for each season and plotted as a function of the marginal occupancy covariates for each species. All variables not included in the plot are assumed fixed at their observed mean. Ribbons represent  $\pm 1$  SE; blue represents the winter season and red represents the autumn season.

### Hosted file

image3.emf available at <https://authorea.com/users/459659/articles/555863-dracula-s-menagerie-a-multispecies-occupancy-analysis-of-lynx-wildcat-and-wolf-in-the-romanian-carpathians>

Figure 3. Co-occupancy probabilities for all pairwise combinations of Eurasian lynx (*Lynx lynx*), European wildcat (*Felis silvestris*), and grey wolf (*Canis lupus*) predicted by the top model for each season (winter = A-C, autumn = D-F) and plotted as a function of the co-occupancy occupancy covariates for each species combination. All variables not included in the plot are assumed fixed at their observed mean.

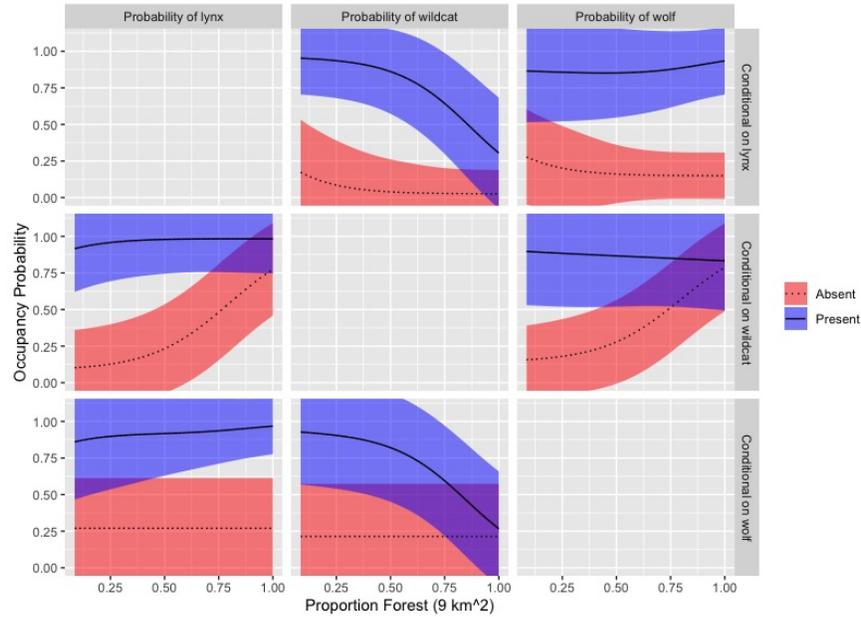


Figure 4. Occupancy probability of lynx, wildcat, and wolf for the winter session, conditional on the presence or absence of each of the other species and proportion of forest in surrounding 9 km. The occupancy probability of the species in each column is conditional on the presence or absence of the species in each row. Lines represent the mean and ribbons represent  $\pm 1$  SE. All variables not included in the plot are assumed fixed at their observed mean.

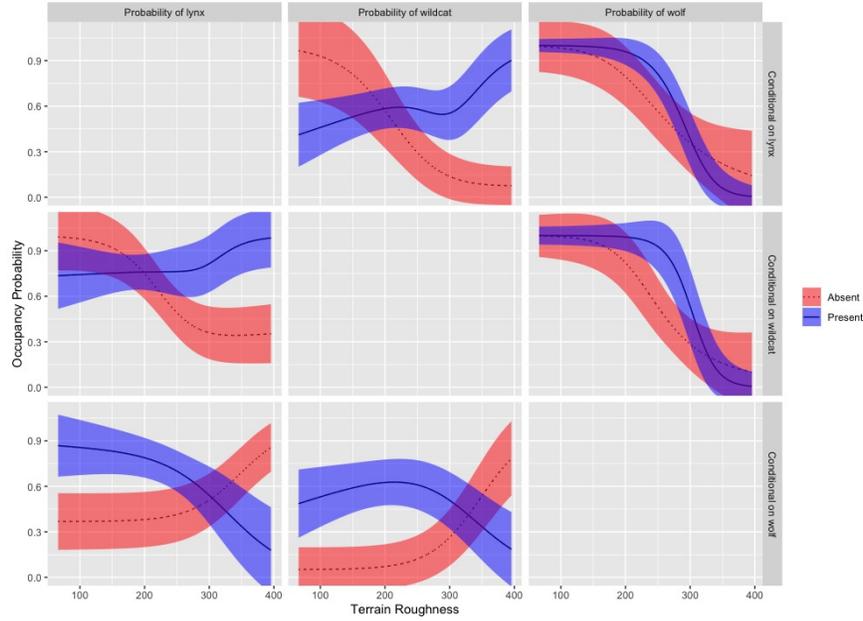


Figure 5. Occupancy probability of lynx, wildcat, and wolf for the autumn session, conditional on the presence or absence of each of the other species and terrain ruggedness.

## Appendix

Table A1. Estimates, standard errors (SE), test statistics (Z), and p-values (p) for detection covariates in top multi-species occupancy models for Eurasian lynx (*Lynx lynx*), European wildcat (*Felis silvestris*), and grey wolf (*Canis lupus*) in winter and autumn sessions in the Romanian Carpathians, Romania, 2018-202.

Species/Season	Covariate	Estimate	SE	z	p
<i>Lynx/Winter</i>	Wolf presence	1.188	0.292	4.07	>0.001
	Wildcat presence	0.526	0.364	1.45	0.148
	Distance to stream	0.207	0.125	1.65	0.099
<i>Wildcat/Winter</i>	Lynx presence	0.432	0.385	1.12	0.262
	Wolf presence	0.095	0.450	0.21	0.833
	Distance to stream	-0.215	0.214	-1.00	0.315
<i>Wolf/Winter</i>	Lynx presence	1.164	0.304	3.83	>0.001
	Wildcat presence	0.305	0.461	0.66	0.509
	Distance to stream	-0.549	0.174	-3.15	0.001
<i>Lynx/Autumn</i>	Wolf presence	0.614	0.305	2.00	0.044
	Wildcat presence	0.745	0.403	1.85	0.065
	Distance to stream	0.010	0.135	0.08	0.938
<i>Wildcat/Autumn</i>	Lynx presence	0.907	0.425	2.13	0.033
	Wolf presence	0.511	0.580	0.88	0.379
	Distance to stream	-1.214	0.352	-3.45	>0.001
<i>Wolf/Autumn</i>	Lynx presence	0.728	0.307	2.38	0.017
	Wildcat presence	0.045	0.503	0.09	0.928
	Distance to stream	0.041	0.137	0.29	0.768

## Hosted file

image6.emf available at <https://authorea.com/users/459659/articles/555863-dracula-s-menagerie-a-multispecies-occupancy-analysis-of-lynx-wildcat-and-wolf-in-the-romanian-carpathians>

Figure A1. Predicted mean occupancy probabilities (with 95% confidence intervals) for Eurasian lynx (*Lynx lynx*), European wildcat (*Felis silvestris*), and grey wolf (*Canis lupus*) for winter (blue) and autumn (red) sessions in the Romanian Carpathians, Romania, 2018-2020.

