

Bottom-up rather than top-down mechanisms determine mesocarnivore interactions in Norway

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Abstract

Interactions among coexisting mesocarnivores can be influenced by different factors such as the presence of large carnivores, land-use, environmental productivity, or human disturbance. Disentangling the relative importance of bottom-up and top-down processes can be challenging, but it is important for biodiversity conservation and wildlife management. The aim of this study was to assess how the interactions among mesocarnivores (red fox *Vulpes vulpes*, badger *Meles meles*, and pine marten *Martes martes*) are affected by large carnivores (Eurasian lynx *Lynx lynx* and wolf *Canis lupus*), land cover variables (proportion of agricultural land and primary productivity), and human disturbance, as well as how these top-down and bottom-up mechanisms are influenced by season. We analyzed three years (2018-2020) of camera trapping data from Norway and used structural equation models to assess hypothesized networks of causal relationships. Our results show that land cover variables are stronger predictors of mesocarnivore activity than large carnivores in Norway. This might be caused by a combination of low density of large carnivores in an unproductive ecosystem with strong seasonality. Additionally, all mesocarnivores showed positive interactions among each other, which were stronger in winter. The prevalence of positive interactions among predators might indicate a tendency to use the same areas and resources combined with weak interference competition. Alternatively, it might indicate some kind of facilitative relationship among species. Human disturbance had contrasting effects for different species, benefiting the larger mesocarnivores (red fox and badger) probably through food subsidization, but negatively affecting apex predators (wolf and lynx) and smaller mesocarnivores (pine marten). In a human-dominated world, this highlights the importance of including anthropogenic influences in the study of species interactions.

INTRODUCTION

The study of interspecific interactions among mammalian carnivores is fundamental to conservation biology (Linnell and Strand, 2000), but the factors influencing these interactions can be complex and difficult to disentangle. Interactions among coexisting species can potentially have large consequences for community structure by influencing the demography, distribution, and behavior of the species within the community (de Satge et al., 2017, Grassel et al., 2015, St-Pierre et al., 2006). The potential top-down effect of large carnivores and their importance in maintaining ecosystem functioning has been widely recognized (Estes et al., 2011, Ripple et al., 2014, Ritchie and Johnson, 2009). Declines in the numbers and distribution of large carnivores due to human persecution and habitat loss in many regions has led to changes in species interactions and food webs, highlighting their ecological role in ecosystems worldwide (Ripple et al., 2014). One commonly proposed outcome following the loss of apex predators is the increase in the abundance of mesopredators. This phenomenon is known as “mesopredator release” (Prugh et al., 2009), and it can potentially have negative impacts on prey species through increased predation from mesopredators, as well as on other smaller carnivores through intraguild predation.

Even though negative interspecific interactions among carnivores seem to be widespread, there is also a growing recognition of the importance of positive interactions in structuring predator communities (Prugh and Sivy, 2020). Large carnivores can facilitate mesocarnivores by providing resource subsidies in the form of carrion (Pereira et al., 2014, Prugh and Sivy, 2020). Scavenging is a widespread behavior that has clear implications for food web structure and population dynamics (Mellard et al., 2021). Carrion subsidies can be important food sources in areas where several opportunistic mesocarnivores coexist (Sivy et al., 2018), or when other food sources are scarce (Jedrzejewski and Jedrzejewska, 1992, Killengreen et al., 2011). Interactions between large carnivores and mesocarnivores can therefore range from facilitation to suppression, and both may even occur simultaneously (Prugh and Sivy, 2020, Wikenros et al., 2017). In addition, the direction and strength of these interactions may be scale dependent (Sivy et al., 2017).

Interactions among predators in human-dominated landscapes can be different from those occurring in undisturbed habitats. Furthermore, ecological phenomena such as mesopredator release can be difficult to separate from land-use changes (Prugh et al., 2009). Mesopredator numbers tend to increase in human-modified habitats, as a response to higher resource availability, while apex predators are more likely to disappear due to direct persecution and habitat loss (Prugh et al., 2009). Unfortunately, large-scale experimental approaches that might help disentangle the relative importance of top-down versus bottom-up effects are rarely logistically possible (Nilsen et al., 2020). However, modeling approaches based on large-scale observational data can be useful (Dorresteijn et al., 2015, Elmhagen and Rushton, 2007). Anthropogenic influence on food webs may operate through diverse processes and influence multiple trophic levels simultaneously. For example, humans can decrease predator density directly through hunting, but they can also trigger behavioral responses at both spatial and temporal scales (e.g., by changing predators' habitat use and activity patterns) (Milner et al., 2007, Ordiz et al., 2012, Ordiz et al., 2021), potentially causing top-down cascades that may affect species at lower trophic levels. On the other hand, humans may also influence predators through bottom-up processes via food subsidization (Gompper and Vanak, 2008, Newsome et al., 2015, Newsome et al., 2014), or by enhancing forage availability of herbivores, thus increasing prey density (Muhly et al., 2013). The effect of such food subsidies may be particularly relevant for systems with low productivity (Melis et al., 2009).

Ecosystem productivity and seasonal change in resource availability can determine the relative strength and direction of trophic interactions (Elmhagen and Rushton, 2007, Ritchie and Johnson, 2009, Stoessel et al., 2018). In particular, Stoessel et al. (2018) found that harsh winter conditions and food scarcity increased the importance of bottom-up constraints on species interactions as compared to top-down factors in an arctic ecosystem. Furthermore, Elmhagen and Rushton (2007) found a stronger degree of bottom-up rather than top-down control of red foxes (*Vulpes vulpes*) in low productivity ecosystems in Sweden. These studies highlight the importance of considering both top-down and bottom-up processes when studying mesopredator interspecific interactions in ecosystems with strong seasonality. The relevance of such insights is of special importance in the face of climate change, which will alter seasonal conditions and species interactions.

Several large carnivore species are now recovering across large parts of Europe (Chapron et al., 2014), with potential cascading effects through the entire carnivore community. In Southern Spain for example, the recovery of the Iberian lynx (*Lynx pardinus*) exerted a strong suppression control of two sympatric mesocarnivores (Burgos et al., 2023). However, the strength of this top-down effect differed for different mesocarnivore species, and it was modulated by prey availability. In Scandinavia, the recovery of Eurasian lynx (*Lynx lynx*) and wolves (*Canis lupus*) in human-modified ecosystems is raising a key question regarding the ecological role that large carnivores play in these anthropogenic landscapes and their importance relative to the effects of humans on mesocarnivores (Dorresteijn et al., 2015, Kuijper et al., 2016). There is some evidence that the recovering lynx populations in Scandinavia significantly limit mesocarnivore populations such as red fox in some areas (Elmhagen et al., 2010, Fedriani et al., 1999, Helldin et al., 2006). This top-down effect has also been observed at a continental scale in Eurasia (Pasanen-Mortensen et al., 2013). However, the presence of lynx may also provide a stable food supply in the form of carrion for red foxes (Helldin and Danielsson, 2007) and other mesocarnivores, which can be vital during winter (Needham et al., 2014). Mesocarnivores are also strongly influenced by anthropogenic food supplies, and red fox and badger (*Meles meles*) densities have been found to be higher, and their home ranges smaller, in urban and suburban

areas compared to semi-natural habitats (Šálek et al., 2015). An increase in red fox numbers might in turn have negative effects on smaller carnivore species, like pine marten (*Martes martes*), through intraguild predation (Lindström et al., 1995).

The aim of this study was to assess how interactions among mesocarnivores are affected by large carnivores, land cover variables (proportion of agricultural land and primary productivity), and human disturbance, as well as how the relative strength of these top-down and bottom-up mechanisms is influenced by season (summer vs winter). The interactions among mesocarnivores were assessed using encounter rates from a national level camera trapping study in Norway. We used three years of camera trapping data to study a carnivore guild that included lynx and wolves as apex predators, red foxes and badgers as dominant mesocarnivores, and pine martens as a subordinate mesocarnivore.

MATERIAL AND METHODS

Study area

We conducted this study within nine different counties in Norway, representing a gradient of landscape productivity and human influence from Troms & Finnmark County in the north (68° N), to Agder County in the south (58° N) (Figure 1). The southern areas are in general more fragmented, with forested areas intermixed with agricultural fields and scattered human settlements, whereas the northern areas are less productive with boreal forests and alpine tundra. Forests are dominated by conifers, mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), intermixed with deciduous species such as birch (*Betula pubescens* and *B. pendula*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), gray alder (*Alnus incana*), and willow (*Salix caprea*), which are more abundant in the south. Mean annual temperatures decrease with latitude, being milder in the south (annual mean temperature 7.8°C in Kristiansand) than in the north (annual mean temperature -0.2°C in Tromsø) (no.climate-data.org), and winter severity (i.e. snow depth and low temperatures) increases with latitude and altitude. Human population densities range from 1642.7 inhabitants per km² in Oslo County to 3.4 inhabitants per km² in Troms & Finnmark (www.ssb.no). Lynx can potentially be found across the entire study area but in higher densities in the southernmost areas. Wolves are restricted to the wolf management zone in southeastern Norway (Figure 1). Wolf density outside the wolf management zone is practically zero, as wolves outside the zone are culled as part of management plans.

Camera trapping

We used three years of data (2018-2020) from 618 camera trap locations as part of an ongoing long-term camera trapping study of lynx (SCANDCAM, viltkamera.nina.no). The SCANDCAM project has volunteer-run camera traps (HC500, HC600, PC800, PC850, PC900 and HP2X, Reconyx, Holmen, Wisconsin, USA), which are distributed with one camera per 50 km² grid cell, covering 30,950 km² in Norway (Figure 1). Local volunteers, in cooperation with trained technicians, placed a minimum of one camera trap inside each grid cell. To maximize the probability of detecting lynx and other predators, the cameras were preferably located on forest roads, trails or natural movement routes for wildlife. Each camera trap was placed 60-120 cm above the ground and aimed at the landscape feature of interest. Memory cards and batteries were switched at least four times a year. All camera traps were set to take a daily time-lapse image at 8 a.m., in addition to being activated by an animal passing, in order to check if the unit functioned correctly and if the field of view was clear. A deep convolutional neural network trained with previous images from the SCANDCAM project was used to classify all images using TensorFlow. All species identifications were in addition manually verified by trained staff and students. All images of humans and vehicles were automatically removed to conform to Norwegian privacy regulations, but we retained information of their passing. A detailed explanation of the pre-processing and classification workflow can be found in Hofmeester et al. (2021).

We calculated species encounter rate as the number of days in which an animal (lynx, wolf, red fox, badger or pine marten) was detected by a camera trap per year and season, corrected for camera effort (i.e., number of days during which the camera trap was active). This encounter rate results from a combination of both local density and activity of predators (Carbone et al., 2001). This is useful for our study because it not only

reflects the number of individuals present, but also the intensity of use of a specific area.

Covariates

All covariates were extracted in ArcGIS (ESRI 2014). We used a Norwegian and a Swedish vegetation map merged together to account for the cameras along the border (Northern Research Institute’s vegetation map, Norway, 30 x 30 m resolution merged with Swedish Corine land cover map Lantmäteriet, Sweden, 25 x 25 m resolution into a 25 x 25-m resolution raster, Mattisson et al., 2013, Ordiz et al., 2015), from which we extracted the proportion of agricultural land. Additionally, we obtained human density (inhabitants/km²) from Statistics Norway as a 250 m resolution raster (www.ssb.no). However, this raster only contained data for urban areas. Given that the cameras were placed at different distances from those areas, we used that data to calculate a proxy for the direct human disturbance at the camera sites. For this, we transformed the raster to a point layer, which we used to predict a planar kernel density map set with bandwidth = 2,000 and cell size = 200 m. We then extracted these two variables (proportion of agricultural land and human disturbance) to a 1-km radius circular buffer around each camera trap.

In order to assess primary productivity, we downloaded the 1-km resolution monthly EVI from the MOD13A3 V061 product (Didan, 2021) using the AppEEARS application (AppEEARS-Team, 2022). We downloaded monthly data for years 2016-2020 and deleted 11 raster cells because of low quality and missing data. We then merged the monthly EVI map layers into one final raster containing average value of overlapping cells. We masked out water to include only terrestrial cells and calculated the mean-EVI for a 10-km radius circular buffer around each camera trap. We used a 10-km buffer for primary productivity in order to focus on the wider region rather than on the micro camera site. Using an environmental productivity variable as a covariate such as EVI can help to correct for biases when considering multiple sites (Hofmeester et al., 2019).

We divided the camera trap data into two six-month periods, from October to March (winter; roughly the months with snow cover) and from April to September (summer; snow free months in most of the study area). We also created an 8-level “study area” covariate based on geographic clusters of camera traps (Figure 1).

Data analysis

All statistical analyses were carried out in R version 3.6.1 (R-Core-Team, 2019). We standardized (scaled) all continuous covariates by subtracting the mean and dividing by one standard deviation. We used Pearson’s correlation tests to check for collinearity among continuous variables, with a limit of $r \leq 0.6$ (Zuur et al., 2010).

We used structural equation modeling (SEM) to test how interactions among mesopredators (red fox, badger and pine marten) were affected by large carnivores (wolf and lynx), land cover variables (proportion of agricultural land and EVI), and human disturbance, as well as how these interactions were affected by season (summer vs winter). SEM provides a multivariate framework to develop and evaluate hypothesized networks of causal relationships, estimating the relative strength of direct and indirect paths within the system (Grace, 2006, Grace et al., 2012).

Model description

We considered top-down and bottom-up pathways based on our predictions and on documented predator interactions in boreal ecosystems (solid lines in Figure 2, Model 1). Large carnivores (lynx and wolf) were expected to limit the dominant mesocarnivores (red fox and badger) through interference competition (Elmhagen and Rushton, 2007). Dominant mesocarnivores, red foxes, were expected to limit pine martens through the same process (Zalewska et al., 2021). We considered that bottom-up factors (proportion of agricultural land and EVI) would affect all species, but expected different strength for different seasons, with bottom-up factors having a stronger effect than top-down factors in winter than in summer (Elmhagen and Rushton, 2007, Stoessel et al., 2018). We anticipated that large carnivores would not interfere with each other, since their interactions appear to be negligible (Wikenros et al., 2012, Schmidt et al., 2009). Humans

were expected to limit large carnivores through disturbance and culling (Dorresteijn et al., 2015), and to have a positive effect on dominant mesocarnivores due to food subsidization (Gompper and Vanak, 2008).

Additionally, we proposed three other alternative models to test against Model 1. This is because there is a large potential for intraguild competition between badger and the other two mesocarnivores (red fox and pine marten). The three of them can occupy similar ecological niches, share the same den sites (Macdonald et al., 2004, Mori et al., 2015) and, being opportunistic generalists, may share foods such as earthworms, smaller vertebrates, eggs and fruits (Macdonald, 1980, Kauhala et al., 1998, Torretta et al., 2016, Prigioni et al., 2008). However, differential use of time and space may enable coexistence (Zalewska et al., 2021). Therefore, we added an additional pathway from badger to red fox (Model 2 in Figure 2) and then a second pathway from badger to pine marten (Model 3 in Figure 2). Moreover, pine martens are considered to avoid urban areas (Goszczyński et al., 2007, Fusillo et al., 2009), although recent research suggest that they can adapt to live in areas with anthropogenic disturbances (Weber et al., 2018). Therefore, we added a third pathway from humans to pine marten (Model 4 in Figure 2).

SEM analysis

To construct the SEM, we used generalized linear mixed models with a negative binomial distribution to model overdispersion, using the Bayesian brms package (Bürkner, 2017) in R version 3.6.1 (R-Core-Team, 2019). We used the number of species encounters (number of days in which an animal was detected by a camera per year and season) as the response variable, with the log-transformed number of active camera trap days as an offset. Depending on the species, explanatory variables included: i) large carnivores (wolf and lynx) encounters and human disturbance, and ii) land cover variables (proportion of agricultural land and EVI). We allowed the model to estimate different values for each pathway for winter and summer by adding the interaction of season with all pathways. We also included a varying intercept by study site and another by camera location by including these two variables as random effects.

We included the default flat priors of brms and fitted the models using 3000 iterations on 3 chains. We used LOO values as indicators of goodness of fit, and for model selection. We checked convergence by looking at the trace plots of the MCMC chains, and with the Gelman and Rubin convergence diagnostic (Gelman and Rubin, 1992). We also calculated a Bayesian R^2 (Gelman et al., 2018) for the best fitting model using the bayes_R2 function in the brms package (Bürkner, 2017) to assess the variance explained by the main factors. Below, we present the posterior median and associated 90% credible interval (CRI) for all parameters, which we discuss in terms of non-overlapping CRI for convenience. The whole posterior distributions can be found in Appendix 1 and 2. We also present the Probability of Direction (pd) as defined in the bayestestR package (Makowski et al., 2019), which represents the (un)certainty with which an effect is either positive or negative, as well as the Region of Practical Equivalence (ROPE; e.g. Kruschke, 2014), which assesses the magnitude and importance of an effect (i.e., its “significance”) (Makowski et al., 2019). These values are in Appendix 3.

RESULTS

In three years of camera trapping we obtained 91,180 non-empty images, of which 62.9% were of people, 19.2% were of red fox, 14.3% were of badger, 1.6% were of pine marten, 1.2% were of lynx and 0.6% were records of wolf.

We tested the baseline model (Model 1, solid lines in Figure 2) with three other models by adding additional pathways. We selected Model 4, which included all the tested pathways, as the best fitting model (Table 1). Bayesian R^2 values for Model 4 were 0.53 for red fox, 0.64 for badger, 0.55 for pine marten, 0.45 for lynx and 0.55 for wolf.

Below, we show coefficients whose 90% CRI did not overlap zero. We allowed the model to estimate different values for each pathway in summer and winter, therefore we show one model for each season (Figure 3). We also present the pd and ROPE for some of the main pathways to ease interpretation. All posterior distributions, pd and ROPE can be found in Appendix 1, 2 and 3.

Top-down vs bottom-up effects

There was a positive relationship between lynx and badger in summer, although the proportion of agricultural land and EVI were stronger predictors of badger encounter rate (Figure 3). There was also a positive association between wolf and red fox encounter rates in summer (Figure 3), but this relationship was weaker (ROPE = 5.8; Appendix 3), and red fox encounter rate was more associated with badger presence and EVI (Figure 3). Both red fox and badger encounter rates were stronger predictors of pine marten encounter rates than land cover variables in winter (Figure 3). Indeed, all mesocarnivores (red fox, badger and pine marten) showed positive interactions among each other, which were stronger in winter (Figure 3).

Land cover variables had contrasting effects for different species and seasons. The proportion of agricultural land was a positive predictor for badger encounter rates in both seasons, and a negative predictor for pine martens, wolves and lynx in summer (Figure 3). Additionally, EVI was a positive predictor of lynx, red fox and badger encounter rates, but only in summer (Figure 3). There was also some evidence of a positive association between EVI and both wolf and pine marten encounter rate. Even though the CRI for the median overlapped zero, only 13% and 39% of the posterior distribution was in the ROPE and $pd = 0.87$ and $pd = 0.71$, respectively for wolf and pine marten in summer (Appendix 3).

The effect of human disturbance

Human disturbance had a positive association with badger encounter rates, which was slightly stronger in winter (Figure 3). There was also some evidence for a positive association between humans and red fox encounter rates in summer, even though the CRI for the median overlapped 0, the probability of direction $pd = 0.94$ indicates a 94% chance that the effect of humans on red fox encounter rates is positive (see whole posterior distribution in Appendix 1). On the other hand, there was some evidence for a negative association between human disturbance and pine marten encounter rates, which was more certain in winter ($pd = 0.75$ in summer and $pd = 0.99$ in winter), even though the median CRI overlapped 0 (Appendix 1 and 3). Human disturbance had a strong negative association with wolf encounter rates, which was stronger in summer (Figure 3). There was also a high probability that the association between humans and lynx would be negative, even though the CRI for the median overlapped 0, only 18% of the posterior distribution was in the ROPE and $pd = 0.91$ (Appendix 3).

DISCUSSION

In this study, we assessed how the combined influences of top-down and bottom-up factors affected the interactions among mesocarnivores in Norway in two different seasons. In general, bottom-up factors were stronger predictors of dominant mesocarnivores' encounter rates (red fox and badger) than top-down factors. Contrary to what we expected, large carnivores apparently had a positive effect on mesocarnivores, with a positive association between lynx and badger and between wolf and red fox in summer (although weak for the last pair). Previous studies also found positive effects of large predators on mesopredators. For instance, Sivy et al. (2017) found a local-scale positive association between wolves and non-apex predators in Canada, which they attributed to carrion facilitation. In Sweden, Wikenros et al. (2017) found a positive effect of lynx on red foxes, which contrasted with previous studies (Pasanen-Mortensen et al., 2013, Pasanen-Mortensen and Elmhagen, 2015). They suggested that this might be caused by a behavioral response of foxes to lynx abundance, where foxes would be using olfactory cues from lynx to increase their possibility to access carrion from prey killed by lynx. Carcasses left by apex predators are known to be an important food supply for smaller predators (Wikenros et al., 2014, Selva et al., 2005, Prugh and Sivy, 2020). These remains can be an important food source during winter, when other food sources are scarce (Carricondo-Sánchez et al., 2016, Helldin and Danielsson, 2007, Needham et al., 2014, Willebrand et al., 2017), or during spring, when animals are usually reproducing (Wikenros et al., 2014). The slight positive effect of wolf on red foxes in summer (which also includes spring months April and May in our analysis) could be related to food provisioning during reproduction time. Regarding the association between lynx and badgers, their positive relationship in summer could be related to their preference for productive environments during that season (Figure 3). There are also no reports of aggressive interactions between these two carnivores (Neal and Chessemann 1996, as cited in Fedriani et al., 1999), and there are several studies documenting a predisposition of badgers to coexist with other apex predators (Fedriani et al., 1999, Garrote and Perez de ayala, 2019, Palomares et al.,

1996).

Both red fox and badger were stronger predictors of pine marten encounter rates than land cover variables in winter. Indeed, the three mesocarnivores (red fox, badger and pine marten), showed positive associations among each other, which were stronger in winter. Food scarcity and challenging winter conditions may force species to use the same resources and areas. Previous studies have found positive associations among competing predators during times of food scarcity in Scandinavia. For instance, Cano-Martínez et al. (2021) found a positive association between red fox, pine marten and weasels (*Mustela nivalis*) during periods of low rodent abundance. Similarly, Stoessel et al. (2018) found a positive association between arctic fox (*Vulpes lagopus*) and red fox during the low rodent phase. However, there is evidence that red foxes kill pine martens (Lindström et al., 1995), which is probably one of the reasons why pine martens avoid open areas (Storch et al., 1990). Pine martens are often described as being more habitat specialists in Scandinavia as compared to other mesocarnivores. Also, pine martens are primarily associated with spruce-dominated forests with large trees at fine spatial scales (Brainerd and Rolstad, 2002), which enables them to avoid predation by climbing trees (Storch et al., 1990). However, at the landscape scale, pine martens seem to be able to live in a mixed landscape of old forest and other habitat types in Norway (Angoh et al., 2023), sharing that landscape with other mesopredators. Pine martens might use small-scale spatiotemporal mechanisms, i.e. avoiding sites only when there is a high risk of encountering a potential enemy, in order to minimize interactions with larger predators and facilitate coexistence (Zalewska et al., 2021). Furthermore, the density of both red fox and pine marten seems to be correlated in Finland, which indicates that the possible effects of interspecific competition do not determine the spatial abundance of pine martens at either a regional or a landscape level (Kurki et al., 1998). This is in opposition to an increase in pine marten density reported by Storch et al. (1990) following a decrease in red fox density during an epizootic of sarcoptic mange (*Sarcoptes scabiei*) in Sweden.

Regarding the positive association between badgers and red foxes, Macdonald et al. (2004) recorded a series of non-aggressive interactions between the two mesocarnivores where foxes seemed to seek the company of badgers at setts. They argued for the possibility that foxes might receive interspecific information from badgers, for example to find good feedings spots. Also, red foxes and badgers are known to share setts/dens (Macdonald 1987 as cited in Macdonald et al., 2004), which indicates some kind of facilitative relationship. Positive associations between competing species may be facilitated by landscape heterogeneity and by mechanisms of niche separation such as temporal partitioning (Bischof et al., 2014, Lesmeister et al., 2015, Viota, 2012). Badgers are considered strictly nocturnal, while red foxes and pine martens are considered facultative nocturnal, since they are more flexible in their use of time (Torretta et al., 2016, Monterroso et al., 2014, Zalewska et al., 2021).

Based on our predictions, we expected environmental productivity to have a stronger positive effect on carnivore encounter rates in winter because of food scarcity (Elmhagen and Rushton, 2007). However, we found a positive association between EVI and some of the carnivores (lynx, red fox and badger) only in summer. Nevertheless, even if the seasonal effect of productivity was not as expected, mesocarnivores in Norway seem to be more influenced by bottom-up rather than by top-down mechanisms, as the effect of large carnivores was weak compared to the effect of land cover. Wikenros et al. (2017) also found that bottom-up processes were more influential on red fox abundance in Sweden than the top-down effect of lynx and wolves, although they emphasized the importance of considering spatial scale. Large carnivores in Norway may occur at too low densities to have an effect on the encounter rates of mesocarnivores at a large scale. The Scandinavian wolf population declined strongly during the 19th century and was declared functionally extinct in 1966 (Wabakken et al., 2001). The population started to recover in the early 1980s in south-central Scandinavia and it has increased in number and geographical distribution since then (Wabakken et al., 2001). However, of the 540 (95% CI = 427-702) individuals estimated during the winter 2021/2022 in Scandinavia, only 88-91 were counted in Norway (Wabakken, 2022). Furthermore, the “wolf zone” only represents 5% of the national territory and is limited to southeastern Norway, and outside this area, wolves are excluded via culling. Lynx numbers are also actively managed through quota regulated hunting to limit their population density and constrict their distribution (Linnell et al., 2010). A reduced predator population

exposed to hunting may not be able to play its full ecological role, limiting both direct and indirect effects on other predators and prey (Ordiz et al., 2013). In this kind of system, it is predicted that bottom-up influence will be stronger than top-down control of mesocarnivores (Pasanen-Mortensen and Elmhagen, 2015). This implies that the abundance of smaller carnivores would be dependent on prey availability, which ultimately is related to bioclimatic factors such as environmental productivity and land use (Pasanen-Mortensen and Elmhagen, 2015).

The proportion of agricultural land also had an important effect on all carnivores, except for red foxes. Actually, agricultural fields in Norway have been found to sustain the lowest abundance of small mammals (Panzacchi et al., 2010), which would explain the lack of effect of this type of landscape on red fox encounter rates. On the other hand, the negative effect of agricultural land found on lynx, wolf and pine marten was expected given that these are predominantly forest species. This negative effect of agriculture was weaker in winter. Agricultural fields vary in usage level by humans over the year, with high activity during late spring and summer, and less activity occurring during autumn and winter (Bunnefeld et al., 2006). This might explain the observed seasonal variation and the strong negative effect of agriculture fields in summer for lynx and wolf. Furthermore, this seasonal variation could also be related to seasonal movements of prey. Moose (*Alces alces*) and roe deer (*Capreolus capreolus*) migrate to areas of lower elevation during winter, in search of higher food availability provided by lower snow depth and artificial feeding sites (Bunnefeld et al., 2006, Singh et al., 2012, Mysterud, 1999). The migration of moose and roe deer to areas of lower elevation during winter could relax the negative effect of fields on lynx and wolf in winter.

Regarding the effect of human disturbance, humans were positively associated with the two dominant meso-carnivores (red fox and badger) in summer. Previous studies have documented positive relationships between red fox abundance and human settlements (e.g., Jähren et al., 2020, Panek and Bresiński, 2002), although they tend to avoid highly urbanized areas (Červinka et al., 2014). Human population density has been suggested to be a good proxy for anthropogenic food subsidies (Oro et al., 2013), which are used by red foxes and badgers (Rosalino et al., 2010, Gomes et al., 2019). Manlick and Pauli (2020) found strong dietary responses by a large variety of generalist carnivores to human disturbance, suggesting substantial use of human subsidies. These human resources can potentially increase dietary overlap (Sévêque et al., 2020), which may increase the probability of interspecific competition and intraguild predation in human-dominated landscapes (Manlick and Pauli, 2020, Newsome et al., 2015). However, these potential effects were not strong enough to prevent both red foxes and badgers from being positively associated with these areas. Pine marten, on the other hand, showed a tendency to avoid areas of high human disturbance mostly in winter. This negative association between humans and pine marten is in line with previous studies (e.g. Fusillo et al., 2009, Goszczyński et al., 2007), suggesting that pine marten is sensitive to human disturbance.

Human disturbance had a negative effect on both large carnivore species, but stronger on wolf in both seasons. Wolves in Norway are strongly managed and restricted to the so-called “wolf zone”, which is located in an area with low human population density. Wolf distribution is therefore strongly influenced by politics and management restrictions. Furthermore, lynx populations in Norway are heavily managed, and human-caused sources of mortality such as hunting, poaching and vehicle collisions are high (Andrén et al., 2006). All those factors may explain the observed negative effect of humans on both wolves and lynx in our study. Yet, it seems that both species are less negatively influenced by humans in winter, which could be related to prey seasonal movements, as explained above. Additionally, high roe deer densities often occur in agricultural, fragmented and disturbed areas (Basille et al., 2009), which are generally associated with higher human densities. Thus, wolves and lynx distribution may be determined by a trade-off between the availability of food and the risk of human presence. A higher availability of main prey closer to more populated areas in winter, when alternative prey is difficult to find, could be attracting both lynx (Bunnefeld et al., 2006, Basille et al., 2009) and wolves to these areas (Carricondo-Sanchez et al., 2020), thus reducing the negative effect of humans. Furthermore, local-scale avoidance and temporal adjustments in habitat use might facilitate large predators sharing the landscape with humans (Thorsen et al., 2022).

It is important to highlight the potential weakness of the use of by-catch data from camera traps from a

study designed to target a single species to study multiple species and their interactions (Hofmeester et al., 2019). However, Hofmeester et al. (2021) showed high detection probability of multiple carnivore species at lynx-targeted camera traps in boreal ecosystems, including high detectability of wolf, red fox and badger. Furthermore, all the camera traps used in this study were deployed with the same sampling design. Therefore, we argue that comparing trapping rates of different species from camera traps within this study design should not result in biased estimates of species interactions.

Conclusion

Land cover variables were stronger predictors of mesocarnivore activity than large carnivores in Norway. This might be caused by a combination of low density of large carnivores in an unproductive ecosystem with strong seasonality. Positive intraguild interactions were predominant in our system, which might indicate a tendency of multiple species to use the same areas and resources (probably facilitated by mechanisms of niche separation such as temporal partitioning and relatively low degrees of interference). Alternatively, these positive interactions might indicate some kind of facilitative relationship between species. Further studies with a more experimental approach and finer scales might help determine the mechanisms behind these positive relationships.

Human disturbance had contrasting effects on different species, benefiting the dominant mesocarnivores probably through food subsidization, but negatively affecting large carnivores and smaller mesocarnivores. Given that ecological interactions are now happening in a human-dominated world, there is a clear need to include anthropogenic influences when studying species interactions.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Rocio Cano-Martinez: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing - original draft preparation (lead); Writing - review and editing (lead). **Neri Horntvedt Thorsen :** Conceptualization (equal); Data curation (supporting); Investigation (supporting); Methodology (equal); Writing - review and editing (supporting). **Tim Hofmeester :** Conceptualization (equal); Data curation (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (equal); Writing - review and editing (supporting). **John Odden :** Conceptualization (equal); Data curation (lead); Funding acquisition (lead); Methodology (supporting); Project administration (supporting); Supervision (supporting); Writing - review and editing (supporting). **John Linnell :** Conceptualization (equal); Data Curation (supporting); Writing - review and editing (supporting). **Olivier Devineau:** Formal analysis (supporting); Methodology (equal); Writing - review and editing (supporting). **Siow Yan Jennifer Angoh :** Investigation (supporting); Writing - review and editing (supporting). **Morten Odden :** Conceptualization (equal); Funding acquisition (supporting);

Methodology (equal); Project administration (lead); Supervision (lead); Writing - review and editing (supporting).

DATA AVAILABILITY STATEMENT

Data and code are available from the Zenodo repository: <https://doi.org/10.5281/zenodo.10005330>

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APPENDIX 1

Posterior median parameter estimates for the final structural equation model (Model 4 in the text) explaining direct associations and interactions of mesopredators (red fox, badger and pine marten) with humans, large predators (wolf and lynx), and bottom-up variables (Agriculture and EVI), together with their associated 50% (thick blue) and 80% (light blue) credible intervals.

APPENDIX 2

Posterior median parameter estimates for the final structural equation model (Model 4 in the text) explaining direct associations and interactions of lynx and wolf with humans and bottom-up variables (Agriculture and EVI), together with their associated 50% (thick blue) and 80% (light blue) credible intervals.

APPENDIX 3

Summary of posterior distributions for the final structural equation model, including the posterior median parameter estimate (Median), the 90% credible interval (90% CRI), the percentage probability of direction (% pd) and the percentage in the Region of Practical Equivalence (% in the ROPE).

Response	Parameter	Median	90% CRI	90% CRI	% pd	% in ROPE
Fox	Badger	0.2	0.14	0.25	1	0
Fox	Wolf	0.09	0.04	0.15	1	0.58
Fox	Lynx	0.06	-0.02	0.13	0.9	0.85
Fox	Humans	0.1	-0.01	0.22	0.94	0.49
Fox	Agriculture	-0.04	-0.15	0.07	0.71	0.84
Fox	EVI	0.18	0	0.35	0.95	0.22
Fox	Badger:Winter	0.27	0.17	0.38	1	0
Fox	Wolf:Winter	-0.06	-0.14	0.02	0.89	0.8
Fox	Lynx:Winter	0	-0.08	0.08	0.53	1
Fox	Humans:Winter	0.02	-0.05	0.08	0.64	1
Fox	Agriculture:Winter	-0.03	-0.11	0.05	0.73	0.96
Fox	EVI:Winter	0.02	-0.07	0.1	0.62	0.98
Badger	Wolf	0.03	-0.05	0.12	0.74	0.92
Badger	Lynx	0.21	0.11	0.3	1	0
Badger	Humans	0.25	0.11	0.38	1	0.01
Badger	Agriculture	0.26	0.12	0.39	1	0.01
Badger	EVI	0.31	0.06	0.56	0.98	0.06
Badger	Wolf:Winter	0.01	-0.12	0.13	0.54	0.86
Badger	Lynx:Winter	-0.03	-0.13	0.06	0.73	0.9
Badger	Humans:Winter	0.07	0	0.13	0.94	0.81
Badger	Agriculture:Winter	0.13	0.05	0.21	1	0.23
Badger	EVI:Winter	-0.01	-0.16	0.14	0.55	0.75
Marten	Fox	0.06	-0.03	0.14	0.87	0.8
Marten	Badger	0.3	0.2	0.39	1	0
Marten	Humans	-0.07	-0.23	0.09	0.75	0.61
Marten	Agriculture	-0.19	-0.38	-0.01	0.96	0.18
Marten	EVI	0.1	-0.2	0.39	0.71	0.39
Marten	Fox:Winter	0.3	0.17	0.43	1	0
Marten	Badger:Winter	0.13	-0.01	0.28	0.93	0.38
Marten	Humans:Winter	-0.34	-0.74	-0.07	0.99	0.06
Marten	Agriculture:Winter	-0.05	-0.22	0.12	0.69	0.64
Marten	EVI:Winter	0.09	-0.1	0.3	0.79	0.49
Lynx	Humans	-0.3	-0.8	0.05	0.91	0.18
Lynx	Agriculture	-0.53	-0.82	-0.26	1	0
Lynx	EVI	0.49	0.1	0.88	0.98	0.03
Lynx	Humans:Winter	0	-0.43	0.43	0.5	0.33
Lynx	Agriculture:Winter	0.43	0.22	0.65	1	0
Lynx	EVI:Winter	-0.04	-0.26	0.18	0.63	0.55
Wolf	Humans	-1.01	-2.26	-0.05	0.96	0.04
Wolf	Agriculture	-0.95	-1.47	-0.49	1	0
Wolf	EVI	0.39	-0.17	0.99	0.87	0.13
Wolf	Humans:Winter	0.51	-0.67	1.69	0.76	0.09
Wolf	Agriculture:Winter	0.07	-0.44	0.56	0.59	0.27
Wolf	EVI:Winter	0.5	0.05	0.95	0.97	0.05

FIGURE LEGENDS

Figure 1. Location of the camera traps in Norway, study areas based on geographic clusters of camera traps, and the wolf zone.

Figure 2. A priori structural equation models describing all hypothesized top-down and bottom-up interactions evaluated. Model 1 (baseline model) is represented by solid lines between variables. Models 2, 3 and 4 are as Model 1, but with added paths from badger to red fox (Model 2, dashed line), from badger to pine marten (Model 3, dotted line), and from humans to pine marten (Model 4, dashed-dotted line).

Figure 3. Structural equation model (SEM) with the best fit showing top-down and bottom-up pathways for large carnivores and mesocarnivores in summer (left figure) and winter (right figure). Values along arrows represent the relative magnitudes of positive (black) and negative (red) standardized path coefficients whose 90% CRI did not overlap zero. Arrows with no coefficients represent those pathways included in the model whose 90% CRI overlap 0. However, we still indicate positive (black) and negative (red) for those pathways that are discussed in the text given their significant *pd* and ROPE values. Grey arrows represent pathways included in the model whose 90% CRI overlap 0 but with very weak evidence according to their *pd* and ROPE.

TABLES

Table 1. Comparison of the four tested models, ranked by relative predictive accuracy (Expected Log-Posterior Density, *elpd_diff*), and associated uncertainty (*se_diff*). Model 4 is “best”, as per Vehtari et al. (2017) and (Sivula et al., 2020). Model 1 corresponds to the baseline model, to which an extra pathway was added for each of models 2-4.

	<i>elpd_diff</i>	<i>se_diff</i>	Added pathways
Model 4	0.00	0.00	Humans -> Pine marten Badger -> Pine marten
Model 3	-2.23	4.03	Badger -> Red fox Badger -> Pine marten
Model 2	-23.06	6.75	Badger -> Red fox
Model 1	-77.99	10.38	Baseline







