Claws and Effect: How Small Carnivore Richness Responds to Habitat Diversity and Ecological Productivity

Emilia Arkdalen
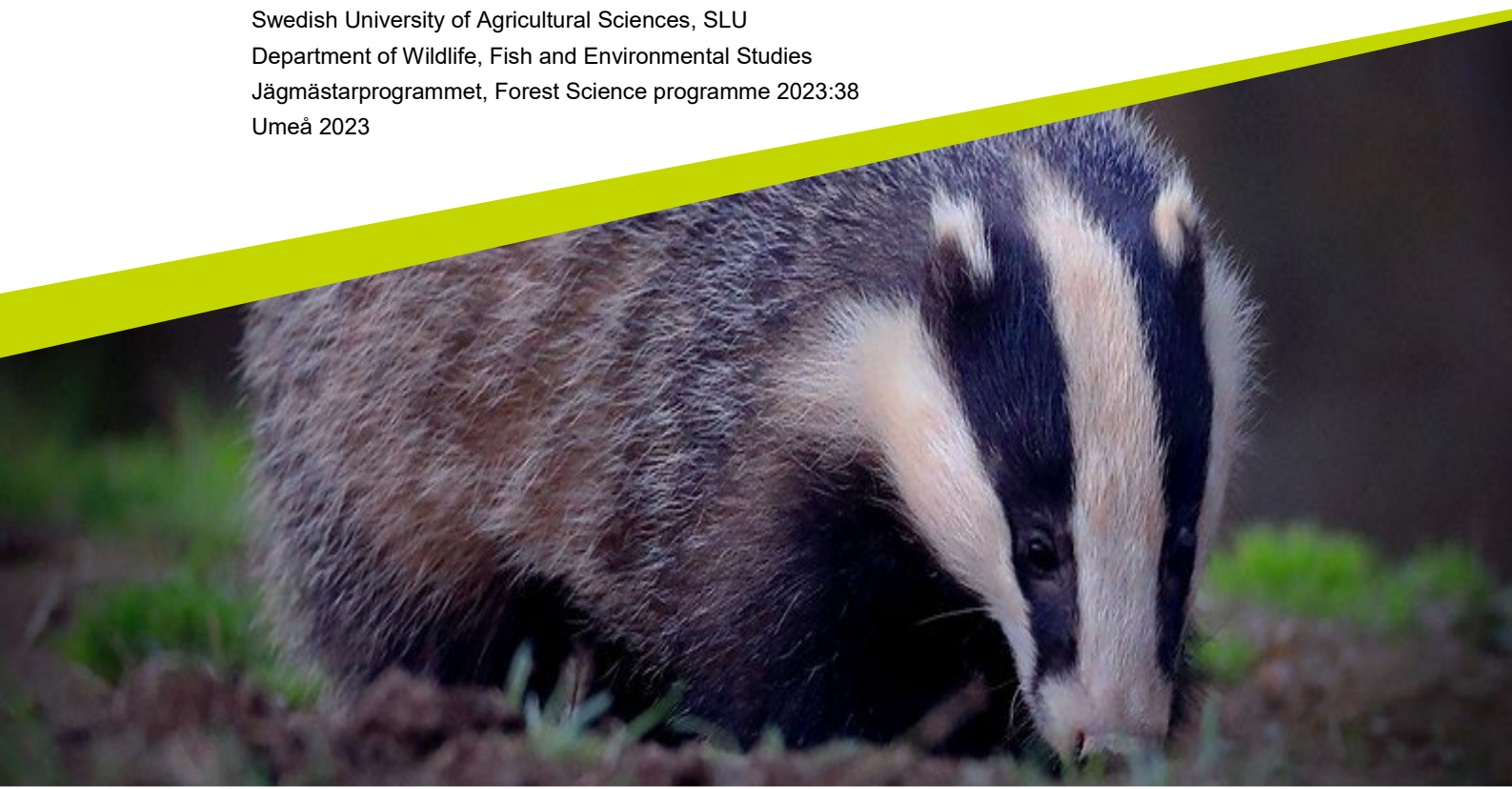
Claws and Effect: How Small Carnivore Richness Responds to Habitat Diversity and Ecological Productivity

Emilia Arkdalen

Abstract

Species distribution and composition research has gained significance in light of global warming and its impact on biodiversity. Understanding the factors shaping species richness is crucial for wildlife ecology and conservation. Previous studies have shown a general pattern of positive correlation between terrestrial species richness and primary productivity. However, the productivity-species richness relationship varies across regions and spatial scales. Additionally, the link between habitat diversity and species richness remains ambiguous, with studies reporting both positive and negative correlations. This thesis focuses on small carnivores, a diverse group with ecological importance and vulnerability to climate change. I aimed to address the knowledge gaps in what shapes the species richness of small carnivores in Europe. I hypothesize that small carnivore species richness increases with study area productivity and habitat richness. I also hypothesize a positive relationship between small carnivore species richness and decreasing habitat evenness.

To test these hypotheses, I employed a multi-scale and multi-species hierarchical modelling approach, estimating the species richness of small carnivores across 64 sites in Europe. These estimates were then used in a meta-analysis that tested the correlation between species richness, productivity, habitat richness and habitat evenness.

The occupancy model performance confirms the accuracy of species richness estimates based on expected associations between species' site-use probabilities and environmental covariates. The result of the meta-analysis found a weak association between productivity and species richness but no association between species richness and habitat richness or evenness. While the productivity-species richness relationship shows uncertain results, previous research suggests the presence of additional factors influencing the correlation. The link between habitat diversity and small carnivore richness is inconclusive, with contrasting findings across different studies and definitions of habitat diversity.

In conclusion, this study provides insights into the species richness of small carnivores in Europe and their relationships with productivity and habitat factors. However, further investigations are required to understand the complex interactions among productivity, habitat diversity, and species richness. Accounting for indirect effects through trophic levels and considering habitat fragmentation and connectivity will enhance future studies. Understanding these factors is vital for effective conservation and management strategies for small carnivores in the face of global change.

Keywords: small carnivore, camera trap, occupancy model, species richness, productivity, habitat richness, habitat evenness

Table of contents

List of tables

List of figures

Abbreviations

CRI   Credible interval

GBIF   Global Biodiversity Information Facility

IUCN   International Union for Conservation of Nature

MODIS   Moderate Resolution Imaging Spectroradiometer (instrument aboard the Terra satellite)

QGIS   Geographic Information System program

1. Background

Extensive research has focused on species distribution and its underlying mechanisms, and its significance has become increasingly apparent in the face of global warming. As climate change progresses, species are forced to track their optimal habitats, leading to rapid shifts in their distribution (Buckley et al. 2012). Such changes can introduce new interactions between species or disrupt already existing ones. As a result, species' distributions have a significant impact on the composition of species in any given location. This highlights the importance of research on species distribution and composition for comprehending the impact of changing environmental conditions on biodiversity and ecosystem stability. Therefore, understanding the factors that shape species richness is fundamental to wildlife ecology and conservation.

The link between primary productivity and terrestrial species diversity can be seen as far back as fossil records. There is strong support for the hypothesis that the relationship between terrestrial diversity and primary productivity is a general pattern in ecology (Fritz et al. 2016). Examining the relationship between species richness and productivity supports that higher productivity enables the persistence of viable populations by increasing the probability of resources occurring. This higher productivity can therefore lead to higher species richness (Bonn et al. 2004). Several studies across the world have found a connection between productivity and species richness and that higher productivity generally results in higher species richness. This positive correlation between productivity and species richness can be seen on various scales such as global (Qian 2010; Coops et al. 2019), regional (Wang et al. 2001; Hortal et al. 2008; Niedziałkowska et al. 2010; McCain et al. 2018; Coops et al. 2019; Cerezer et al. 2021) and local scale (Hortal et al. 2008; Niedziałkowska et al. 2010).

Productivity-species richness relationships differ across regions, ranging from linear to humped-shaped (Coops et al. 2019). The relationship between species richness and productivity can also vary over spatial scales. Wang et al. (1999) found a unimodal relationship between small mammal species richness and productivity at a larger spatial scale. At the smaller scale, no relationship could be found at all, suggesting movement and spatial use patterns are important factors to consider. On the contrary, Hortal et al. (2008) found that productive energy could

explain the species richness on a regional scale but also between sites. They found that the variation of species richness was explained by the productive energy to a greater degree in the larger sites, but the pattern was consistent over all scales. When looking at small mammals on a local and regional scale in Poland, Niedziałkowska et al. (2010) found that there was a positive linear relationship between small mammal diversity and the productivity of the forest habitat they lived in. This relationship could be seen on both the local and regional scales.

The link between habitat and species richness seems to not be as clear as that of productivity. A positive relationship between species diversity, habitat diversity and habitat heterogeneity has been seen as fundamental within ecology based on the island biogeography theory (Losos & Ricklefs 2009). This theory is however based on isolated islands and although research has been done using this theory on a fragmented landscape, using the habitats patches as "islands" (Bueno & Peres 2019) the application on the mainland is debated. A study on small mammals in the Colorado Rocky Mountains in the USA found no relationship between mammal richness and habitat diversity or heterogeneity (McCain et al. 2018). Though different studies have found that the relationship between habitat heterogeneity or diversity and species diversity can be either negative or positive, a literature review showed that the relationship is mostly positive (Tews et al. 2004). What is defined as the variation in habitats also varies between studies. Habitat heterogeneity in the form of elevation range was a significant variable in predicting species richness of all different vertebrate groups although its contribution was minor compared to other variables (Qian 2010). Studies on habitat richness and heterogeneity in Europe have shown a positive relationship between habitat richness and the richness of species (Fløjgaard et al. 2011; Cervellini et al. 2021). The effect that habitat richness or diversity has on species richness can sometimes also be hard to separate from the effect that area has on species richness. This is shown by Kallimanis et al. (2008) who in their study found that area was significantly correlated with the number of habitat types. This means that these variables should not be used as independent variables. However, Kallimanis et al. (2008) also found that both area and habitat diversity significantly affect species richness independently of each other. They then concluded that habitat diversity is affecting how fast species accumulate as the area increase.

As the impacts of global warming can greatly influence both productivity and habitat, it is crucial to explore the intricate relationship between these factors and their potential effects on species richness. Understanding the factors that shape species richness is particularly important as changes in species interactions can have significant consequences for ecosystem functioning, including trophic disruptions (Buckley et al. 2012).

One group of species that is especially vulnerable to the compounded bottom-up effect climate change can initiate are carnivores because of their high trophic position (Van Valkenburgh & Wayne 2010). The mammalian order Carnivora has a large variety of species, and they have the largest range in body size of any living order. Carnivores are not only diverse in size but also in their distribution and behaviour. They are distributed from pole to pole and can range from solitary to seemingly obligate social. This diversity and ecological importance have made carnivores a popular order to research (Van Valkenburgh & Wayne 2010). The most attention in research has been given to the large apex predators (Roemer et al. 2009; Van Valkenburgh & Wayne 2010) but most species in the order Carnivora are not the large apex predators, but the medium to small-sized carnivores that are under 15 kg (Roemer et al. 2009). The impact small carnivores have within communities is generally assumed to be relatively minor despite them being more abundant than larger carnivores. A decline of larger carnivores caused by global warming may however change this fact as there are examples where this decline led to small carnivores driving community structures to a larger extent and becoming de facto apex predators (Roemer et al. 2009). The ecological role of the mammalian small carnivore can be far greater than previously thought and theoretical and empirical research suggest that small carnivores may be fundamentally important drivers of ecosystem function (Roemer et al. 2009). Small carnivores can also in themselves be used as sentinels of global environmental change and are more appropriate to use as such than larger carnivores (Marneweck et al. 2022). The variety in taxa and life histories of small carnivores makes them sentinels for different processes within ecosystems and the wider range of ecological niches causes them to have a wider variety of sensitivity to environmental change. A shorter lifespan and higher reproduction rate also make small carnivores more suitable as indicators of environmental change as their populations are more responsive to fluctuations in environmental conditions. It is not only the responsiveness to environmental change that makes the small carnivores so useful as sentinels of change, but they also have a higher abundance and can be easier to monitor. Management of small carnivores also tends to be less likely to cause conflict than that of larger carnivores (Marneweck et al. 2022).

1.1 Aim

Studying the response of small carnivore communities to the factors that shape their species richness is crucial due to their growing ecological importance as sentinels of global change. Investigating how productivity and habitat diversity affect small carnivorous mammal diversity is necessary, particularly considering small carnivores' abundance and ecological significance. This thesis explores the impact of primary productivity and habitat diversity on small carnivores' species richness,

providing insights into the factors shaping species composition in ecosystems. Understanding how small carnivores respond to environmental factors can help conserve their populations and overall ecosystem health.

I hypothesize that:
1. Small carnivore species richness in Europe increases with the productivity of the study area.
2. Small carnivore species richness in Europe increases with the habitat richness of the study area.
3. Small carnivore species richness in Europe increases with a decreasing habitat evenness of the study area.

2. Method

To test my hypotheses, I conducted a two-step analysis using small carnivore detections in Europe and indexes of productivity and habitat diversity. The first step involved creating a model that estimated species richness from detection-non-detection data from camera traps, while the second step involved using these estimates to examine the relationship between species richness, primary productivity, habitat richness, and habitat evenness.

2.1 Study area

The study area of this thesis was the same as that of the Snapshot Europe Project in 2021 (Max Planck Institute of Animal Behaviour & EUROMAMMALS n.d.) from which I got my detection data of small carnivores. Snapshot Europe aimed to collect data on mammals in Europe using a coordinated and standardized camera trap effort during September and October 2021. Anyone could register a subproject with a study site and contribute if they followed the requirements according to the standards set by the Snapshot Europe protocol. Sixty-four study sites were included in my thesis, located in 21 countries in Europe (Figure 1). The study sites covered a variety of biomes, ranging from the boreal forests in northern Europe to Mediterranean woodland in Portugal and Greece. They also span over several different climate zones in Europe, with study sites placed in maritime subtropical climates to intermediate cold climates (Pinborg 2002).
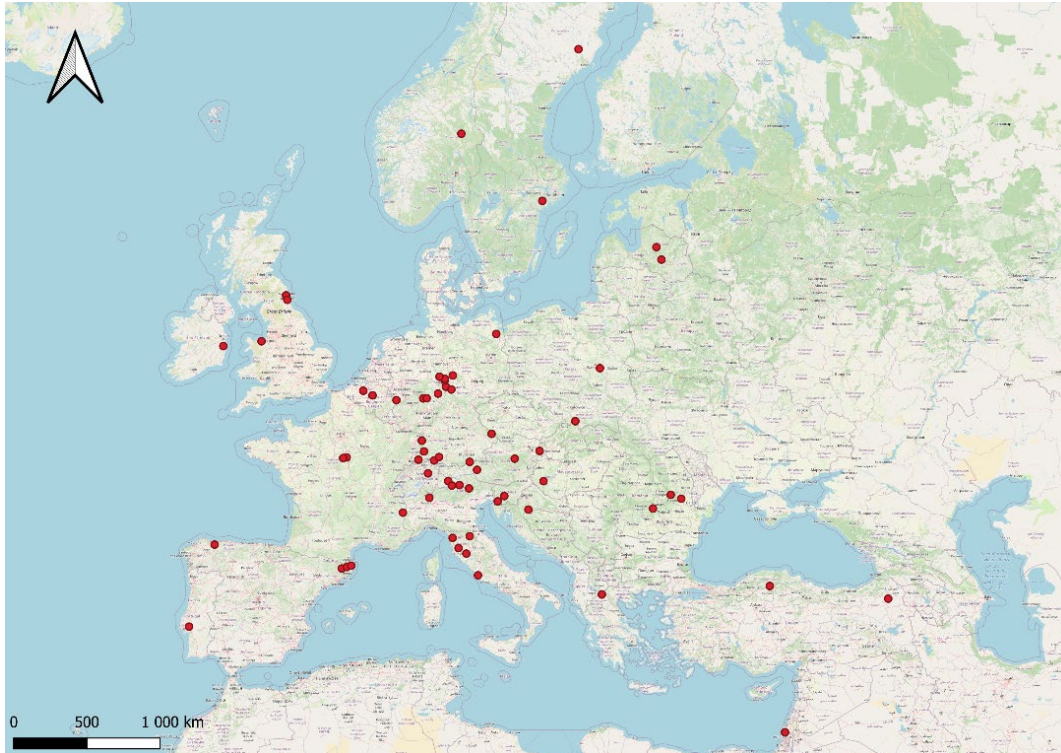
Figure 1: Map over the study area with the 64 study sites marked. Background map data from OpenStreetMap.

2.2 Camera data

The data used in this thesis were placements and sequence data from the camera trap project Snapshot Europe in 2021 (Max Planck Institute of Animal Behaviour & EUROMAMMALS n.d.). The requirements of the cameras to contribute to the Snapshot Europe project were:

- Have an infrared flash
- Can fire bursts of pictures
- Have a trigger speed of less than or equal to 0.5 seconds
- Placed 50 cm off the ground
- No bait is used
- Take at least three pictures per burst in rapid-fire mode
- Placed in 10 to 50 sites during September – October
- Deployed for at least 3 weeks per site
- At least 400 camera trap days across all sites
- Deployed at least 200 m apart but less than 5 km apart

The images were uploaded to wildlife insights (Wildlife Insights n.d.) where an AI reviewed all the unclassified images and identified species. This automatic identification was then approved or edited by a member of the subproject that submitted the images. All camera locations were grouped in study sites.

2.3 Preparing data for analysis

2.3.1 Deployment and sequence data

The data derived from the Snapshot Europe project came in two CSV files. One held the sequence data with information on the sequences of images the individual cameras had taken and the other held the deployment data with information about the individual deployed cameras within the study site. All preparations of the detection data were made in R (R Core Team 2022).

I filtered the deployment data file to only keep the deployments that were active during the study period of 2021-09-01 to 2021-10-31. This filtering was necessary because some study sites had active deployments outside the study period set by the Snapshot Europe Project. Additionally, I removed cameras marked as not functioning and only kept cameras placed at knee height and with a parallel sensor orientation.

To ensure the accuracy of the data, I visually inspected all deployments and study sites in QGIS (QGIS.org 2022). During this inspection, I removed a few deployments due to mistyped coordinates, which resulted in the deployment being far from the rest in the study site. Furthermore, study sites with fewer than three cameras after the initial filters were applied were also removed. Lastly, I removed one study site where cameras were placed well over the limit of 5 km apart, set by the Snapshot Europe Project protocol.

I filtered the sequence data according to the study period between 2021-09-01 to 2021-10-31. Fourteen species of small carnivores were identified within the data (Table 1). There were only a few subprojects that had identified pine marten (*Martes martes*) and beech marten (*Martes foina*) to species level, so I changed all observations to be classified at the genus level (*Martes sp.*) and included these two species as a single species in the model.

Table 1: List of species included in the species richness estimation.

Species	Common name
Martes foina	Beech marten
Martes martes	Pine marten
Genetta genetta	Common genet
Herpestes ichneumon	Egyptian mongoose
Meles meles	Eurasian badger
Lutra lutra	Eurasian otter
Canis aureus	Golden jackal
Mustela nivalis	Least weasel
Procyon lotor	Northern raccoon
Nyctereutes procyonoides	Raccoon dog
Vulpes vulpes	Red fox
Mustela erminea	Stoat
Mustela putorius	Western polecat
Felis silvestris	Wild cat

The northern raccoon (*Procyon lotor*) and the raccoon dog (*Nyctereutes procyonoides*) are alien invasive species in Europe (EU 2022). Therefore, their current distribution might be largely determined by where they were originally introduced, and the time since introduction, rather than environmental factors. To test if this might influence the estimated patterns in small carnivore species richness, I ran the models twice, once with and once without these two species.

I performed several tasks to convert the sequence data into detection histories of the small carnivore species. Firstly, I assigned zeros for non-detection and ones for detection. Then, I grouped the detection histories based on calendar days into one-week occasions, resulting in the study period consisting of 9 occasions (weeks 35 - 43). I corrected the detection histories by taking into account the time when the cameras were active, and set all other occasions to NA values, as some study sites did not have all deployments active simultaneously. For species that were not

detected at a camera location within its geographical range, I included them with a detection history of zeroes for all active occasions. In study sites where the species could not occur, I set the detection histories to NA values to ensure that non-detections outside of the geographical range did not affect the overall detection probability of the species.

To obtain the range data, I used the distribution maps from IUCN (IUCN (International Union for Conservation of Nature) 2008, 2014, 2015, 2016a, b, c, d, e, f, g, h, 2018; Gerngross, P. et al. 2022) and observations of the species from the GBIF archive (GBIF.org 2023). I determined that the species was possibly present in a study site if the site was within 10km of the range set by IUCN or if there were at least two observations of the species according to the GBIF data within the site or within 10km of the site. Finally, I used the combined range of pine marten and beech marten to determine the range for Martes sp.

2.3.2 Covariates

I prepared the environmental covariates used in the occupancy models and analyses connected to the aim using the Geographic Information System program QGIS (QGIS.org 2022). For modelling the likelihood of a species occurring at a camera location, I selected three covariates: tree cover percentage, distance to water, and human footprint. The tree cover percentage was chosen to explain the different species' preferences for habitats with different forest covers. For instance, martens are known to prefer woodlands with an incomplete canopy (Herrero et al. 2015). The distance to water was used to estimate the occupancy of semi-aquatic species, such as otters (Kruuk 2006). Lastly, the human footprint was included to account for the likelihood of the species living in areas affected by human activity. For example, wild cats prefer to live in relatively undisturbed habitats (Oliveira et al. 2018), while golden jackals can venture into human settlements in search of food (Ćirović et al. 2016). All of these variables were extracted for each camera location.

Tree cover percentage had a pixel resolution of 250 m and a yearly temporal resolution (DiMiceli, et al. 2015). I calculated distance to water using Open Street Map data on waterways and wetlands using the QGIS plugin QuickOSM. Shapefiles of wetlands, lakes and waterways were rasterized to a pixel resolution of 100 m with a fixed value classified as water that covered all study sites and an additional 10 km buffer around them. I then used the QGIS tool Proximity to create a new raster of the same resolution with pixel values that reflected the distance in meters of each cell to those that were classified as water. I extracted the human footprint covariate from a raster of cumulative human pressure on the environment from 2009 (Venter et al. 2016). The spatial resolution was 1 km, and the values of the raster were based on eight different pressures variables: 1) the extent of built

environments, 2) population density, 3) electric infrastructure, 4) croplands, 5) pasture lands, 6) roads, 7) railways, and 8) navigable waterways. I also used the mean body mass of each species (Smith 2004) and the camera effort in days deployed in the modelling. I used the mean body mass of the individual species to account for the different probabilities a species would have of being detected by the cameras due to its size. I used the camera effort in days to correct for the fact that all deployments were not active for the whole study period.

The site-specific covariates used to test the hypotheses were land cover evenness, land cover richness and productivity per site. I defined the study site geographically by using the minimum bounding geometry tool in QGIS on the deployments of each study site with the geometry type convex hull. Then, I buffered the area by 1 km (Figure 2) since this is the approximate mean radius of the home range of the species included based on data from the PanTHERIA database (Jones et al. 2009). I derived the land cover evenness and richness by using the EUNIS (European Nature Information System) habitat type raster with a 100 m spatial resolution and a yearly temporal resolution (European Environment Agency 2019). Using the zonal statistics tool in QGIS, I extracted the variation and richness of land cover types in each study site. The land cover evenness was calculated using Pielou's evenness (Pielou 1966). For the index of productivity, I used NDVI, which has been used in several other studies investigating species richness and productivity (Bonn et al. 2004; Hurlbert & White 2005; Qian 2010; Coops et al. 2019; Feng et al. 2021; Li et al. 2022). I calculated the mean NDVI of each site from MODIS data (Didan 2021), using the zonal statistics tool in QGIS. This dataset had a 500 m spatial resolution and a 16-day temporal resolution. I calculated a yearly mean for each cell from the multiple 16-day rasters, and the reason for using the yearly mean instead of the study period was that I assumed it would more accurately explain the Europe-wide variation in species richness at the study site level. Finally, I standardized all covariates before using them in the models by subtracting the mean and dividing them by the standard deviation.
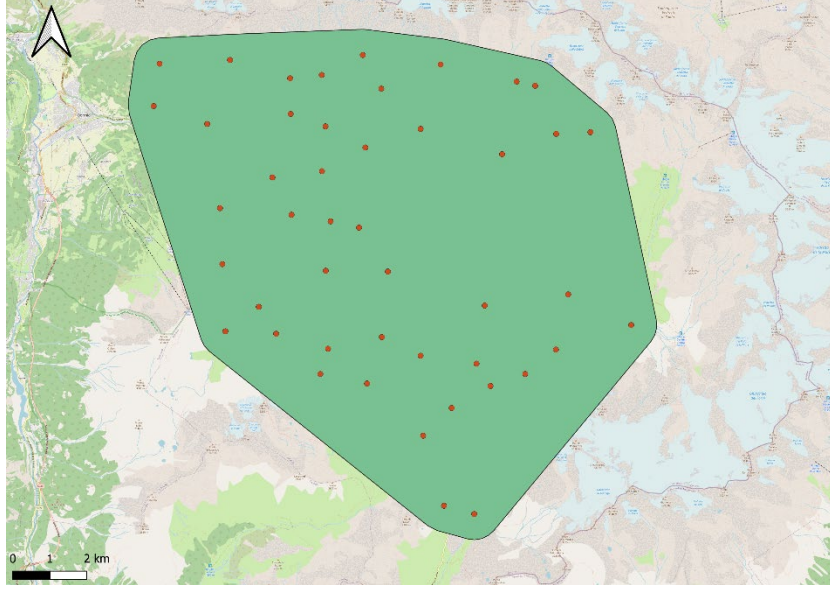
Figure 2: Example of one of the study sites with a buffer of 1 km around the camera deployments shown by the red dots. This study site was located in Stelvio National Park in Italy. Background map data from OpenStreetMap.

2.4 Modelling framework

Differences in the number of camera traps and the time these cameras were deployed among study sites could lead to biased estimates of species richness when using the observed number of species. Therefore, I used a multi-species occupancy model to estimate the species richness in each study site. The framework used for estimating the species richness in the study sites was a combination of multi-scale and multi-species occupancy models described by Kéry and Royle (2016). I combined a multi-scale approach with the multi-species occupancy model to account for my study design that used smaller units (the deployments) nested in larger units (the study sites). The model of the occupancy of a species at study site level was a simple Bernoulli model:

$$z_{ij} \sim \text{Bernoulli}(\psi_{ij}) \tag{1}$$

Where ψ_{ij} is the occupation probability of species i in study site j and $\psi_{ij} = \text{Pr}(z_{ij}=1)$. The sum of z_i per site is the estimated species richness per site. The site-use of the area around the individual cameras (deployment area) within each study site was then conditional on the occupancy of a species in the study site:

$$a_{ijk}|z_{ij} \sim \text{Bernoulli}(z_{ij} \text{ x } \theta_{ijk}) \tag{2}$$

Where a_{ijk} is the site-use of species i in study site j and deployment area k. This had the probability of Θ_{ijk} given that the study site was occupied by the species ($z_{ij}=1$).

The probability of detecting a species given that it is using the deployment area is described as:

$$y_{ijkl}|a_{ijk} \sim \text{Bernoulli}(a_{ijk} \; x \; p_{ijkl}) \qquad (3)$$

Where y_{ijkl} is the detection or non-detection of species i in study site j and deployment area k during occasion l. The detection had the probability of p_{ijkl} given that the deployment area was used by the species (a_{ijk}=1).

To accommodate for the different effects the species, deployment placements and survey duration had on the site-use and detection probability this was modelled using a series of logistic regression equations with species-specific intercepts. The occupancy probability was not modelled with any covariates, to assure independent estimates for the second step (see below), but had a species-specific intercept (*lpsi*):

$$logit(\psi_{ij}) = lpsi_i \qquad (4)$$

The site-use probability Θ was modelled as species-specific and influenced by tree cover, distance to water and human footprint.

$$
\begin{aligned}
logit(\theta_{ijk}) = {} & ltheta_{0i} + beta.ltheta_{1i} * tree.cover_{ijk} + \\
& beta.ltheta_{2i} * \log(distance.to.water_{ijk}) + \\
& beta.ltheta_{3i} * \log(human.footprint_{ijk})
\end{aligned} \qquad (5)
$$

The detection probability p was modelled with survey effort in days:

$$logit(p_{ijkl}) = lp_{0i} + beta.lp_1 * effort_{ijkl} \qquad (6)$$

The betas in the site-use model were species-specific while the beta in the detection probability model was not and they represent the different slopes of the covariates. Body mass was modelled as linear regressions directly on the means and variances of the random intercepts of the site-use and detection probabilities:

$$ltheta_i \sim Normal(\mu_{ltheta,i}, \sigma^2_{ltheta,i}) \qquad (7)$$
$$lp_i \sim Normal(\mu_{lp,i}, \sigma^2_{lp,i}) \qquad (8)$$

$$\mu_{ltheta,i} = delta.ltheta_0 + delta.ltheta_1 * \log_{10}(mass_i) \qquad (9)$$
$$\mu_{lp,i} = delta.lp_0 + delta.lp_1 * \log_{10}(mass_i) \qquad (10)$$

$$\log(\sigma^2_{ltheta,i}) = phi.ltheta_0 + phi.ltheta_1 * \log_{10}(mass_i) \qquad (11)$$
$$\log(\sigma^2_{lp,i}) = phi.lp_0 + phi.lp_1 * \log_{10}(mass_i) \qquad (12)$$

Where the deltas and phis are the intercepts and slopes of the body mass covariate and mass$_i$ is the mean body mass (g) of species *i*. This use of the body mass covariate made it possible to use observations from more common species to estimate likely detection and site-use probabilities of less common species through an expected relationship with body mass. I mostly used vague priors of normal distribution except for the hyperpriors of the standard deviations. The priors of the standard deviations had a uniform distribution with a limit that was set by trial and error (Appendix 1). I checked the frequency of values that the posterior of the standard deviation had taken after every time the model had run and if the values varied close to the limit set in the uniform distribution, the limit was extended in the next run. This was done until the prior no longer varied up to the set limit. I set the initial values of the occupancy and the site-use using the observed values and the initial values of the hyperpriors were sampled from a normal distribution.

I ran the model for 80 000 iterations on 8 cores with a thinning rate of 10 and 7 000 burn-in iterations. I checked for successful convergence based on Rhat values of below 1.1 and the trace plots were also checked to ensure convergence of the Markov chains.

I then tested for relationships between estimated species richness and my covariates of interest in a second step, following the method described by Kéry and Royle (2016). This analysis propagates the estimation uncertainty of the estimates of species richness from the occupancy model. I extracted the posterior means of the species richness per site from the occupancy model result, as well as the standard deviations. Next, I performed a simple regression with NDVI as the index of productivity, land cover evenness, and land cover richness, and fitted it with two residual components. The first residual component accounted for the uncertainty from the occupancy model (i.e., the standard deviation), while the second component accounted for the usual lack of fit component, estimated from the data.

$$N_j \sim Normal\left(\mu_{N,j}, \sigma_j^2\right) \tag{13}$$

$$\mu_{N,j} = beta_1 + beta_2 * LCE_j + beta_3 * LCR_j + beta_4 * NDVI_j + eps_j \tag{14}$$

Where N$_j$ is the estimated species richness in study site j from the occupancy model and the posterior standard deviation of the estimated species richness per site is used as σ^2. LCE is the land cover evenness, LCR is the land cover richness, NDVI is the mean NDVI in the study site and eps is the lack of fit component. I used vague priors of a normal distribution with a mean of 0 and precision of 0.001 for the betas. I also used a normal distribution for the eps variable but with a mean of 0 and a precision that had a hyperprior with a uniform distribution between 0 and 2. The initial values of the betas were sampled from a normal distribution. I ran this model

for 12 000 iterations on 3 cores with a thinning rate of 10 and 2 000 burn-in iterations. The convergence of the Markov chains was checked in the same way as for the occupancy model. This analysis ignored covariances of the estimates of species richness between sites. To test that there was no covariance, the joint posteriors of the richness estimates were plotted for pairs of sites to visually inspect the likelihood of this assumption.

3. Results

A total of 1 230 deployments in 64 sites were used in the occupancy modelling. This added up to 543 309 camera trap days during the study period. The estimated species richness was slightly higher than the observed species richness across all sites. The estimated species richness ranged from 4.7 to 10.4 species while the observed species richness ranged from 1 to 8 species (Appendix 2). The exotic species were kept in the final version of the occupancy model since the response of the environmental covariates on the species richness was very similar with or without the species included. The site with the highest species richness was in Hungary and the site with the lowest richness was in Germany. The regional patterns in species richness were not very clear as sites with varying richness were located quite close to each other. Great Britain, Ireland and Scandinavia had a low to medium species richness and eastern Turkey and Israel had low species richness (Figure 3). There also tended to be a low to medium species richness in southern Germany and Switzerland.
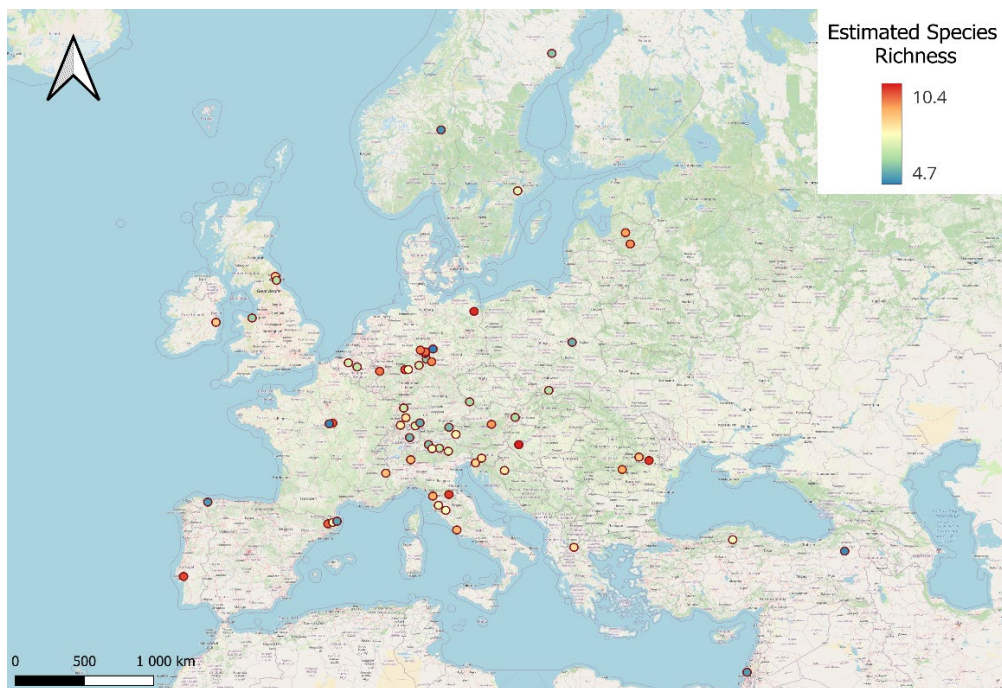

Figure 3: Overview of all sites and the estimated species richness of small carnivores at each site, Sep-Oct 2021. Background map data from OpenStreetMap.

3.1 Occupancy model

I found generally low detection probabilities for all species. The mean detection probability of the species community was 0.09 and ranged from 0.01 to 0.19 (Appendix 3). The among-species variation in site-use probability was a little larger than that of the detection probability with a mean of 0.28, ranging from 0.04 to 0.54. The occupancy probability had the largest variation, varying from very low to very high occupancy probability. The mean occupancy probability was 0.52 ranging from 0 to 1. The variation in the occupancy probability suggested that several species are widespread but also several that have very limited distribution.

3.1.1 Detection probability

The average effect of effort on the detection probability was negligible with large uncertainty (mean 0.03, 95% CRI -18.16 to 18.15). The standard deviation of the effect of effort on the detection probability was very high. It was in reality even higher as no upper limit to the variation in the posterior of the standard deviation was found during the modelling. The upper limit of the prior for the standard deviation of the effect of effort on the detection probability was increased until other estimates no longer changed. It was decided to stop the increase there as the upper limit already was very high and the posteriors seemed to continue to vary into infinity.

As the effort increased, the detection probability for all species showed an upward trend. Among the studied species, the Eurasian otter, golden jackal, and red fox had the highest detection probabilities ranging between 0.19 – 0.51, 0.18 - 0.49 and 0.16 – 0.46 respectively. The least weasel had the lowest detection probability, regardless of the level of effort, varying between 0.02 - 0.07 (Appendix 4).

3.1.2 Site-use probability

The median effect of the covariates on the site use probability and the detection probability of the entire community of species was low and all credible intervals (CRI) of the posteriors were overlapping zero. The tree cover percentage had a median effect of 0.001 and 95% CRI between -0.32 and 0.29. The distance to water had the largest median effect on the entire community of -0.16 and 95% CRI between -0.59 and 0.25. The median effect of the human footprint was -0.09 with 95% CRI between -0.5 and 0.25.

The percentage of tree cover had different effects on different species and the mean slope was positive for some species and negative for others. This meant that if the mean slope was positive, the species tended to have a higher probability of using the site around the deployment when the tree cover percentage was higher and vice versa. None of the species-specific effects were strong however as all the 95% credible intervals overlapped zero. Some species had a bigger overlap than others (Figure 4). The red fox had the generally highest site-use probability of all species, but it was not affected by a changing tree cover percentage. Only the golden jackal had a higher site-use probability than the red fox but only in the lowest tree cover percentages. The least weasel had the lowest site use probability of all species and that was not affected by the tree cover either (Appendix 4).
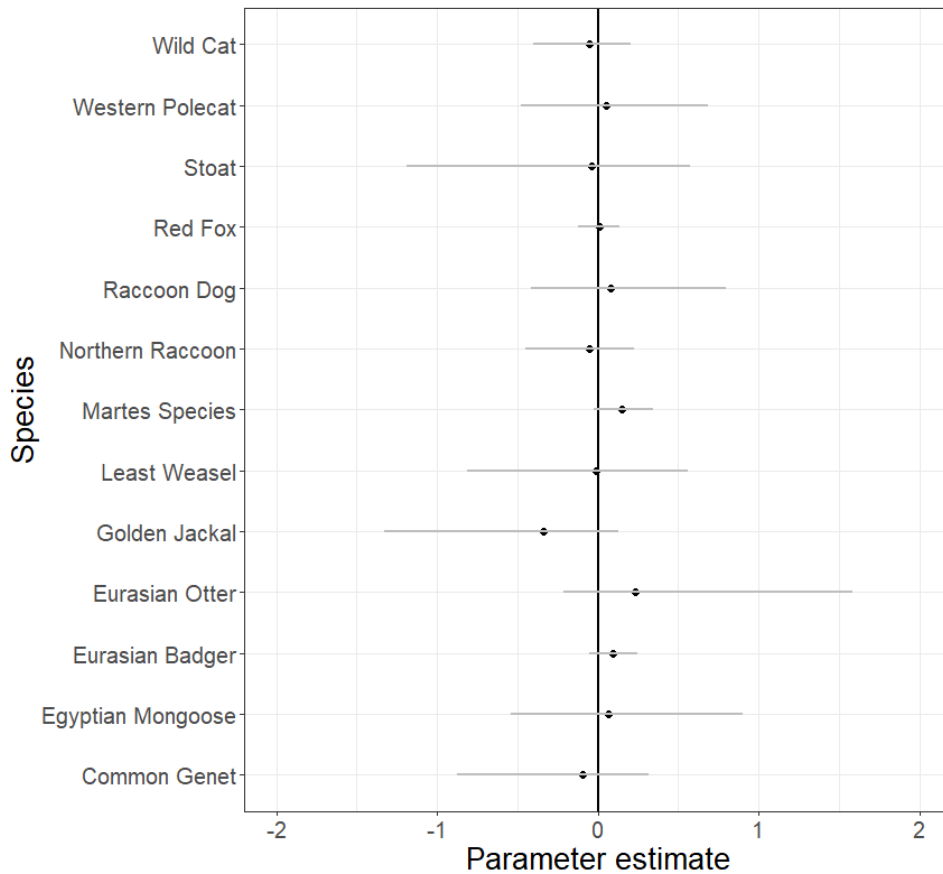
Figure 4: The effect the percentage of tree cover has on the individual species in the occupancy model. The black dots are the mean effect, and the lines represent the credible interval. Credible intervals that don't overlap zero are highlighted in blue.

The effect of the log-transformed water distance on the species-specific site-use probability was strong for three species. An increasing distance to water had a positive effect on the site use of golden jackals with a slope of 0.5 but a negative effect on the site use of otters and badgers with slopes of -1.49 and -0.17 respectively (Figure 5). The otter had the highest site-use probability of all species where the distance to water was the lowest but also the lowest site-use probability at a high distance to water. The red fox had a high site-use probability across all different distances to water (compared to other species) and the site-use probability was unaffected by the distance to water. When there is a long distance to water, the golden jackal had the highest site-use probability (Appendix 4).
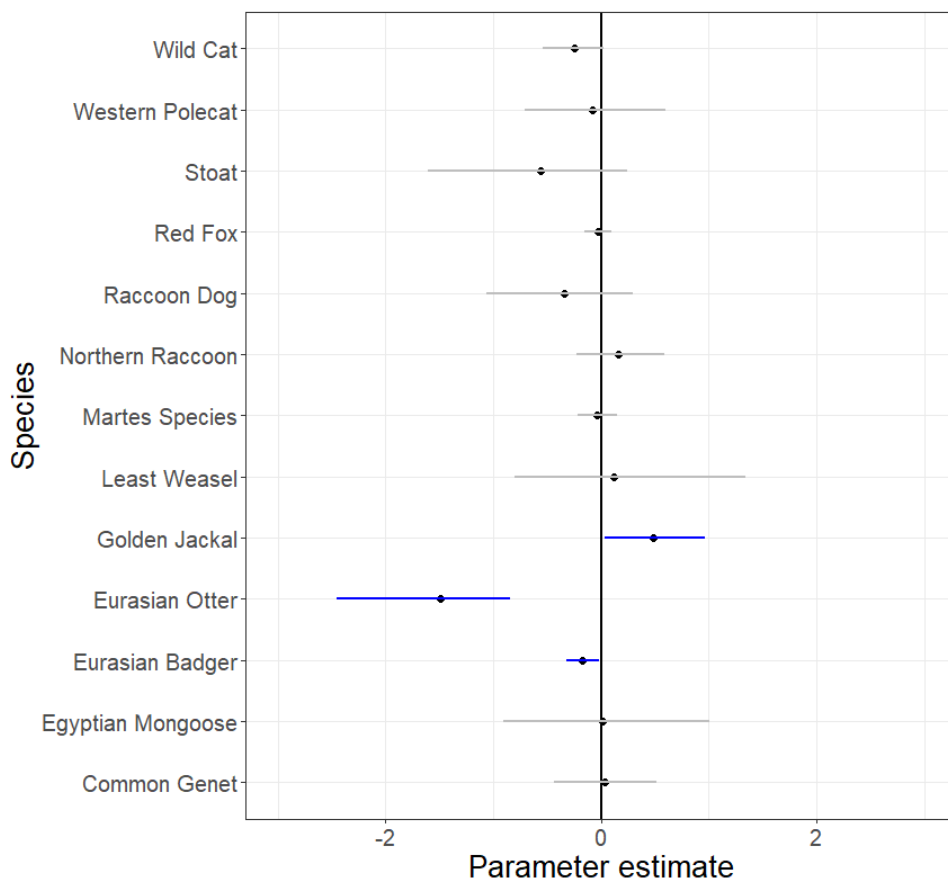
Figure 5: The effect the log-transformed distance to water has on the individual species in the occupancy model. The black dots are the mean effect, and the lines represent the credible interval. Credible intervals that don't overlap zero are highlighted in blue.

The log-transformed human footprint index had a significant effect on the site-use of two species. An increasing human footprint index had a negative effect on the site-use of the wild cat with a slope of -0.41 but a positive effect on the site use of red foxes with a slope of 0.27 (Figure 6). The wild cat had the highest site-use probability of all species at the lowest human footprint index. The golden jackal

had the highest site-use probability at the highest levels of human pressure while the least weasel had the lowest. The stoat had the lowest site-use probability at a low human footprint index (Appendix 4).
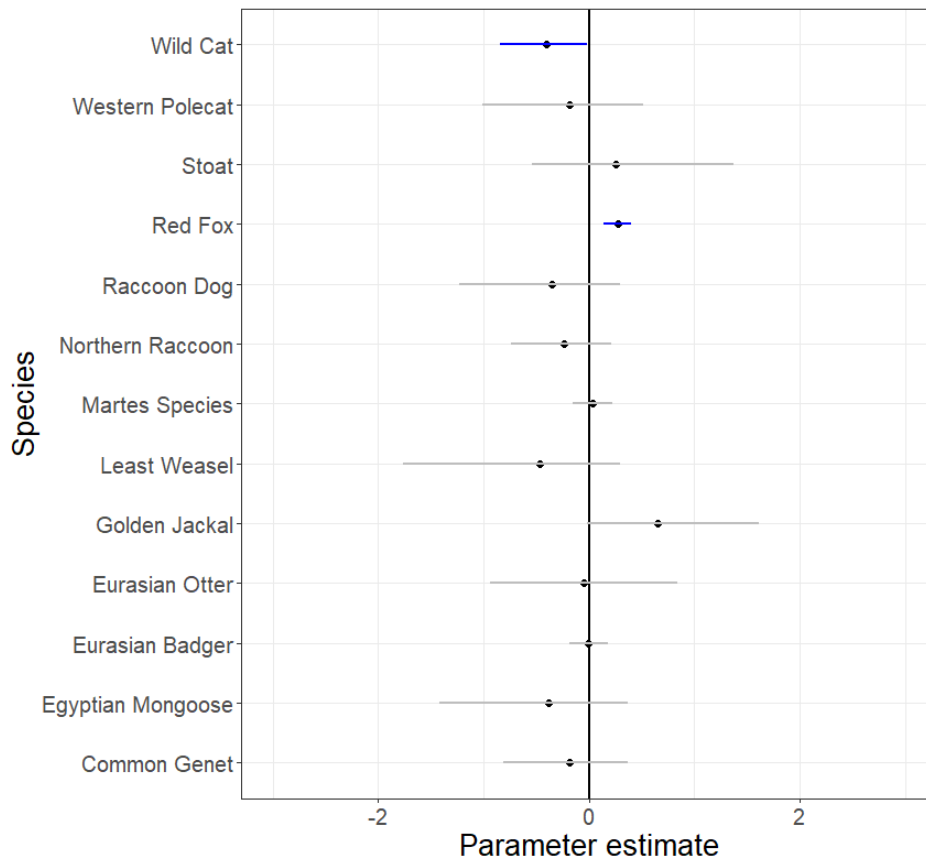
Figure 6: The effect the log-transformed human footprint index has on the individual species in the occupancy model. The black dots are the mean effect, and the lines represent the credible interval. Credible intervals that don't overlap zero are highlighted in blue.

3.1.3 Patterns of species richness

The final model that tested the hypotheses gave no strong conclusions as to how the estimated species richness was related to the environmental covariates. All estimates of the slopes of the covariates were relatively low and the credible interval overlapped zero for all estimates. When visually inspecting the plotted relationship between each parameter and the estimated species richness, no clear relationship could be seen. The area of the study sites was initially intended to be included but because of the high correlation to both habitat covariates, it was excluded.

There was a weak positive response between the estimated species richness and productivity in the form of NDVI with a mean slope of 0.20. This relationship was however still not conclusive with a credible interval between -0.13 and 0.53 (Figure 7) but 89% of the posterior had the same positive sign as the mean (Appendix 5).

Figure 7: The relationship between productivity and estimated species richness. The error bars denote the 95% CRI of the species richness estimates from the occupancy model. The red line is the regression line estimated from the two-step analysis that accounts for both posterior standard deviations and residual variation around the regression line. The dashed red line is the 95% CRI of the regression.

There was no relationship between estimated species richness and the land cover evenness. The estimated mean slope was 0.001 with a 95% CRI of -0.32 to 0.32 (Figure 8). 50% of the posterior had the same positive sign as the mean (Appendix 5).

Figure 8: The relationship between land cover evenness and estimated species richness. The error bars denote the 95% CRI of the species richness estimates from the occupancy model. The red line is the regression line estimated from the two-step analysis that accounts for both posterior standard deviations and residual variation around the regression line. The dashed red line is the 95% CRI of the regression.

The response estimated species richness had on the changing land cover richness was very low. The estimated mean slope was 0.048 with a 95% CRI between -0.26 and 0.36 (Figure 9). The proportion of the posterior that had the same positive sign as the mean was 62% (Appendix 5).

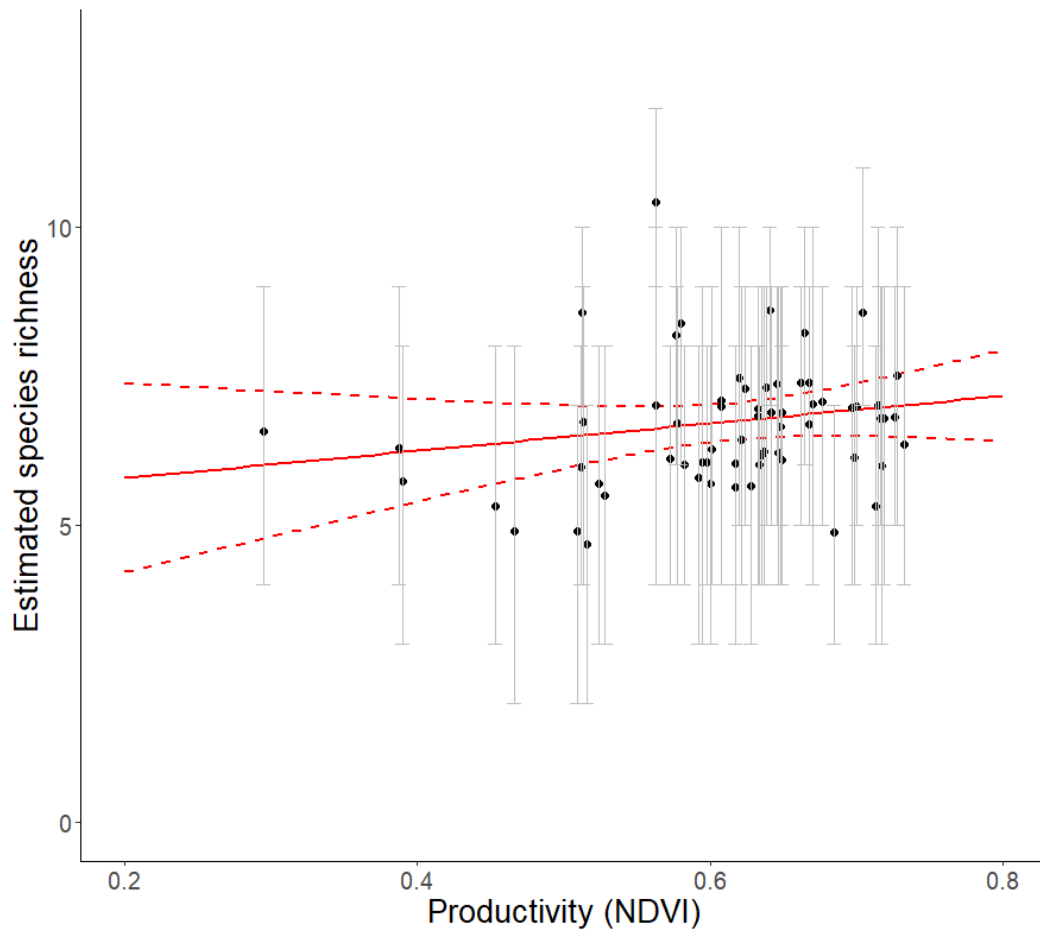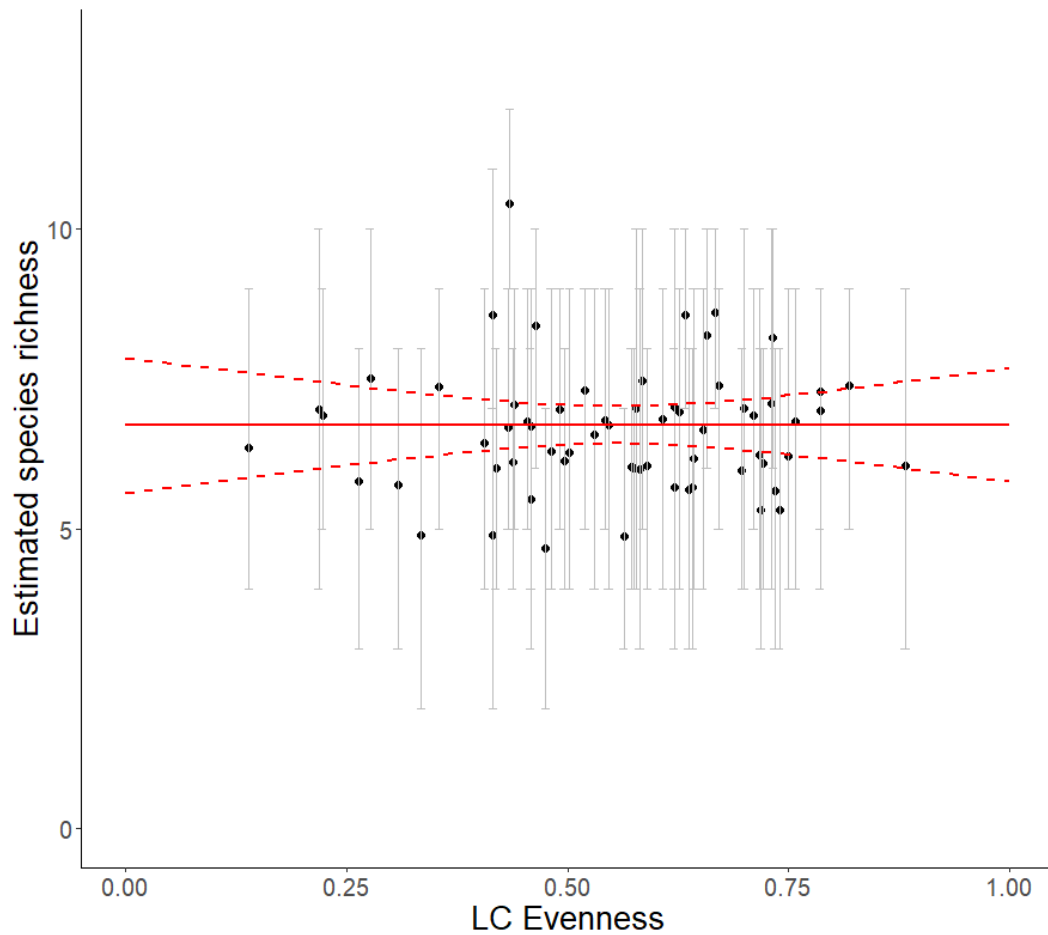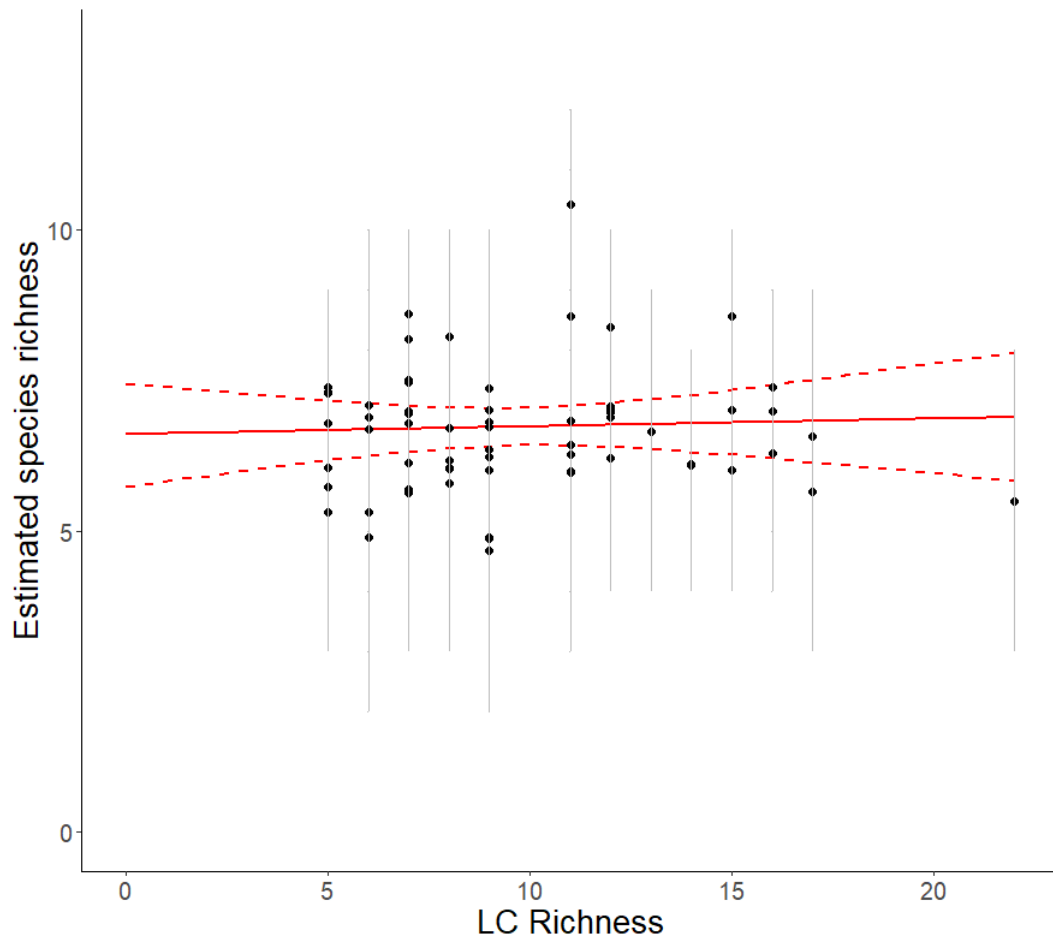*Figure 9: The relationship between land cover richness and estimated species richness. The error bars denote the 95% CRI of the species richness estimates from the occupancy model. The red line is the regression line estimated from the two-step analysis that accounts for both posterior standard deviations and residual variation around the regression line. The dashed red line is the 95% CRI of the regression.*

4. Discussion

Using a multi-scale and multi-species method of hierarchical modelling, the species richness of small carnivores was estimated in 64 sites across Europe. These species richness estimates were then modelled with three explanatory environmental variables in a meta-analysis. The occupancy model showed that the covariates used had a different effect on the site-use probability of different species but not on the community. The final meta-analysis that tested the hypotheses found weak evidence for an increase in species richness with study site productivity but no evidence of habitat richness or evenness having an impact on species richness.

4.1 Occupancy model performance

The species richness estimates can be considered accurate based on the response that individual species' detection and site-use probability had to the environmental covariates. The detection probabilities are consistent with previous studies using occupancy models on both mammals in general (Tobler et al. 2015; Feng et al. 2021) and small carnivores in particular (Li et al. 2022). The detection probability was highest for the larger species and that also meets the expectations since those both have larger home ranges and are easier to capture on camera because of their body size. Most of the species-specific site-use probabilities had associations with tree cover, distance to water and human footprint that was expected from a biological standpoint. While not all covariates had a strong association with the increase or decrease in site-use probability of a certain species, none of the effects went against the species' known preferences in terms of habitats. Most notable was the expected decrease in site-use probability of the Eurasian otter with increased distance to water since this is a clear habitat preference of the species (Kruuk 2006). Also, the associations that were not as strong still confirmed species' known habitat preferences such as the golden jackals' preference for arid grasslands and proximity to human settlements (Ćirović et al. 2016). This consistency in expected associations between the site-use probabilities and the covariates used in the occupancy model showcases the robustness of the model and the credibility of the species richness estimates on a site level.

4.2 Productivity and small carnivore richness

The hypothesis that species richness should increase with increasing productivity was probably the most solid of the hypotheses when it came to previous research. There was however no strong response to the estimated species richness of small carnivores with changing productivity in the analysis done in this thesis. The estimated species richness tended to increase with increasing productivity, which was expected according to empirical research, but the uncertainty is too great to make any definitive conclusions. The relationship between productivity and species richness has been seen to vary between different spatial scales where some scales exhibit no relationship at all (Wang et al. 1999). What is contradictory to the findings in this thesis is that it has been in smaller spatial scales some researchers have not found a relationship between productivity and species richness, but they have found a relationship at larger scales. This implies that it should be even more likely that a correlation would have been shown since all of Europe was analysed but that was not the case. Other factors than the spatial scale have therefore most likely played a role in the lack of correlation.

The sampling of study sites may have added to the uncertainty of the relationship between productivity and small carnivore species richness. The study sites were not distributed evenly across Europe and not across the gradient of productivity either. This can be seen in the point estimates in figure 7 where most of the points are at around the same productivity level and very few sites were at a very high or low productivity area. This is also illustrated by the larger credible interval, especially in the lower productivity sites. Future studies that test the correlation between species richness of small carnivores and productivity should have a more even distribution of sites in different productivity areas to be able to make sure the lack of correlation is not the cause of the sampling of study sites.

Assuming the lack of correlation between small carnivore species richness and productivity is not because of the sampling effort, the trophic level of the small carnivores can be a contributing factor. Because of the trophic level that small carnivores are in, the effect of higher productivity will not be as direct on their available resources as for herbivorous mammals. This additional step in the relationship between productivity and species richness may be the cause of the weaker evidence for a correlation compared to studies made on all mammal species together. This explanation for the lack of a strong correlation between productivity and small carnivore species richness is supported by Sandom et al. (2013) which found decreasing importance of productivity and climate to species richness when ascending the trophic levels. Li et al. (2021) also found that there was no direct correlation between productivity and carnivore species richness but an indirect correlation through the positive effect the productivity had on the abundance of

prey species. This suggests that in further studies, the abundance of prey species should be accounted for in the models using productivity as a predictor for carnivore species richness to account for the indirect effects through trophic levels.

4.3 Habitat and small carnivore richness

The connection between species richness and different measures of habitat diversity and heterogeneity have been seen to vary in intensity between studies and sometimes there has been no definitive correlation at all. This lack of consensus in the research is reflected in these analyses as well as there was very little to no association between the habitat factors and species richness of small carnivores. Although the review Tews et al. (2004) made showed that there is a majority of studies made on habitat heterogeneity and species richness or diversity that show a positive correlation, they point out a possible influence of publication bias towards positive results. The far fewer studies that saw no effect of habitat heterogeneity on species richness such as the case in the analysis done in this thesis could also possibly be because of the tendency that studies with larger effects are more likely to be published (Parker et al. 2016).

The measurements of what is classified as habitat richness also vary between studies and this could have an impact on the results. The use of methods of measuring habitat diversity also has an impact on the scale and precision of the habitat measurements. The differences in methods can make it difficult to make comparisons of results between different studies and different species may react differently to the same measure of habitat heterogeneity (Tews et al. 2004). The span of species looked at in this thesis is far narrower than in many other studies on habitat heterogeneity and species richness. This can result in these species by themselves not exhibiting the same patterns in species richness as when for example all mammal species are included. Several of these species of small carnivores are adaptive to a wide arrange of habitat types and this can cause the relationship with habitat richness and evenness to be less pronounced. The spatial scale of the measurements of the structural variable is also crucial when it comes to relating it to species richness (Tews et al. 2004). It is however difficult to discern if that is a contributing factor to the results in this thesis as studies both using habitat measurements that have lower resolution satellite data (Fløjgaard et al. 2011; Cervellini et al. 2021) and higher resolution on-site measurements (Kallimanis et al. 2008) that have found positive relationships between habitat diversity and species richness or diversity.

The temporal aspect of the measurements that I used to classify the richness and evenness of the habitats can also have impacted the results. Since the data set of

land cover is several years old by the time of the study period, the evenness and richness measurements may not be accurate anymore at all the sites.

The size or connectivity of the different types of habitats was not considered in the correlation between habitat richness, evenness and species richness. This may result in there being a high habitat richness and low evenness but only because the landscape is highly fragmented with small patches of habitats that cannot sustain a significant number of species. As a high habitat richness or a low evenness also can represent fragmentation that may have a negative effect on the species richness in a site. Higher fragment isolation and reduced fragment area reduce species richness (Haddad et al. 2015). The degree of fragmentation and connectivity should therefore be included in future studies exploring the correlation between habitat structure and small carnivore species richness to account for the quality of the habitat richness available in the study sites. The effect of fragmentation on carnivore occupancy can however differ between different species (Crooks 2002) making these factors best to implement as species-specific.

4.4 Limitations

No data augmentation, adding unseen species, was done in these analyses and this resulted in only the species that were detected at any of the study sites to be included. This excluded some of the other small carnivores that can be found in Europe such as the steppe polecat (*Mustela eversmanii*) and the Marbled polecat (*Vormela peregusna*). An added number of missed species can however make the species richness estimates unreasonably high (Guillera-Arroita et al. 2019), therefore, adding more species that were missed could make the richness estimates more unreliable than when they are excluded. The decision was made to keep the exotic species northern raccoon (*Procyon lotor*) and the raccoon dog (*Nyctereutes procyonoides*). The results did not differ and none of the environmental factors made a significant impact on the species richness when they were included or excluded.

There are also additional factors that can affect the species richness at any given study site that was not accounted for in the models. The impact that larger carnivores could have on the species richness of the small carnivores, in general, was not considered in this study. The distributions of larger carnivores differ between study sites (Chapron et al. 2014) and since the presence of large carnivores can have a negative effect on the presence of smaller carnivores (Prugh & Sivy 2020) this could also impact the final results as it was not considered in the models. Human activities other than the human footprint index were not accounted for either. There could be a varying effect of hunting of some of the small carnivores

included that could influence the species richness in a study site. This effect could both be direct by the number of individuals of a particular species being reduced and by the change in interactions. The change in the density of one carnivore species can greatly affect the density of other carnivores (Linnell & Strand 2000) and this possible change in dynamics based on human interference has not been accounted for.

The design of the method may have been a contributing factor to the vague nature of the results of the relationship between the estimated species richness and the productivity and habitat factors. Using a two-step analysis and propagating the uncertainty makes the analysis more robust but it has a larger overall uncertainty, making vague results more likely to be not significant.

Some of the study sites had fewer cameras after the filtering of the placements and removal of non-functioning cameras than the protocol for the Snapshot Europe project demanded. These were still included as the number of study sites would be decreased if the ones below the limit of active cameras were removed. Having sites with as few as 5 cameras could add uncertainty. The number of cameras was however accounted for in the occupancy model by including the camera effort and the site-use probability around the individual cameras. Because the sites with very few cameras were accounted for in the occupancy model and would be given a higher uncertainty to the richness estimates, it was decided that keeping them would not seriously affect the credibility of the richness estimates. The extent of the uncertainty was also carried over to the final model where the richness estimates were checked for correlation with the productivity and habitat factors, making sure they were accurately represented.

Though there was a general standardization of how the cameras should be set up there is variation in methods of choosing placements, where some may use a strictly systematic placement whereas others use random placements. Some cameras were placed on different kinds of trails which would affect the detection probability. This is something that probably should have been corrected for in the modelling of detection probability, especially since carnivore species show a higher probability of being caught on camera at game trail placements (Cusack et al. 2015). The potential error is then that the model assumes that the detection probability of a species should be the same between deployments, only depending on the effort, which may not have been the case.

4.5 Conclusion

The occupancy model performance showed a consistency in the expected associations between the site-use probabilities and the environmental covariates, indicating the credibility of the species richness estimates on a site level. However, the final meta-analysis did not find any strong relationships between the estimated species richness and the environmental covariates.

The hypothesis that species richness should increase with increasing productivity was not strongly supported in this study. Although the estimated species richness tended to increase with increasing productivity, the uncertainty was too great to make any definitive conclusions. The trophic level of the small carnivores may be a contributing factor, as the effect of higher productivity on their available resources may not be as direct as for herbivorous mammals.

The connection between habitat diversity and small carnivore richness was also not strongly supported in this study, with very little to no association found between the habitat factors and species richness of small carnivores. The effect of fragmentation on habitat heterogeneity may, however, had an impact on the results.

Overall, this study provides insights into the species richness of small carnivores in Europe and the factors that may affect it. However, further studies with a stratified sample of sites through the range of the studied environmental factors that are accounting for the indirect effects through trophic levels and habitat composition are needed to draw more definitive conclusions.

References

Bonn, A., Storch, D. & Gaston, K.J. (2004). Structure of the Species-Energy Relationship. *Proceedings: Biological Sciences*, 271 (1549), 1685–1691

Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, 21 (9), 873–885. https://doi.org/10.1111/j.1466-8238.2011.00737.x

Bueno, A.S. & Peres, C.A. (2019). Patch-scale biodiversity retention in fragmented landscapes: Reconciling the habitat amount hypothesis with the island biogeography theory. *Journal of biogeography*, 46 (3), 621–632. https://doi.org/10.1111/jbi.13499

Cerezer, F.O., Cáceres, N.C. & Dambros, C.S. (2021). Effect of Productivity on Community Size Explains the Latitudinal Diversity Gradient of South American Small Mammals. *The American Naturalist*, 198 (4), E111–E121. https://doi.org/10.1086/716171

Cervellini, M., Di Musciano, M., Zannini, P., Fattorini, S., Jiménez-Alfaro, B., Agrillo, E., Attorre, F., Angelini, P., Beierkuhnlein, C., Casella, L., Field, R., Fischer, J.-C., Genovesi, P., Hoffmann, S., Irl, S.D.H., Nascimbene, J., Rocchini, D., Steinbauer, M., Vetaas, O.R. & Chiarucci, A. (2021). Diversity of European habitat types is correlated with geography more than climate and human pressure. *Ecology and Evolution*, 11 (24), 18111–18124. https://doi.org/10.1002/ece3.8409

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., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D. & 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

Ćirović, D., Penezić, A. & Krofel, M. (2016). Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes. *Biological conservation*, 199, 51–55. https://doi.org/10.1016/j.biocon.2016.04.027

Coops, N.C., Bolton, D.K., Hobi, M.L. & Radeloff, V.C. (2019). Untangling multiple species richness hypothesis globally using remote sensing habitat indices. *Ecological Indicators*, 107, 105567. https://doi.org/10.1016/j.ecolind.2019.105567

Crooks, K.R. (2002). Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation. *Conservation biology*, 16 (2), 488–502. https://doi.org/10.1046/j.1523-1739.2002.00386.x

Cusack, J.J., Dickman, A.J., Rowcliffe, J.M., Carbone, C., Macdonald, D.W. & Coulson, T. (2015). Random versus Game Trail-Based Camera Trap Placement Strategy for Monitoring Terrestrial Mammal Communities. *PLOS ONE*, 10 (5), e0126373. https://doi.org/10.1371/journal.pone.0126373

Didan, K. (2021). MODIS/Terra Vegetation Indices 16-Day L3 Global 500m SIN Grid V061. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MOD13A1.061

DiMiceli, C., Carroll, M., Sohlberg, R., Kim, D.-H., Kelly, M. & Townshend, J. (2015). MOD44B MODIS/Terra Vegetation Continuous Fields Yearly L3 Global 250m SIN Grid V006. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MOD44B.006

EU (2022). *Commission Implementing Regulation (EU) 2016/1141 of 13 July 2016 adopting a list of invasive alien species of Union concern pursuant to Regulation (EU) No 1143/2014 of the European Parliament and of the Council*. 1–9. http://data.europa.eu/eli/reg_impl/2016/1141/2022-08-02/eng [2023-06-18]

European Environment Agency (2019). Ecosystem types of Europe 2012 - Terrestrial habitats. https://sdi.eea.europa.eu/catalogue/srv/eng/catalog.search#/metadata/7c0cf3f2-ab54-4cd0-a635-b322df7197f6 [2023-05-12]

Feng, J., Sun, Y., Li, H., Xiao, Y., Zhang, D., Smith, J.L.D., Ge, J. & Wang, T. (2021). Assessing mammal species richness and occupancy in a Northeast Asian temperate forest shared by cattle. *Diversity and Distributions*, 27 (5), 857–872. https://doi.org/10.1111/ddi.13237

Fløjgaard, C., Normand, S., Skov, F. & Svenning, J.-C. (2011). Deconstructing the mammal species richness pattern in Europe – towards an understanding of the relative importance of climate, biogeographic history, habitat heterogeneity and humans. *Global Ecology and Biogeography*, 20 (2), 218–230. https://doi.org/10.1111/j.1466-8238.2010.00604.x

Fritz, S.A., Eronen, J.T., Schnitzler, J., Hof, C., Janis, C.M., Mulch, A., Böhning-Gaese, K. & Graham, C.H. (2016). Twenty-million-year relationship between mammalian diversity and primary productivity. *Proceedings of the National Academy of Sciences of the United States of America*, 113 (39), 10908–10913

GBIF.org (2023). GBIF Occurrence Download. https://doi.org/10.15468/dl.f6dv4r [2023-01-31]

Gerngross, P., Ambarli, H., Angelici, F.M., Anile, S., Campbell, R., Ferreras de Andres, P., Gil-Sanchez, J.M., Götz, M., Jerosch, S., Mengüllüoğlu, D., Monterroso, P., & Zlatanova, D. (2022). Felis silvestris (spatial data) Version 2022-2.

Guillera-Arroita, G., Kéry, M. & Lahoz-Monfort, J.J. (2019). Inferring species richness using multispecies occupancy modeling: Estimation performance and interpretation. *Ecology and Evolution*, 9 (2), 780–792. https://doi.org/10.1002/ece3.4821

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X. & Townshend, J.R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1 (2). https://doi.org/10.1126/sciadv.1500052

Herrero, J., Kranz, A., Skumatov, D., Abramov, A., Maran, T. & Monakhov, V.G. (2015). IUCN Red List of Threatened Species: Martes martes. *IUCN Red List of Threatened Species,*. https://www.iucnredlist.org/en [2023-04-02]

Hortal, J., Rodríguez, J., Nieto-Díaz, M. & Lobo, J.M. (2008). Regional and environmental effects on the species richness of mammal assemblages. *Journal of Biogeography*, 35 (7), 1202–1214. https://doi.org/10.1111/j.1365-2699.2007.01850.x

Hurlbert, A.H. & White, E.P. (2005). Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. *Ecology Letters*, 8 (3), 319–327. https://doi.org/10.1111/j.1461-0248.2005.00726.x

IUCN (International Union for Conservation of Nature) (2008). Genetta genetta (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2014). Mustela putorius (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2015). Lutra lutra (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2016a). Herpestes ichneumon (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2016b). Martes foina (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2016c). Martes martes (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2016d). Meles meles (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2016e). Mustela erminea (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2016f). Mustela nivalis (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2016g). Nyctereutes procyonoides (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2016h). Vulpes vulpes (spatial data) Version 2022-2. https://www.iucnredlist.org

IUCN (International Union for Conservation of Nature) (2018). Canis aureus (spatial data) Version 2022-2. https://www.iucnredlist.org

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C.A., Price, S.A., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O.R.P., Gittleman, J.L., Mace, G.M. & Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90 (9), 2648–2648. https://doi.org/10.1890/08-1494.1

Kallimanis, A.S., Mazaris, A.D., Tzanopoulos, J., Halley, J.M., Pantis, J.D., Sgardelis, S.P. & McGill, B. (2008). How Does Habitat Diversity Affect the Species-Area Relationship? *Global Ecology and Biogeography*, 17 (4), 532–538

Kéry, M. & Royle, J.A. (2016). *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS*. Boston: Academic Press. https://doi.org/10.1016/B978-0-12-801378-6.00011-4

Kruuk, H. (2006). *Otters Ecology, Behaviour and Conservation*. Oxford: University Press, UK.

Li, J., Li, D., Hacker, C., Dong, W., Wu, B. & Xue, Y. (2022). Spatial co-occurrence and temporal activity patterns of sympatric mesocarnivores

guild in Qinling Mountains. *Global Ecology and Conservation*, 36, e02129. https://doi.org/10.1016/j.gecco.2022.e02129

Li, X.Y., Bleisch, W.V., Liu, X.W., Hu, W.Q. & Jiang, X.L. (2021). Human disturbance and prey occupancy as predictors of carnivore richness and biomass in a Himalayan hotspot. *Animal Conservation*, 24 (1), 64–72. https://doi.org/10.1111/acv.12600

Linnell, J.D.C. & Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions*, 6 (4), 169–176. https://doi.org/10.1046/j.1472-4642.2000.00069.x

Losos, J.B. & Ricklefs, R.E. (2009). *The Theory of Island Biogeography Revisited*. Course Book. Princeton, NJ: Princeton University Press. https://doi.org/10.1515/9781400831920

Marneweck, C.J., Allen, B.L., Butler, A.R., Do Linh San, E., Harris, S.N., Jensen, A.J., Saldo, E.A., Somers, M.J., Titus, K., Muthersbaugh, M., Vanak, A. & Jachowski, D.S. (2022). Middle-out ecology: small carnivores as sentinels of global change. *Mammal Review*, 52 (4), 471–479. https://doi.org/10.1111/mam.12300

Max Planck Institute of Animal Behaviour & EUROMAMMALS (n.d.). *Snapshot Europe*. *Snapshot Europe*. https://app.wildlifeinsights.org/initiatives/2000166/Snapshot-Europe. [2022-09-06]

McCain, C.M., King, S.R.B., Szewczyk, T. & Beck, J. (2018). Small mammal species richness is directly linked to regional productivity, but decoupled from food resources, abundance, or habitat complexity. *Journal of Biogeography*, 45 (11), 2533–2545. https://doi.org/10.1111/jbi.13432

Niedziałkowska, M., Kończak, J., Czarnomska, S. & Jędrzejewska, B. (2010). Species Diversity and Abundance of Small Mammals in Relation to Forest Productivity in Northeast Poland. *Ecoscience*, 17 (1), 109–119. https://doi.org/10.2980/17-1-3310

Oliveira, T., Urra, F., López-Martín, J.M., Ballesteros-Duperón, E., Barea-Azcón, J.M., Moléon, M., Gil-Sánchez, J.M., Alves, P.C., Díaz-Ruíz, F., Ferreras, P. & Monterroso, P. (2018). Females know better: Sex-biased habitat selection by the European wildcat. *Ecology and evolution*, 8 (18), 9464–9477. https://doi.org/10.1002/ece3.4442

Parker, T.H., Forstmeier, W., Koricheva, J., Fidler, F., Hadfield, J.D., Chee, Y.E., Kelly, C.D., Gurevitch, J. & Nakagawa, S. (2016). Transparency in Ecology and Evolution: Real Problems, Real Solutions. *Trends in Ecology & Evolution*, 31 (9), 711–719. https://doi.org/10.1016/j.tree.2016.07.002

Pinborg, U. (2002). *Europe's biodiversity - biogeographical regions and seas — European Environment Agency*. (1/2002). European Environment Agency. https://www.eea.europa.eu/publications/report_2002_0524_154909 [2023-05-08]

Prugh, L.R. & Sivy, K.J. (2020). Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. *Ecology Letters*, 23 (5), 902–918. https://doi.org/10.1111/ele.13489

QGIS.org (2022). *QGIS Geographic Information System* (3.28.0). QGIS Association. http://www.qgis.org

Qian, H. (2010). Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. *Ecological Research*, 25 (3), 629–637. https://doi.org/10.1007/s11284-010-0695-1

R Core Team (2022). *R: A Language and Environment for Statistical Computing* (4.2.2). Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Roemer, G.W., Gompper, M.E. & Valkengurgh, B.V. (2009). The Ecological Role of the Mammalian Mesocarnivore. *BioScience*, 59 (2), 165–173. https://doi.org/10.1525/bio.2009.59.2.9

Sandom, C., Dalby, L., Fløjgaard, C., Kissling, W.D., Lenoir, J., Sandel, B., Trøjelsgaard, K., Ejrnæs, R. & Svenning, J.-C. (2013). Mammal predator and prey species richness are strongly linked at macroscales. *Ecology*, 94 (5), 1112–1122. https://doi.org/10.1890/12-1342.1

Smith, F. (2004). Macroecological database of mammalian body mass. National Center for Ecological Analysis and Synthesis. https://knb.ecoinformatics.org/view/doi:10.5063/AA/nceas.196.3 [2023-01-13]

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004). Animal Species Diversity Driven by Habitat Heterogeneity/Diversity: The Importance of Keystone Structures. *Journal of Biogeography*, 31 (1), 79–92

Tobler, M.W., Hartley, A.Z., Carrillo-Percastegui, S.E. & Powell, G.V.N. (2015). Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *Journal of Applied Ecology*, 52 (2), 413–421

Van Valkenburgh, B. & Wayne, R.K. (2010). Carnivores. *Current Biology*, 20 (21), R915–R919. https://doi.org/10.1016/j.cub.2010.09.013

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A. & Watson, J.E.M. (2016). Global terrestrial Human Footprint maps for 1993 and 2009. *Scientific Data*, 3 (1), 160067. https://doi.org/10.1038/sdata.2016.67

Wang, G., Wang, Z., Zhou, Q. & Zhong, W. (1999). Relationship between species richness of small mammals and primary productivity of arid and semi-arid grasslands in north China. *Journal of Arid Environments*, 43 (4), 467–475. https://doi.org/10.1006/jare.1999.0572

Wang, G., Zhou, Q., Zhong, W., Sun, C. & Chen, Z. (2001). Species richness — primary productivity relationship of plants and small mammals in the Inner Mongolian steppes, China. *Journal of Arid Environments*, 49 (3), 477–484. https://doi.org/10.1006/jare.2001.0814

Wildlife Insights (n.d.). *Home | Wildlife Insights*. https://www.wildlifeinsights.org/ [2023-03-14]

Acknowledgements

I would like to express my deepest gratitude and appreciation to my supervisor, Tim Hofmeester, for his invaluable guidance, support, and encouragement throughout the entire process of completing this thesis. His expertise, patience, and dedication have been instrumental in shaping my research and academic journey. I am truly grateful for the time and effort he invested in me.

I am also immensely thankful to my friends and family who have stood by my side during this whole endeavour. Their belief in my abilities and constant encouragement has provided me with the strength and motivation to overcome obstacles and reach the finish line.

Appendix 1: Description of the multi-species multi-scale occupancy model in JAGS

```
# Priors
for(i in 1:n.spec){

  # psi

  lpsi[i] ~ dnorm(mu.lpsi, tau.lpsi)

  # theta

  ltheta[i] ~ dnorm(mu.ltheta[i], tau.ltheta[i])
  mu.ltheta[i] <- delta0.ltheta + delta1.ltheta * logmass[i]
  tau.ltheta[i] <- 1/var.ltheta[i]
  log(var.ltheta[i]) <- phi0.ltheta + phi1.ltheta * logmass[i]

  betaltheta1[i] ~ dnorm(mu.betaltheta1, tau.betaltheta1)
  betaltheta2[i] ~ dnorm(mu.betaltheta2, tau.betaltheta2)
  betaltheta3[i] ~ dnorm(mu.betaltheta3, tau.betaltheta3)

  # p

  lp[i] ~ dnorm(mu.lp[i], tau.lp[i])
  mu.lp[i] <- delta0.lp + delta1.lp * logmass[i]
  tau.lp[i] <- 1/var.lp[i]
  log(var.lp[i]) <- phi0.lp + phi1.lp * logmass[i]
}
betalp1 ~ dnorm(mu.betalp1, tau.betalp1)

# Priors for regression params for means
delta0.ltheta ~ dnorm(0, 0.01)
delta1.ltheta ~ dnorm(0, 0.01)
delta0.lp ~ dnorm(0, 0.01)
delta1.lp ~ dnorm(0, 0.01)
```

```
# Priors for regression params for variances
phi0.ltheta ~ dnorm(0, 0.01)
phi1.ltheta ~ dnorm(0, 0.01)
phi0.lp ~ dnorm(0, 0.01)
phi1.lp ~ dnorm(0, 0.01)

## Hyperpriors
# For the model of site-use

mu.lpsi ~ dnorm(0,0.01)
tau.lpsi <- pow(sd.lpsi, -2)
sd.lpsi ~ dunif(0,6)

# For the model of site-use

mu.betaltheta1 ~ dnorm(0, 0.1)
tau.betaltheta1 <- pow(sd.betaltheta1, -2)
sd.betaltheta1 ~ dunif(0,1.5)
mu.betaltheta2 ~ dnorm(0, 0.1)
tau.betaltheta2 <- pow(sd.betaltheta2, -2)
sd.betaltheta2 ~ dunif(0,2)
mu.betaltheta3 ~ dnorm(0, 0.1)
tau.betaltheta3 <- pow(sd.betaltheta3, -2)
sd.betaltheta3 ~ dunif(0,2)

# For the model of detection

mu.betalp1 ~ dnorm(0, 0.01)
tau.betalp1 <- pow(sd.betalp1, -2)
sd.betalp1 ~ dunif(0,700)

# Occurrence in study area j

for(i in 1:n.spec) {
  for (j in 1:n.site) {
  z[i,j] ~ dbern(psi[i,j])
  logit(psi[i,j]) <- lpsi[i]
  }
}
```

```
# site-use probability at cam k

for(i in 1:n.spec) {
  for(j in 1:n.site) {
    for(k in 1: n.cams) {
    a[i,j,k] ~ dbern(mu.a[i,j,k])
    mu.a[i,j,k] <- z[i,j] * theta[i,j,k]
    logit(theta[i,j,k]) <- ltheta[i] + betaltheta1[i] * TC[i,j,k] + betaltheta2[i] *
WD[i,j,k] + betaltheta3[i] * HFP[i,j,k]
    }
  }
}

# detection probability during survey l

for(i in 1:n.spec) {
  for(j in 1:n.site) {
    for(k in 1:n.cams) {
      for(l in 1:n.surveys) {
      y[i,j,k,l] ~ dbern(mu.y[i,j,k,l])
      mu.y[i,j,k,l] <- a[i,j,k] * p[i,j,k,l]
      logit(p[i,j,k,l]) <- lp[i] + betalp1 * effort[i,j,k,l]
      }
    }
  }
}
```
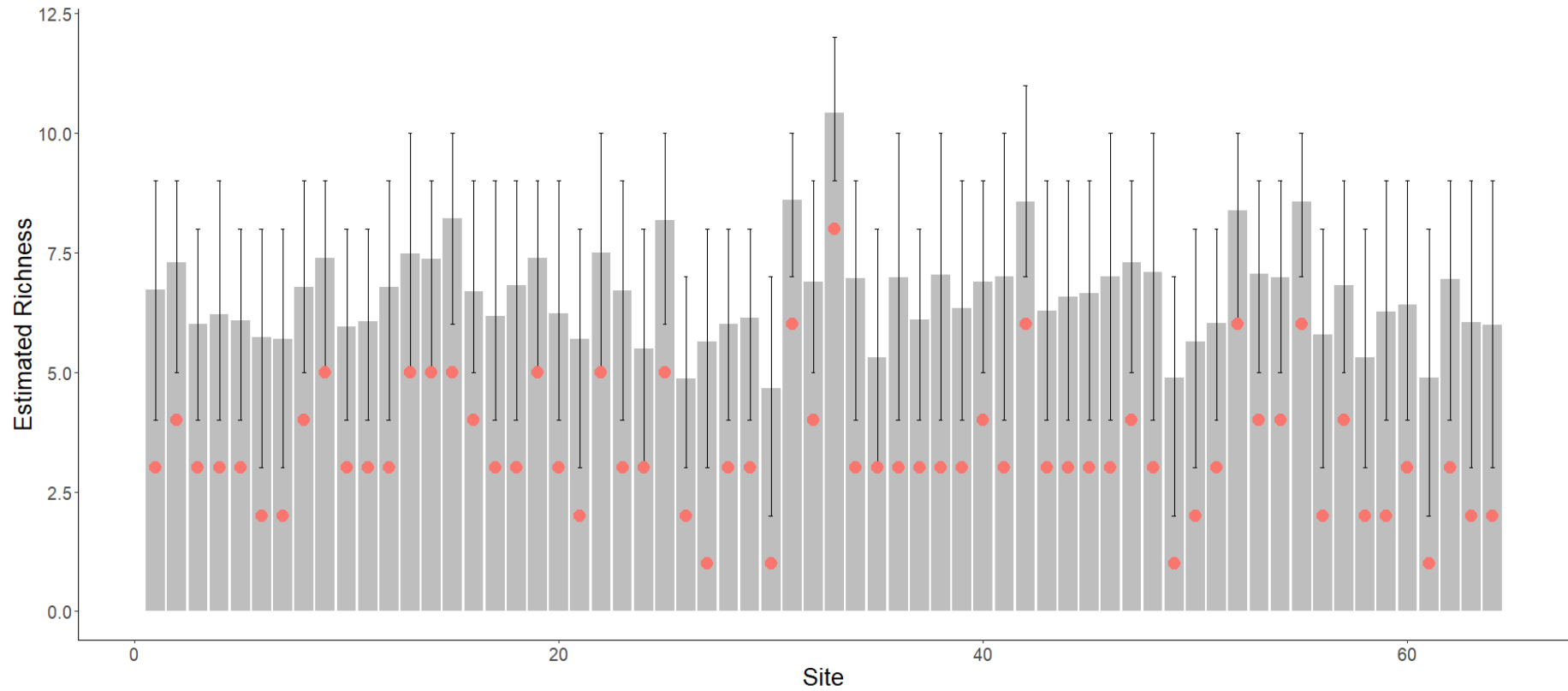
# Appendix 2: Comparison of observed and predicted species richness

The estimations of species richness in the 64 sites across Europe with error bars showing the CRI of the estimates. Observed species richness in each site is marked with a red dot.

Appendix 3: Mean detection probability per species

*Results of the mean detection probability per species from the occupancy model.*

Species	Detection probability
Martes sp.	0.08
Common genet	0.06
Egyptian mongoose	0.07
Eurasian badger	0.12
Eurasian otter	0.19
Golden jackal	0.18
Least weasel	0.01
Northern raccoon	0.09
Raccoon dog	0.10
Red fox	0.16
Stoat	0.04
Western polecat	0.04
Wild cat	0.07

Appendix 4: Species-specific effects on detection and site-use probability
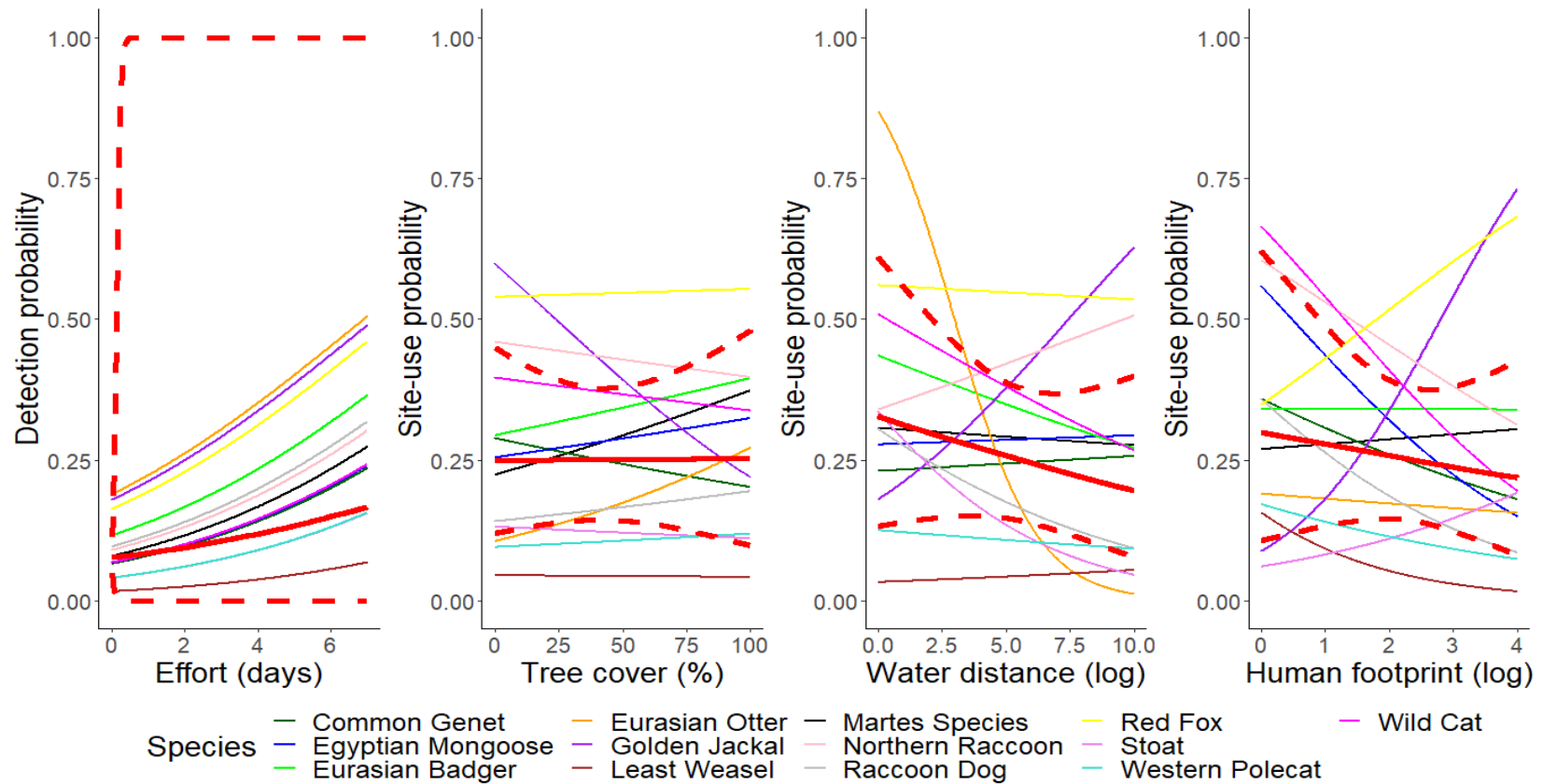
The species-specific effects the covariates had on the detection and site-use probability in the occupancy model. Community median effect is shown as a solid red line and the CRI is represented by the red dashed lines.

Appendix 5: Distribution of posteriors of effects on species richness
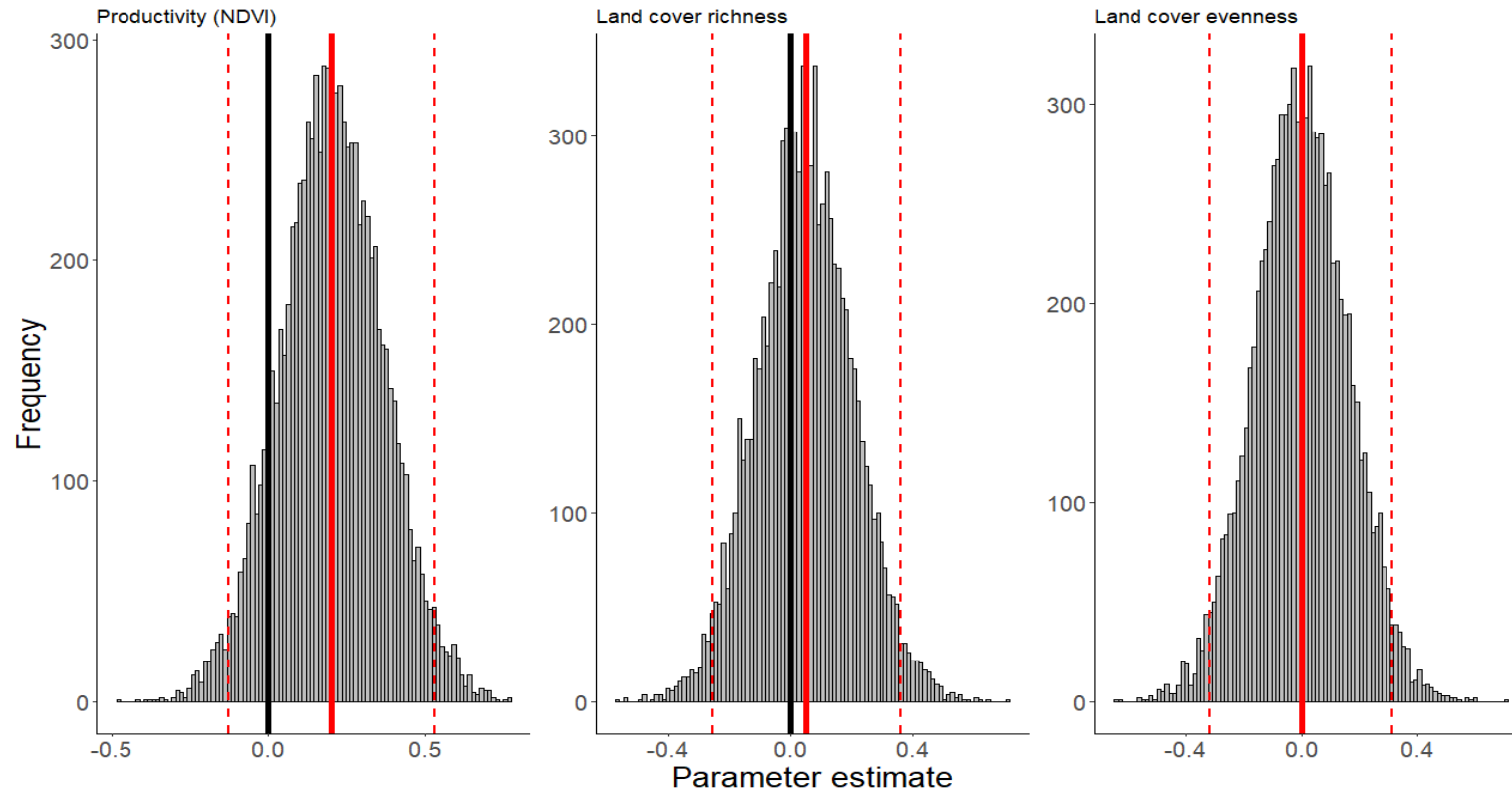
Distribution of the posterior of the effect the productivity and habitat covariates had on the species richness of small carnivores. The mean is marked with a solid red line and the red dashed lines represent the CRI.

Publishing and archiving

Approved students' theses at SLU are published electronically. As a student, you have the copyright to your own work and need to approve the electronic publishing. If you check the box for **YES**, the full text (pdf file) and metadata will be visible and searchable online. If you check the box for **NO**, only the metadata and the abstract will be visible and searchable online. Nevertheless, when the document is uploaded it will still be archived as a digital file. If you are more than one author, the checked box will be applied to all authors. You will find a link to SLU's publishing agreement here:

- https://libanswers.slu.se/en/faq/228318.

☒ YES, I/we hereby give permission to publish the present thesis in accordance with the SLU agreement regarding the transfer of the right to publish a work.

☐ NO, I/we do not give permission to publish the present work. The work will still be archived and its metadata and abstract will be visible and searchable.