



Impacts of zoning and landscape structure on the relative abundance of wild boar assessed through a Bayesian N-mixture model

Bollen Martijn^{a,b,c,*}, Neyens Thomas^{b,d}, Beenaerts Natalie^a, Casaer Jim^c

^a Centre for Environmental Sciences, UHasselt – Hasselt University, Diepenbeek, Belgium

^b Data Science Institute, UHasselt – Hasselt University, Diepenbeek, Belgium

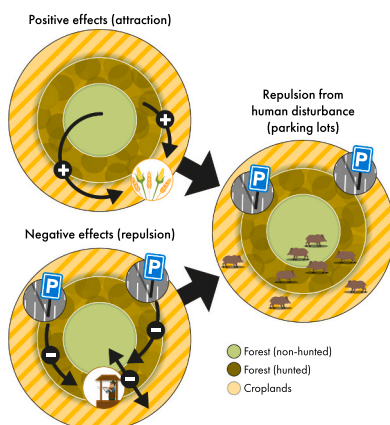
^c Research Institute for Nature and Forest, Brussels, Belgium

^d Leuven Biostatistics and statistical Bioinformatics Centre, KU Leuven, Leuven, Belgium

HIGHLIGHTS

- Wild boar land-use intensities vary across hunting management zones
- Environmental, management and anthropogenic factors drive wild boar land-use
- Wild boar land-use intensity was negatively affected by non-lethal human disturbances
- Wild boar land-use intensity increased towards the centre of the forest

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Rafael Mateo Soria

Original content: [Supplementary data to "Impacts of zoning and spatial confounders of zones on the abundance of wild boar assessed through a Bayesian N-mixture Model" \(Original data\)](#)

Keywords:

Agricultural crops
Agro-ecosystem
Camera traps
Human-wildlife interaction

ABSTRACT

Increasing human-wild boar interactions have led to damage to agricultural crops, traffic collisions and disease transmissions. Dividing natural areas in zones with differential hunting pressure is one of the currently adopted management strategies. However, the effectiveness of this approach is under debate. Hence, there is a need to better understand how to mitigate negative human-wild boar interactions effectively.

Camera traps are cost-efficient, and non-invasive tools to monitor animal populations. N-mixture models can reliably estimate spatial variation in relative abundances when animals are imperfectly detected and/or cannot be individually identified. Thus, they are useful tools to infer the impacts of several factors on the land-use intensity of wild boar, based on camera trap data.

In a nature area in central Belgium, we compare “summer” (April–September) land-use intensity of wild boar from 2018 until 2021 between three zones: a hunting free core zone, a winter hunting zone where hunting only takes place between November and March, and a year-round hunting zone. The latter is also close to the forest edge, agricultural crops and settlements. We compare spatial abundance models that capture these zone effects,

* Corresponding author at: Agoralaan, Building D, Diepenbeek, Belgium.

E-mail address: martijn.bollen@uhasselt.be (B. Martijn).

<https://doi.org/10.1016/j.scitotenv.2023.168546>

Received 26 June 2023; Received in revised form 8 November 2023; Accepted 11 November 2023

Available online 17 November 2023

0048-9697/© 2023 Elsevier B.V. All rights reserved.

or attractive effects of croplands, repulsive effects of hunting and repulsive effects of non-lethal human disturbances.

We reveal between zone differences in wild boar land-use intensities across all summers. Additionally, we find that non-lethal human disturbance and croplands also explain variation in wild boar land-use intensity, but do not find negative associations with hunting locations. Our results suggest that the effects of zoning on wild boar land-use patterns are relevant in medium-sized natural areas. Moreover, we identify the need to install additional cameras outside of the managed area in order to assess the impacts of hunting in combination with non-lethal human activities on wild boar to mitigate negative human-wild boar interactions in the future.

1. Introduction

During recent decades, humans have conditioned the success of mammal populations (Tucker et al., 2021). Human disturbance, loss of habitats, and other factors have led to the (near) extinction of species that were unable to adapt to contemporary landscapes (“human-avoiders”). Conversely, species that succeeded in adapting to these human-dominated landscapes (“synanthropic”) have expanded their geographical ranges and/or increased in density (Ledger et al., 2022). Most likely, these synanthropic species have learned to exploit some of the benefits associated with contemporary land-use changes and other recent changes, such as supplemental food and water resources, shelter and altered climates. Wild boar is exemplary of a synanthropic species, with strong increases in boar population size observed during recent decades (Barrios-Garcia and Ballari, 2012; Massei et al., 2015). Higher food availability due to agricultural intensification, as well as milder winters have been suggested as the main reasons for these strong increases in wild boar population size (Barrios-Garcia and Ballari, 2012; Vetter et al., 2020).

As a consequence, human-wild boar interactions are increasing, which leads to both positive and negative encounters. The latter include damage to agricultural crops, traffic collisions and disease transmission (Schley et al., 2008; Jägerbrand et al., 2018; Triguero-Ocaña et al., 2021). In an attempt to mitigate these impacts, hunting regimes are commonly regarded as the most important strategy (Keuling et al., 2008). Although the effectiveness of current hunting practices is challenged by Massei et al. (2015), hunting remains the prime source of wild boar mortality in European countries (Keuling et al., 2013). For hunting to be effective, sufficient hunting posts should be occupied at the same time (Vajas et al., 2020; Fernandez-De-Simon et al., 2023). Under these circumstances, hunting can act as a good method for population control (Quirós-Fernández et al., 2017). Moreover, hunting has been reported to alter the spatial behaviour of ungulates including wild boar, which seek refuge in areas adjacent to hunting grounds, in which hunting is prohibited (Tolon et al., 2009; Grignolio et al., 2011; Colomer et al., 2021). However, there is an ongoing debate about this “reserve effect”, as other studies did not find evidence of wild boar adjusting their spatial behaviour in relation to the presence of hunters (Brogi et al., 2020; Reinke et al., 2021). This suggests that the reserve effect should be evaluated case-by-case, and is likely modulated by the method of hunting, the size of the refuge area (*i.e.*, the reserve), landscape composition, and other forms of anthropogenic disturbance (Fattebert et al., 2017; Brogi et al., 2020). The presence of nearby reserves has been linked to increased crop damage by wild boar (Amici et al., 2012). As the economic impacts of crop damage are extensive, successfully confining wild boar into nature areas should be a prime management concern (Schley et al., 2008). One option to achieve this is to focus hunting efforts in a “buffer zone” around a protected “core zone”, *i.e.*, the reserve. Ideally, this leads to a higher risk perception in the buffer zone, preventing movement across this zone towards adjacent croplands (Linderoth, 2010).

Camera traps (CTs) allow to investigate a possible reserve effect in a cost-effective and non-invasive way (Colomer et al., 2021; Reinke et al., 2021). Although they are less useful to record finer-scale movements than tracking devices (Ferrer-Ferrando et al., 2023), modelling

differences in space use or abundance may suffice to confirm or dismiss the impacts of zoning (Bollen et al., 2021; Reinke et al., 2021). The N-mixture model (NMM; (Royle, 2004)) is a convenient method allowing corrections for imperfect detection and covariate effects, which has been applied successfully in camera trapping studies aimed at ungulate populations (Keever et al., 2017; Bubnicki et al., 2019). The NMM is a mixture of two submodels, one for the latent state (*i.e.*, abundance N), and another for the actual observations, conditional on N (Kéry and Royle, 2016). Typically, the observation process is formulated through a binomial distribution, while abundances are commonly assumed to be Poisson random variables. However, other distributions have been used for both of the submodels (Joseph et al., 2009; Martin et al., 2011; Bubnicki et al., 2019; Mimmagh et al., 2022). In most realistic settings, abundances should be viewed as relative measures of intensity of site-use (or land-use) rather than a reflection of the true population size (Barker et al., 2018; Kéry, 2018; Nakashima, 2020). Hereafter, we will consistently use the term “land-use intensity” to refer to the relative abundances obtained from NMM.

In this study, we apply NMM to CT data from a study area in central Belgium to investigate whether “summer” (April – October) land-use intensities differ among zones with differential hunting pressure: a year-round hunting zone, a winter hunting zone and hunting-free core zone. We focus on the summer period, as we are primarily interested if wild boar can be successfully confined to the core zone when crops are growing, and hence the attractiveness of croplands perceived by wild boar is at its peak. During the summer, hunting is prohibited in both the winter hunting zone and hunting-free core zone, which may therefore act as a reserve. Additionally, we assess if wild boar land-use intensity can be explained by continuous fear effects caused by hunting (Keuling et al., 2008; Kohl et al., 2018). Finally, we also identify the possible impacts of other factors that may drive wild boar land-use intensity. These include landscape composition (Fattebert et al., 2017), the proximity of croplands (Keuling et al., 2009) and human disturbance (Podgórski et al., 2013).

2. Materials and methods

2.1. Study area

The study area (longitudes: 4.650°W - 4.750°W; latitudes: 50.788°N - 50.824°N) is situated in a Natura 2000 reserve called “Meerdaal” in central Belgium (Fig. 1). It has a total surface area of ~15 km², consisting of a mosaic of coniferous (mainly *Pinus sylvestris*) and broad-leaved (mainly *Quercus sp.*, *Fagus sylvatica* and *Carpinus betulus*) forest stands. The forested area in Meerdaal is surrounded by a rich mosaic of croplands, with crops growing predominantly during April–September. The most common crops are wheat, maize, potato and sugar beet, of which the former two are particularly attractive to wild boar (Herrero et al., 2006). Meerdaal has altitudes ranging from 35 to 103 m above sea-level, and is characterized by locally steep slopes. The study area has a cool temperate and moist climate, with a mean annual temperature of 11 °C and 773.2 mm rainfall (Klimaatstatistieken van de Belgische gemeenten Oud-Heverlee (nis24086), n.d). Hunting in Meerdaal is restricted to fixed locations (*i.e.* hunting posts), and must take place from 19:00 until 9:00 during Daylight Saving Time, and from 16:00 until

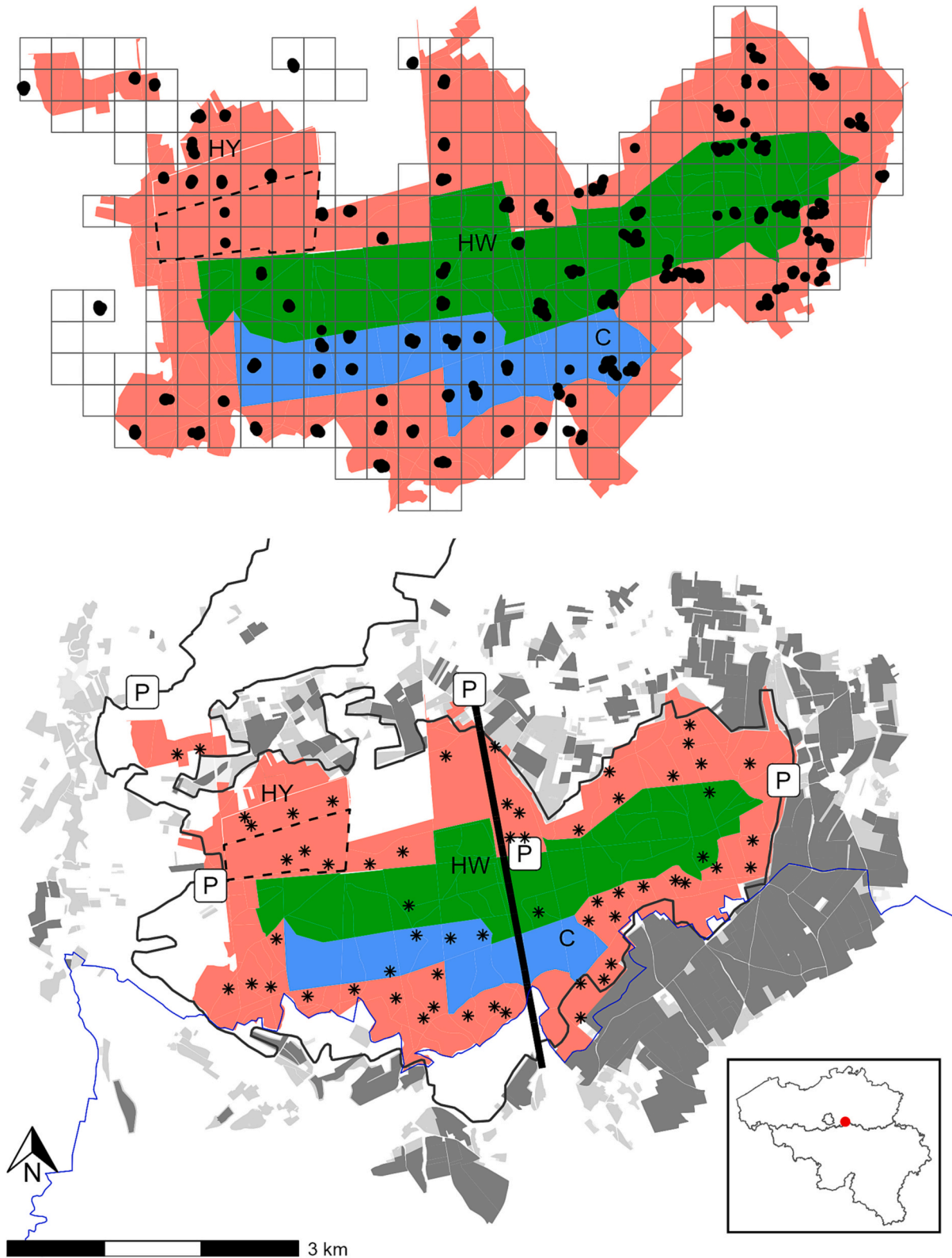


Fig. 1. Map of the study area with the overlaying square grid cells. Camera deployments are indicated by the black dots (upper). The dashed black lines encompass an area where access for humans is prohibited. Colors represent management zones; year-round hunting zone (“HY” – red), winter hunting zone (“HW” – green) and hunting-free core zone (“C” – blue). Hunting locations (asterisks), major parking lots (“P”), the major road intersecting the study area (thick black line), the forest edge (thin black line) and croplands (< 1 km from the border of the study area; gray patches) are also mapped (lower). Darker patches correspond to higher availability of crops preferred by wild boar (*i.e.*, maize and cereals). The blue line marks the administrative border between Flanders and Wallonia. The inset map (lower right) shows the study area within Belgium.

10:00 during Winter Time. In the year-round hunting zone ($\sim 9 \text{ km}^2$), wild boar is hunted year-round. In the winter hunting zone ($\sim 4 \text{ km}^2$), hunting is restricted to the time period from November until March. In the core zone ($\sim 2 \text{ km}^2$), hunting is prohibited year-round (Fig. 1). Wild boar density in and around Meerdaal, in the context of a European observatory of wildlife project by *ENETWILD*, is estimated at 7.88 ± 3.50 individuals/ km^2 using the random encounter model (Rowcliffe et al., 2008; Guerrasio et al., 2023).

2.2. Camera trapping network and data

As part of a larger monitoring framework, a subset of 13 CTs is deployed in Meerdaal, since March 2018 (Fig. 1). Cameras are placed at the centre of a subset of randomly selected $250 \text{ m} \times 250 \text{ m}$ grid cells (0.0625 km^2) from a grid overlaying the study area. All CTs are relocated monthly to a new grid cell location. Annually, the same set of grid cells is visited twice. A first time during the summer (April–September) and a second time during winter (October–March). All CTs are mounted on the nearest tree $\sim 50 \text{ cm}$ above ground, facing North. None of the CTs was baited to lure animals, or placed along a trail. Each camera trigger was followed by a sequence of ten consecutive photos, with a 0 s recovery time between triggers. We considered sequences (10 photos/trigger) to be independent if they were at least 2 min apart. Non-independent sequences were aggregated and annotated as a single sequence of >10 photos. We considered each independent sequence to display an independent group of wild boar, and defined the raw counts as the number of unique individuals in these groups. Annotation was done using the Agouti software platform (www.agouti.eu). For our analysis, we only considered images from a six months “summer” period (April – October), for the years 2018 to 2021. Taken together, we retained data from 303 deployments, yielding a total of 10,086 24-h observation periods, in which 1873 independent groups of wild boar were captured (total count: 4505, average group size: 2.34).

2.3. Statistical models

The data collected by our CT network was analysed through a range of Poisson NMMs, which were fitted within a Bayesian estimation framework using the dynamic Hamiltonian Monte Carlo sampler in *Stan* via the R package *cmdstanr* (Carpenter et al., 2017). From our camera trapping network, we retained replicated counts y_{ijt} of wild boar by aggregating all the raw counts collected at sites $i = 1, 2, \dots, R$, on day $j = 1, 2, \dots, J$, in year $t = 1, 2, \dots, T$. Now, our model assumes that daily counts of wild boar y_{ijt} are independent and identically distributed Poisson random variables,

$$y_{ijt} | N_{it} \sim \text{Poisson}(N_{it} p_{ijt}), \quad (1)$$

where the mean is a product of the latent number of individuals N_{it} and p_{ijt} , the expected detection/trapping rate per individual per day. Given that we restrict our study period to the same summer period each year, we assume that p_{ijt} is constant over J days and across T years ($p_{ijt} \approx p_i$). Furthermore, we assume that N_{it} is Poisson-distributed with a mean λ_{it} ,

$$N_{it} \sim \text{Poisson}(\lambda_{it}) \quad (2)$$

Without further restrictions, the likelihood of this model involves an infinite sum over N_{it} , which we needed to restrict in order to sample from it. Therefore, we set an upper bound (K) vastly larger than the expected local population size. Moreover, we construct the likelihood by marginalising over N_{it} 's with upper bound K given that *Stan* cannot sample discrete latent variables. Both p_i and λ_{it} may be modelled in function of covariates, by using appropriate link functions (logit and log respectively). The specific covariate structure depends on the candidate model, all of which are listed in Table 1. In all of these models we consider a subset of the following general effects:

Table 1

Abundance (i.e., land-use intensity) submodels and their mathematical structure. Part I: models with management zones as a fixed effect. Part II: models with combinations of covariates of interest.

| Name | $\text{Log}(\lambda_{it})$ |
|----------------------------|--|
| Part I | |
| zone | $\beta_{0,\text{zone}} + f(t) + v_{i,2}$ |
| zone (spatial) | $\beta_{0,\text{zone}} + f(t) + u_i + v_{i,2}$ |
| zone (spatiotemporal) | $\beta_{0,\text{zone}} + f(t) + u_{it} + v_{i,2}$ |
| zone-year (spatial) | $\beta_{0,\text{zone}} + \beta_1 \cdot (\text{zone} \cdot t) + f(t) + u_i + v_{i,2}$ |
| zone-year (spatiotemporal) | $\beta_{0,\text{zone}} + \beta_1 \cdot (\text{zone} \cdot t) + f(t) + u_{it} + v_{i,2}$ |
| Part II | |
| Forest | $\beta_0 - g(D_{\text{fedge}}) + f(t) + v_{i,2}$ |
| Crops | $\beta_0 + \beta_1 \cdot \% \text{crops} + f(t) + v_{i,2}$ |
| Road | $\beta_0 - g(D_{\text{road}}) + f(t) + v_{i,2}$ |
| Parking | $\beta_0 - g(D_{\text{park}}, \mathbf{w}) + f(t) + v_{i,2}$ |
| Parking (# spaces) | $\beta_0 - g(D_{\text{park}}, \mathbf{w}_p) + f(t) + v_{i,2}$ |
| Hunting | $\beta_0 - g(D_{\text{hunt}}, \mathbf{w}) + f(t) + v_{i,2}$ |
| Hunting (# effort) | $\beta_0 - g(D_{\text{hunt}}, \mathbf{w}_e) + f(t) + v_{i,2}$ |
| Hunting (# shot) | $\beta_0 - g(D_{\text{hunt}}, \mathbf{w}_s) + f(t) + v_{i,2}$ |
| Hunting (# yearly effort) | $\beta_0 - g(D_{\text{hunt}}, \mathbf{w}_{e(t)}) + f(t) + v_{i,2}$ |
| Hunting (# yearly shot) | $\beta_0 - g(D_{\text{hunt}}, \mathbf{w}_{s(t)}) + f(t) + v_{i,2}$ |
| Forest-crops | $\beta_0 + \beta_1 \cdot \% \text{crops} - g(D_{\text{fedge}}) + f(t) + v_{i,2}$ |
| Forest-road | $\beta_0 - g(D_{\text{fedge}}) - g(D_{\text{road}}) + f(t) + v_{i,2}$ |
| Forest-parking | $\beta_0 - g(D_{\text{fedge}}) - g(D_{\text{park}}, \mathbf{w}) + f(t) + v_{i,2}$ |
| Crops-road | $\beta_0 + \beta_1 \cdot \% \text{crops} - g(D_{\text{road}}) + f(t) + v_{i,2}$ |
| Crops-parking | $\beta_0 + \beta_1 \cdot \% \text{crops} - g(D_{\text{park}}, \mathbf{w}) + f(t) + v_{i,2}$ |
| Road-parking | $\beta_0 - g(D_{\text{road}}) - g(D_{\text{park}}, \mathbf{w}) + f(t) + v_{i,2}$ |
| Forest-crops-road | $\beta_0 + \beta_1 \cdot \% \text{crops} - g(D_{\text{fedge}}) - g(D_{\text{road}}) + f(t) + v_{i,2}$ |
| Forest-crops-parking | $\beta_0 + \beta_1 \cdot \% \text{crops} - g(D_{\text{fedge}}) - g(D_{\text{park}}, \mathbf{w}) + f(t) + v_{i,2}$ |
| Forest-crops-road-parking | $\beta_0 + \beta_1 \cdot \% \text{crops} - g(D_{\text{fedge}}) - g(D_{\text{road}}) - g(D_{\text{park}}, \mathbf{w}) + f(t) + v_{i,2}$ |

$$\begin{aligned} \text{Logit}(p_i) &= \alpha_0 + v_{i,1} \\ \log(\lambda_{it}) &= \beta_1 \cdot \mathbf{X}_i + f(t) + u_i + v_{i,2} - g(\mathbf{D}, \mathbf{w}) \\ v_i | \Sigma &\sim \text{MVN}(0, \Sigma) \end{aligned} \quad (3)$$

where α_0 is a general intercept, β_1 is a vector of a general intercept and $l - 1$ slope parameters, v_i captures spatially unstructured between-site variation in trapping rates ($v_{i,1}$) and in land-use intensity ($v_{i,2}$), which are correlated with correlation coefficient ρ , and variance-covariance matrix $\Sigma = \begin{pmatrix} \sigma_{v1} & 0 \\ 0 & \sigma_{v2} \end{pmatrix} \begin{pmatrix} \rho & 1 \\ 1 & \rho \end{pmatrix} \begin{pmatrix} \sigma_{v1} & 0 \\ 0 & \sigma_{v2} \end{pmatrix}$. To make sure that the random effects $v_{i,1}$ and $v_{i,2}$ are identifiable, we only estimate these term for sites that contain a CT (i.e. that are sampled). $f(t)$ models a smooth trend in land-use intensity across years, using an exact Gaussian process (GP) (Golding and Purse, 2016), u_i captures spatially structured between-site variation in wild boar land-use intensities. For computational efficiency, we use the Hilbert-space reduced-rank Gaussian process (HSGP) approach to model u_i (Solin and Särkkä, 2020). We performed a prior sensitivity analysis for the length scale of the HSGP, as u_i may possibly confound with fixed effects of interest (Mäkinen et al., 2022). However, we found that posteriors of fixed effects are almost invariant to the considered prior specifications (results not shown). Finally $g(\mathbf{D}, \mathbf{w}) = \log(h(\mathbf{D}) \cdot \mathbf{w})$, with $h(\mathbf{D})$ a negative-exponential decay-function of Euclidean distance to M locations of interest:

$$h(\mathbf{D}) = \gamma_0 \exp(-\gamma_1 \mathbf{D}) \quad (4)$$

where,

$$\mathbf{D} = \begin{bmatrix} d_{11} & \dots & d_{1M} \\ \vdots & \ddots & \vdots \\ d_{R1} & \dots & d_{RM} \end{bmatrix} \quad (5)$$

represent an $R \times M$ distance matrix, which has entries d_{im} (i.e., the

distance from the i^{th} grid centroid to the m^{th} location). The parameter γ_0 determines the effect at distance $d_{im} = 0$, while γ_1 controls the decay rate. Note that when only one location is present, \mathbf{D} reduces to an R -sized vector of entries d_i , i.e., $\mathbf{D} = [d_1 \dots d_R]$. In cases where $M > 1$, the joint effect of all individual locations is obtained by multiplying Eq. (5) by a vector of M weights, i.e., $\mathbf{w} = [w_1 \dots w_M]$. Note that the weights \mathbf{w} can also be a $M \times T$ matrix of entries w_{mt} (instead of w_m), when there is reason to assume that individual effects differ between years. In both cases, \mathbf{w} can (i) be defined as a vector/matrix of equal weights, (ii) be estimated by a model, or (iii) informed by data.

Our analysis consists of two parts. First, we attempt to capture the effect of hunting management zones on wild boar land-use intensities in the face of additional spatial and temporal autocorrelations in detections. After having estimated these effects, we try to identify possible confounding factors by fitting a range of models that do not include the management zones, but instead model land-use intensity in function of environmental covariates. Hence, depending on the analysis, we specify different candidate models for λ_{it} , retaining the same detection model (Table 1). Thus, we consider covariates that express (i) the proportion of cropland containing maize or cereals in a 1500 m buffer around grid centroids ('crop'), the Euclidean distance(s) from grid centroids to (ii) the forest edge ('fedge'), (iii) a major road that intersects the study area ('road'), (iv) the main parking lots in the study area ('park'), and (v) hunting locations in the study area ('hunt'). Note that the 'crop' covariate (i) summarizes average proportions across all years, since this yields nearly the same pattern than annual proportions. Covariates (i-ii) hold information on the landscape composition, while covariates (iii-v) map different forms of lethal and non-lethal human disturbances.

For distances, i.e., 'fedge', 'road', 'park' and 'hunt', we make the assumption that their effects dissipate according to $h(\mathbf{D})$, a negative-exponential function decaying with distance (Whittington et al., 2011; Royle et al., 2013). We model 'park' with a vector of equal weights and with weights according to the number of available spaces at a parking lot. For 'hunt', we test a vector of equal weights, a vector of weights according to the hunting effort per location and one based on the number of wild boar shot per location, a matrix of weights for the yearly hunting effort per location, and finally, another weight-matrix for the yearly number of wild boar shot per location (Table 1; Appendix C).

We mostly use vague priors, which are detailed in Appendix A. For all models, we run three parallel MCMC chains with 4000 iterations, which included 2000 iterations that are discarded as burn-in iterations; this always results in satisfactory convergence (Tables A1 and A2), following the guidelines by Vehtari et al. (2021). After model fitting, we perform a model selection using the expected log-predictive density (ELPD) and WAIC based on the leave-one-out procedure developed by Vehtari et al. (2017). For convenience, we will refer to the top-ranking model of part 1 and part 2 of our analysis as \mathcal{M}_1 and \mathcal{M}_2 respectively. We will regard a threshold in ΔELPD of $>1.96 \text{ SE}(\Delta\text{ELPD})$ as substantial. Hence, models with differences in ELPD that do not reach this threshold will be considered equally informative about the true state. Finally, we also compute annual total "summer" land-use intensity for both models as the summation across R sites of expected population sizes $E(N_t) = \sum_{i=1}^R E(N_{it})$.

3. Results

3.1. Management zones model

A model with a zone-year interaction term ('zone-year (spatial)', hereafter referred to as \mathcal{M}_1) is the best ranked by ELPD, followed by the 'zone' model, which has a non-substantial ΔELPD with \mathcal{M}_1 . The high percentage ($>50\%$) of divergent transitions (leading to incomplete exploration of the posterior distribution) of the 'zone (spatial)', 'zone (spatiotemporal)' and 'zone-year (spatiotemporal)' models likely inflated the estimated number of parameters, causing their poor predictive

performance indicated by ELPD (Table 2). According to \mathcal{M}_1 , 95 % of site-averaged daily trapping rates lie between 0.132 and 0.141 based on posterior quantiles (Fig. B1). However, there is substantial variation (captured by $v_{i,1}$) in the daily trapping rates among CT locations (Fig. 2a), with respectively 0.004 and 0.988 being the minimum and maximum posterior trapping rates observed at any location. Moreover, the estimated unstructured spatial random effects of the detection and land-use intensity submodels are negatively correlated ($\rho = -0.56$) (Fig. 2a-b). Given that a zone effect is present in the model, there is still a relevant extra-variability in wild boar land-use intensity captured by a structured spatial random effect (Fig. 2c). Posterior means of the main zone effects are provided in Fig. 2d. Differences in land-use intensity are substantial between the year-round hunting zone (HY) and the winter hunting zone (HW), and between the year-round hunting zone and the core zone (C), but not between the winter hunting zone and the core zone for most of the years (Fig. 2e). The hunting pressure among years remains similar throughout the study period (Table C3).

3.2. Covariate model

The best-ranking combination of covariates, according to ELPD, is that of model 'Forest-parking' (hereafter referred to as \mathcal{M}_2) followed by those of 'Crops-parking' and 'Parking' (Table 2). The ΔELPD is non-substantial for most of the models in Table 1 (Table 2). As also the ΔELPD between \mathcal{M}_2 and lower ranking model is non-substantial we will restrict the discussion to the potential contributions of factors tested in our candidate covariate models. However, to better understand the implications of a different model on the wild boar land-use intensities for summers of 2018–2021, we visualise the spatial predictions for the top four ranking models (Fig. 3).

3.3. Management zones vs. Covariate model

Despite the uncertainty about which covariate model is most consistent with the data, we report the predictions from \mathcal{M}_2 to compare against those of \mathcal{M}_1 . Overall, \mathcal{M}_2 produces higher point estimates of the total land-use intensity of wild boar than \mathcal{M}_1 . However, there is still a large portion of overlap between their 95 % Bayesian credible intervals (BCI). Under both models, wild boar total land-use intensity increased from 2018 to 2019, and returned to approximately the initial values after 2019 (Fig. 4a). Spatial patterns in land-use intensity are significantly correlated according to Kendall's tau correlations between \mathcal{M}_1 and \mathcal{M}_2 for all of the years (Fig. 4b). Differences in land-use intensity after z-transformation reveal that model \mathcal{M}_1 tends towards higher land-use intensities in the north-west and south-east of the study area as compared to model \mathcal{M}_2 (Fig. 4c). Average residuals for these models reveal more clusters of high values for \mathcal{M}_1 , as compared to \mathcal{M}_2 (Fig. B3). Finally, the root mean square errors (RMSE) of \mathcal{M}_1 and \mathcal{M}_2 are 0.122 and 0.086 respectively.

4. Discussion

The aims of this study were (i) to investigate the impacts of the hunting management through zoning in Meerdaal, (ii) to identify possible factors that may explain differential land-use intensities among zones. We were able to reveal differences in posterior mean land-use intensity of wild boar for all summers between the outer "year-round hunting" zone and the inner "core" and "winter hunting" zones (Fig. 2d). This finding may indicate that the two inner zones in which hunting is prohibited during the summer months (although we found some records of hunting for these zones, see C3 and Fig. 1), can act as a refuge area for wild boar. However, for some of the summers 95 % BCIs for the zone-specific land-use intensities reveal that there is some posterior uncertainty about differential intensities across management zones. The inner zones (core zone $\sim 2\text{km}^2$ and winter hunting zone $\sim 4\text{km}^2$) combined make up an area of $\sim 6\text{km}^2$, which could be large enough for wild boar

Table 2
Ranking of models in Part I and II, based on their expected log predictive density (ELPD). Stacked model weights (Wt) based on ELPD.

| Model | Wt | ΔELPD | SE(ΔELPD) | ΔWAIC | SE(WAIC) | # Par. |
|-----------------------------------|------|---------|-----------|---------|----------|--------|
| Part I | | | | | | |
| Zone-year (spatial) | 0.61 | 0.00 | 0.00 | 0.00 | 0.00 | 272 |
| Zone | 0.39 | -67.85 | 71.14 | -103.49 | 69.01 | 28 |
| Zone (spatial) | 0.00 | -3E+03* | 445.12* | -3E+04* | -1E+04* | 3441* |
| Zone-year (spatiotemporal) | 0.00 | -9E+04* | 1E+04* | -3E+07* | 6E+06* | 91476* |
| Zone (spatiotemporal) | N/A* | N/A* | N/A* | N/A* | N/A* | N/A* |
| Part II | | | | | | |
| Forest-parking | 0.22 | 0.00 | 0.00 | -0.37 | 3.70 | 137 |
| Crops-parking | 0.19 | -1.90 | 3.71 | -0.51 | 1.13 | 140 |
| Parking | 0.13 | -2.39 | 4.07 | 0.00 | 0.00 | 141 |
| Forest-crops-road-parking | 0.11 | -3.84 | 5.13 | -1.29 | 5.39 | 141 |
| Forest-crops-parking | 0.09 | -4.42 | 1.85 | -2.82 | 3.67 | 142 |
| Road-parking | 0.08 | -4.96 | 7.09 | -2.73 | 4.61 | 141 |
| Forest-crops | 0.08 | -6.94 | 5.13 | -7.13 | 6.01 | 137 |
| Crops | 0.04 | -7.01 | 6.00 | -7.79 | 4.76 | 137 |
| Parking (# parking spaces) | 0.03 | -7.80 | 6.37 | -6.66 | 5.15 | 138 |
| Forest-road | 0.02 | -8.70 | 7.43 | -7.90 | 7.58 | 137 |
| Road | 0.02 | -10.48 | 9.58 | -10.42 | 7.41 | 138 |
| Forest-crops-road | 0.00 | -10.86 | 7.19 | -9.42 | 7.51 | 140 |
| Forest | 0.00 | -11.60 | 5.74 | -8.06 | 6.15 | 141 |
| Hunting | 0.00 | -11.92 | 8.22 | -11.16 | 6.39 | 138 |
| Hunting (# shots) | 0.00 | -12.75 | 5.76 | -11.97 | 5.98 | 139 |
| Crops-road | 0.00 | -13.37 | 8.55 | -11.90 | 6.98 | 140 |
| Hunting (yearly effort) | 0.00 | -13.62 | 5.82 | -13.12 | 5.95 | 140 |
| Hunting (# yearly shots) | 0.00 | -13.82 | 6.55 | -11.61 | 6.13 | 140 |
| Hunting (effort) | 0.00 | -14.55 | 6.37 | -11.00 | 5.86 | 141 |

Par: Number of effective parameters. Models for which the $|\Delta\text{ELPD}| > 1.96 \text{ SE}(\Delta\text{ELPD})$ are indicated in bold. *failed to properly converge. N/A: 100 % of transitions ended with a divergence.

to satisfy all of its requirements (Podgórski et al., 2013; Fattebert et al., 2017; Brogi et al., 2020). However, higher land-use intensity in the inner zones does not confirm causality with the higher hunting pressure in the surrounding year-round hunting zone. Alternatively, wild boar may simply use these zones more frequently because of their central locations relative to the forested area. Furthermore, still a lot of variation in wild boar land-use intensity is unexplained by the zone effects in model \mathcal{M}_1 (Fig. 2c). This suggests that also other factors may influence wild boar land-use intensity in Meerdaal. Both food availability (Bubnicki et al., 2019), as well as landscape composition (Fattebert et al., 2017) have been suggested as primary drivers of wild boar space use. Additionally, inter-specific or intra-specific competition for resources may force wild boar to visit locations outside of the inner zones (Ballari and Barrios-García, 2014). Model \mathcal{M}_1 reveals that differences in posterior mean land-use intensity between the two inner zones and the outer year-round hunting zone remain similar across the study period (Fig. 2e), which may also explain why the ΔELPD between ‘zone’ and ‘zone-year (spatial)’ models did not reach the threshold (Table 2). Moreover, differences in hunting pressure among the management zones also remain stable throughout the study period (C3). In summary, these findings seem to indicate that the hunting management zones, as defined in Meerdaal, have a relevant impact on wild boar land-use intensity but that also other factors not captured by \mathcal{M}_1 may be associated with (and potentially driving) the observed land-use patterns.

Despite difficulties with assigning a clear best-performing covariate model, \mathcal{M}_2 has a better predictive performance than \mathcal{M}_1 in terms of ELPD and based on the average residuals. This suggests that other factors than the hunting management zones may influence the land-use patterns of wild boar in Meerdaal. The consistent appearance in the six best-ranking models of the distance-dependent effects of parking lots seem to suggest an effect of human disturbance on wild boar land-use intensity. According to \mathcal{M}_2 (and other models that include effects of parking lots), wild boar avoid areas with higher human disturbance, which is in accordance with Bubnicki et al. (2019). The effect of parking lots dissipates nor very rapidly, nor very slowly in space ($\gamma_1 = 1.92$, resulting in a half-life distance of $\tau_{1/2} = 0.36 \text{ km}$ for \mathcal{M}_2 ; Fig. B2). This

result aligns with our expectations assuming that recreational activities such as hiking, horseback riding or biking happen within a perimeter of their starting locations. Therefore, if wild boar prefer places that are undisturbed by humans, very rapid distance-decays from parking lots are unlikely. Weighing individual contributions to the distance-dependent effect of parking lots, based on the available parking spaces produced the lowest ELPD from all models with effects of parking lots (Table 2 ‘Parking (# parking spaces)’). This could suggest that the size of a parking lot is a bad indicator of the intensity of recreational activities within its vicinity, or alternatively that wild boar avoid human disturbance without discriminating between areas that are (in)frequently disturbed. While the effects of non-lethal recreational activities on the land-use intensity of ungulates are likely context-dependent, generally negative effects, as we observed here, dominate over positive effects (Larson et al., 2016). Nevertheless, wild boar are reported to adapt to urban environments by tolerating human disturbances (Stillfried et al., 2017b; Castillo-Contreras et al., 2018) and possibly also taking advantage of anthropogenic food resources, thereby increasing their body mass, size, condition and reproductive success (Castillo-Contreras et al., 2021). In that regard, the avoidance of human disturbance in our area could be a consequence of the possible rewards not outweighing the risks (e.g. anthropogenic food sources to scarce in relation to human disturbance, traffic, etc.). Alternatively, it could be that wild boar in our study area still need to habituate to high levels of human disturbance, and that it is a matter of time before they learn to adapt to these environments. Other studies find that wild boar in urban environments still forage on natural rather than anthropogenic food sources, and that source-sink dynamics may explain why wild boar use urban environments (Stillfried et al., 2017a; Stillfried et al., 2017c). Assuming that source-sink dynamics are at play, wild boar in our study area may not use urban environments (sinks) frequently, if the source population has not yet reached its carrying capacity (i.e. there are no excess individuals).

Effects other than those of parking lots that may influence wild boar land-use intensities include effects of crops within 1500 m, distance-dependent effects of the forest edge, major road or distance to the

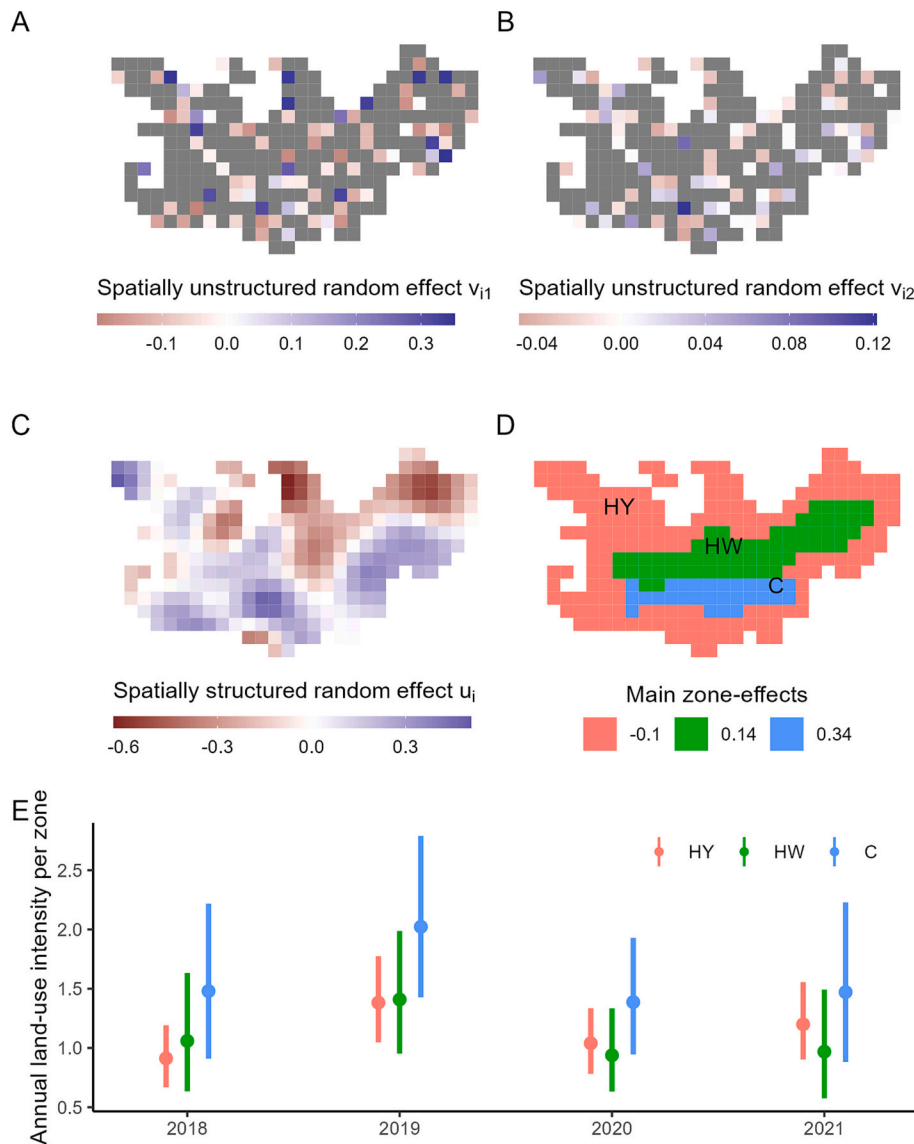


Fig. 2. Posterior means of the fixed and random effects of model M_1 . Spatially unstructured random effects of the trapping rate (A) and land-use intensity (B). Spatially structured random effect of the land-use intensity (C). Main management zone effects – year-round hunting zone HY, winter hunting zone HW and core zone C (D). The resulting posterior means and 95 % credible intervals of the zone-specific annual land-use intensities (E). The effects in A are on the logit-scale, the effects in B–D are on the log-scale, the effects in E are on the unit scale.

hunting locations (Table 2). Except for ‘Hunting’, all the models including the effects of hunting locations produced a substantially poorer fit than M_2 . This seems to suggest that non-lethal human disturbances (and possibly a range of other factors) trump the effects of hunting in our study area. Possibly negative impacts of hunting are obscured by hunters preferentially visiting locations with high wild boar abundance, or because of hunters using baits or scent marks to lure individuals (Ohashi et al., 2013; Wevers et al., 2020). Additionally, the impact of hunting could have been masked by the distance-dependent effects of parking lots. The greatest distances from parking lots and highest hunting pressure largely coincide (Figs. B4 and B5), but appear to have opposite effects on wild boar land-use intensity. Hence, in our study area, wild boar may trade-off the risk from hunting pressure with the fear of non-lethal human disturbance. This would suggest that human disturbance induces a stronger fear in wild boar compared to the generally low hunting pressure in Meerdaal (Tables C2 and C3). In Meerdaal, hunting is restricted to fixed locations and the number of hunting posts occupied at the same time is usually low. Synchronised hunting attempts or drive hunts with dogs have the potential to

drastically improve the hunting efficacy and likely also induce stronger fear effects in the future (Vajas et al., 2020; Colomer et al., 2021; Fernández-De-Simon et al., 2023). Even if the fear effects of hunting and non-lethal human disturbance are equal, wild boar may still prefer areas with high hunting pressure, which are closer to croplands, when fear effects mutually cancel with attraction to croplands for food. This may explain why models including the effects of proportion of crops within a 1500 m buffer did not rank higher. Also note that there are reports from crop damage in the croplands surrounding Meerdaal. Lastly, the absence of an effect from hunting in our study area could be a consequence of the configuration of the hunting locations, which are more abundant and randomly spread around the study area relative to that of other variables.

Previous studies on wild boar revealed forest or more specifically forest type (coniferous/deciduous) as a main driver of their spatial distribution (Fattebert et al., 2017; Rutten et al., 2019; Wevers et al., 2020; Fernández-López et al., 2022). However, we were unable to assess the affinity of wild boar for forest (type) in our study area, since it consists almost exclusively of a complex matrix of both coniferous and deciduous

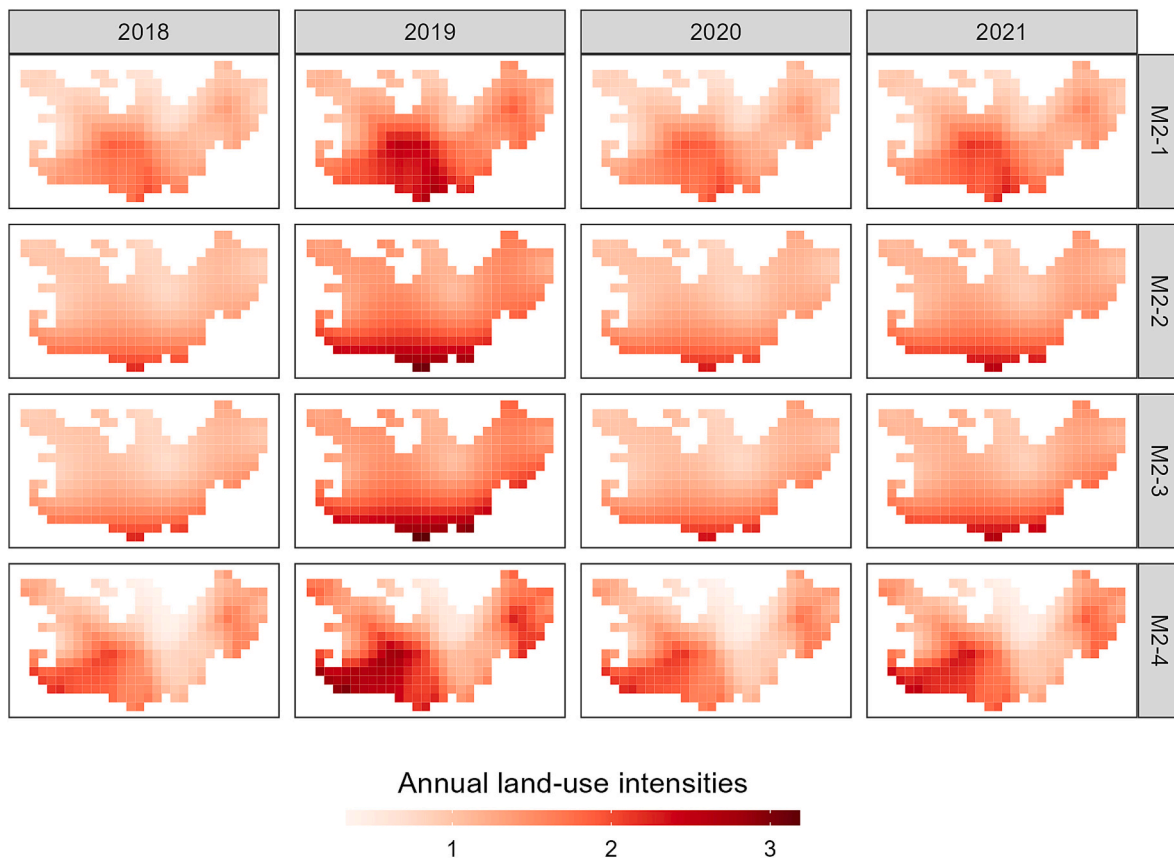


Fig. 3. Posterior means for the annual land-use intensities based on the top four ranking models (according to ELPD) of model \mathcal{M}_2 .

trees. Instead, we find that wild boar land-use intensity increases with increasing distance to the forest edge (*i.e.* close to the centre of the forest), but that the effect is limited. However, the majority of photographs from wild boar near the centre of Meerdaal were captured during daytime, when they are mostly resting/inactive. Hence, it could be that wild boar have a stronger preference for resting sites in the centre of the forest than we observe, since animals not actively moving in front of the CT will not be captured (Johann et al., 2020; Fradin and Chamailé-Jammes, 2023).

Both \mathcal{M}_1 and \mathcal{M}_2 indicate that the bulk of wild boar activity is located towards the centre and South of Meerdaal. The relatively lower land-use intensity close to the forest edges could be a consequence of more directed movements when commuting to and from adjacent croplands (Keuling et al., 2009). This could lead to relatively fewer sightings around forest edges compared to areas where wild boar are actively foraging, and thus performing searching behaviour. Finally, it could be that some wild boar in Meerdaal choose to stay the summer permanently inside either the (inner) forest or the croplands (this possibly also in response to lethal and non-lethal human pressure), which would result in fewer observations close to the forest edge (Keuling et al., 2009). To investigate this hypothesis (and intensity of cropland use in general) we suggest that future studies deploy tracking devices to model fine-scale movement patterns, or that CTs are placed inside these croplands (Thurfjell et al., 2009).

4.1. Management applications

Although our results indicate that wild boar show a higher use of areas towards the centre of the forest, and less disturbed by human activities, some caution is warranted when using our results to inform future hunting management. First, our findings result from an area characterized by a high non-lethal human pressure, combined with a

relative low and sporadic hunting pressure, possibly resulting in complex and difficult to understand patterns of tolerances towards human activities (Courbin et al., 2022). Furthermore, our findings suggest that hunting efforts in Meerdaal might not be sufficiently effective at modulating the spatial behaviour of wild boar. However, we stress they are based on an observational study, making it impossible to know which wild boar land-use patterns would have emerged in Meerdaal when hunting would have been prohibited completely during the summer (*i.e.*, also in the year-round hunting zone). Possibly, a lower risk of mortality in the year-round hunting zone could have led to higher wild boar land-use intensities in this zone and the surrounding croplands (Quirós-Fernández et al., 2017). As such, it may be that the currently adopted hunting management strategy in Meerdaal is at least partially successful in reducing wild boar damages to agricultural crops. Furthermore, we identified several factors, most notably the distance to parking lots and distance to the forest edge that possibly obscured the impacts of the hunting strategy, which makes our study area suboptimal for evaluating the effect of hunting disturbances. In the future, a pseudo-experimental design, where some of these factors are manipulated can increase the power to detect an effect of hunting disturbances. Finally, our results do not reflect the behaviour/vigilance of wild boar or the time at which they use particular zones. Therefore, if the objective is to gain insight in differential activity or behaviour of wild boar between zones at the individual level or at small spatial scales we advise to use tracking devices instead of CTs (Keuling et al., 2008; Johann et al., 2020; Ferrer-Ferrando et al., 2023).

CRedit authorship contribution statement

MB: conceptualisation, methodology, formal analysis, visualisation and writing – original draft preparation. TN and NB: supervision. JC: validation and project administration. All authors: writing - review &

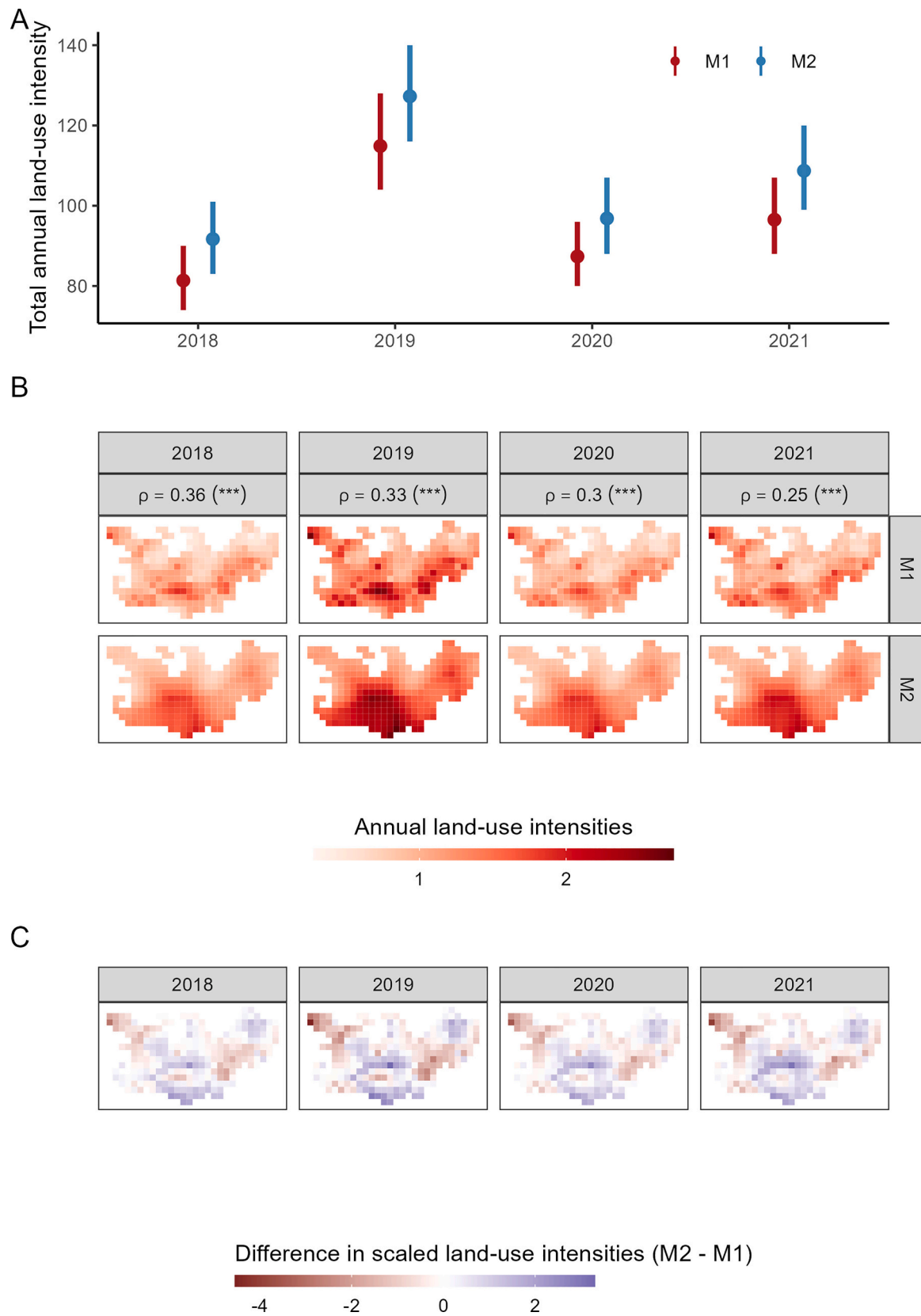


Fig. 4. Posterior means and 95 % credible intervals for the total annual land-use intensity (A). Posterior means for the annual land-use intensities (B). Results are displayed for models \mathcal{M}_1 and \mathcal{M}_2 of our analysis. The Kendall's tau correlations ρ between land-use intensities of these models are provided in panel (B). > 0.05 (ns), ≤ 0.05 (*), ≤ 0.01 (**), and ≤ 0.001 (***)

editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Supplementary data to "Impacts of zoning and spatial confounders of zones on the abundance of wild boar assessed through a Bayesian N-mixture Model" (Original data) (Figshare)

Acknowledgements

This work makes use of data and/or infrastructure provided by INBO

and funded by Research Foundation Flanders (FWO) as part of the Belgian contribution to LifeWatch. The services used in this work were provided by the VSC (Flemish Supercomputer Center), funded by the FWO and the Flemish Government. MB is a PhD fellow funded by a BOF mandate at Hasselt University. TN gratefully acknowledges funding by the FWO (G0A4121N) and by the Internal Funds KU Leuven (project number 3M190682). We are grateful to the Flemish Agency for Nature and Forest and the local nature conservation NGO "Vrienden van Heverleebos en Meerdaalwoud" to allow us to place camera traps on their properties. Further, we thank all volunteers and students that aided in the field or processed and annotated pictures. Finally, we are grateful for the insightful comments that we received from three anonymous reviewers, which have improved the clarity and quality of this article.

Appendix A. Priors, model convergence and diagnostics

For the Poisson N-mixture model, which is described in the main paper, we mostly used vaguely informative priors. For the length scale parameter of the GPs we have used distributions that avoid values near zero (*i.e. inverse gamma*), or that avoid both values near zero and larger values (*i.e. generalized inverse Gaussian*). For regression parameters $\{\alpha_0, \beta_{0,zone}, \beta_0, \beta_1\}$ and for γ_0 , controlling the magnitude of the negative exponential decay at $d = 0$, we used *normal*(0, 1) priors. For γ_1 , which controls the decay rate of the negative exponential function, we used an inverse gamma *IG*(5, 5) prior. We used *half normal*(0, 1) priors, and an inverse gamma *IG*(11, 4) prior for respectively the marginal standard deviation σ_{f_i} and the length scale ρ_{f_i} , the hyperparameters of the GP. For the same hyperparameters of the HSGP, *i.e.*, σ_{u_i} and ρ_{u_i} , we used respectively a non-negative *student t*⁺(3, 0, 5) and a generalized inverse Gaussian *GIG*(3, 13, 0.01) prior. For the GPs coefficients $\{\eta_{f_p}, \eta_{f_s}, \eta_{u_i}\}$ we used *normal*(0, 1) priors. For numerical efficiency, we decomposed the variance-covariance matrix as $\Sigma = L \cdot \Omega \cdot L$, with Cholesky factor $L = \begin{pmatrix} \sigma_{v1} & 0 \\ 0 & \sigma_{v2} \end{pmatrix}$ and correlation matrix $\Omega = \begin{pmatrix} \rho & 1 \\ 1 & \rho \end{pmatrix}$, where $L \sim LKJ(1)$ and $\sigma_v \sim half\ normal(0, 1)$.

Table A1
Posterior mean, and quantiles (0.025 and 0.975) for the Rhat, ESS bulk and ESS tail of model \mathcal{M}_1 .

| Variable | Rhat | | | ESS bulk | | | ESS tail | | |
|----------------|--------|---------|---------|----------|---------|---------|----------|---------|---------|
| | Mean | 0.025 % | 0.975 % | Mean | 0.025 % | 0.975 % | Mean | 0.025 % | 0.975 % |
| α_0 | 1.0006 | 1.0006 | 1.0006 | 7789 | 7789 | 7789 | 2884 | 2884 | 2884 |
| σ_{f_i} | 1.0007 | 1.0007 | 1.0007 | 2033 | 2033 | 2033 | 2537 | 2537 | 2537 |
| σ_{u_i} | 1.0072 | 1.0072 | 1.0072 | 235 | 235 | 235 | 399 | 399 | 399 |
| β_0 | 1.0010 | 1.0002 | 1.0020 | 3099 | 2102 | 4158 | 3253 | 2204 | 3849 |
| β_1 | 1.0018 | 1.0011 | 1.0023 | 3570 | 2167 | 4397 | 3362 | 2192 | 4177 |
| ρ_{f_i} | 1.0006 | 1.0006 | 1.0006 | 6002 | 6002 | 6002 | 3501 | 3501 | 3501 |
| ρ_{u_i} | 1.0057 | 1.0057 | 1.0057 | 316 | 316 | 316 | 882 | 882 | 882 |
| σ_v | 1.0021 | 1.0016 | 1.0026 | 2024 | 409 | 3640 | 2309 | 893 | 3724 |

Rhat: potential scale reduction factor, ESS: effective sample size (in the tail or bulk of the distribution).

Table A2
Posterior mean, and quantiles (0.025 and 0.975) for the Rhat, ESS bulk and ESS tail of model \mathcal{M}_2 .

| Variable | Rhat | | | ESS bulk | | | ESS tail | | |
|----------------|--------|---------|---------|----------|---------|---------|----------|---------|---------|
| | Mean | 0.025 % | 0.975 % | Mean | 0.025 % | 0.975 % | Mean | 0.025 % | 0.975 % |
| α_0 | 1.0006 | 1.0006 | 1.0006 | 10,932 | 10,932 | 10,932 | 4502 | 4502 | 4502 |
| σ_{f_i} | 1.0020 | 1.0020 | 1.0020 | 1741 | 1741 | 1741 | 1766 | 1766 | 1766 |
| β_0 | 1.0007 | 1.0007 | 1.0007 | 4055 | 4055 | 4055 | 3687 | 3687 | 3687 |
| β_1 | 1.0017 | 1.0017 | 1.0017 | 3840 | 3840 | 3840 | 4431 | 4431 | 4431 |
| γ_0 | 1.0002 | 1.0002 | 1.0002 | 4917 | 4917 | 4917 | 3395 | 3395 | 3395 |
| γ_1 | 0.9998 | 0.9998 | 0.9998 | 7851 | 7851 | 7851 | 4604 | 4604 | 4604 |
| ρ_{f_i} | 1.0006 | 1.0006 | 1.0006 | 9970 | 9970 | 9970 | 4385 | 4385 | 4385 |

Rhat: potential scale reduction factor, ESS: effective sample size (in the tail or bulk of the distribution).

Appendix B. Supplementary figures

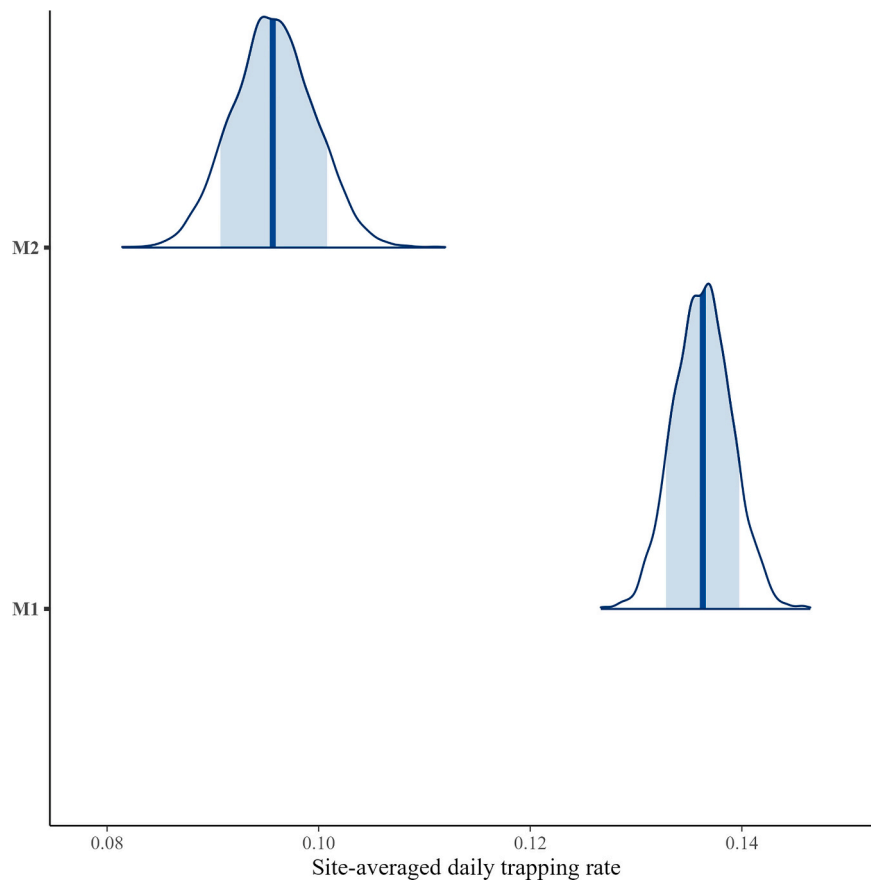


Fig. B1. Posterior distribution for the site-averaged daily trapping rate per individual. The vertical lines represent the posterior means and the shaded area show the 95 % credible intervals.

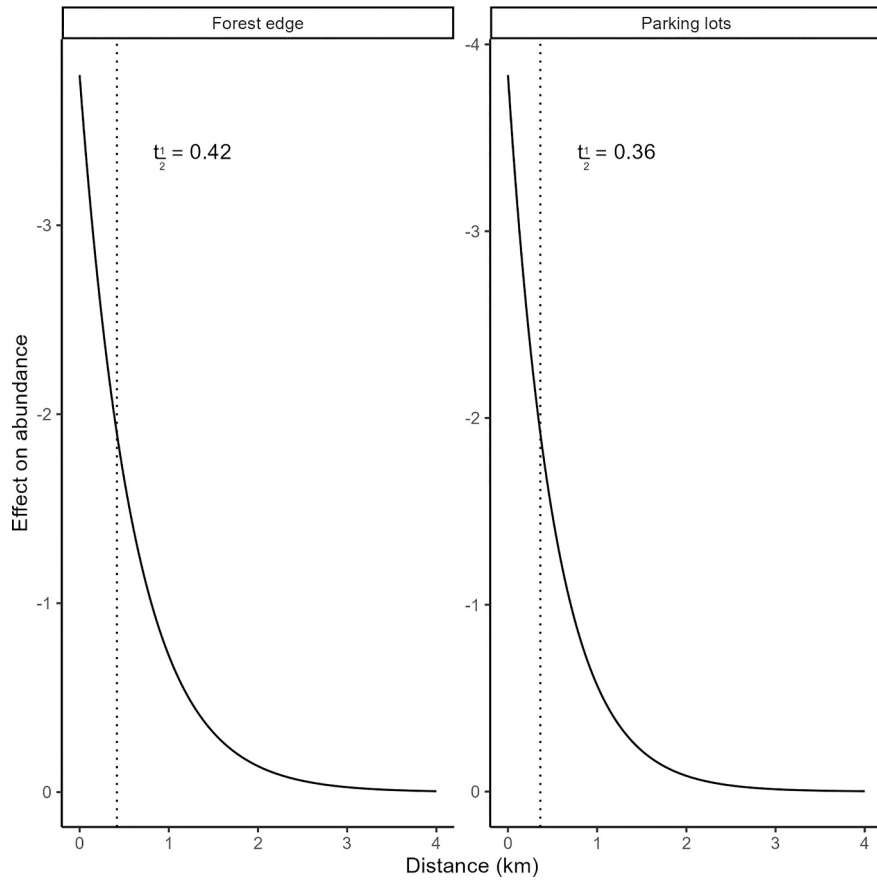


Fig. B2. Negative exponential decay function for the distance (in km) to forest edge (left) and to parking lots (right). The half-life distance $\tau_{1/2}$ is indicated by the dotted line.

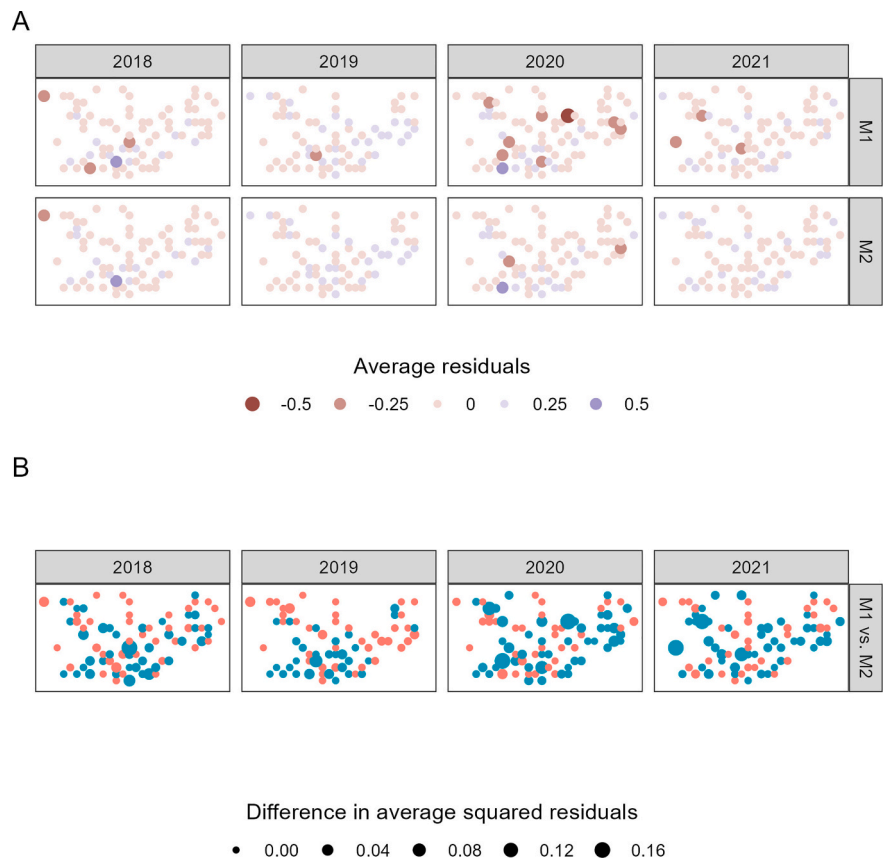


Fig. B3. Average spatial residuals for models \mathcal{M}_1 and \mathcal{M}_2 (A). Difference in average spatial residuals, with greens indicating $res(\mathcal{M}_1) > res(\mathcal{M}_2)$ and reds indicating $res(\mathcal{M}_1) < res(\mathcal{M}_2)$ (B).

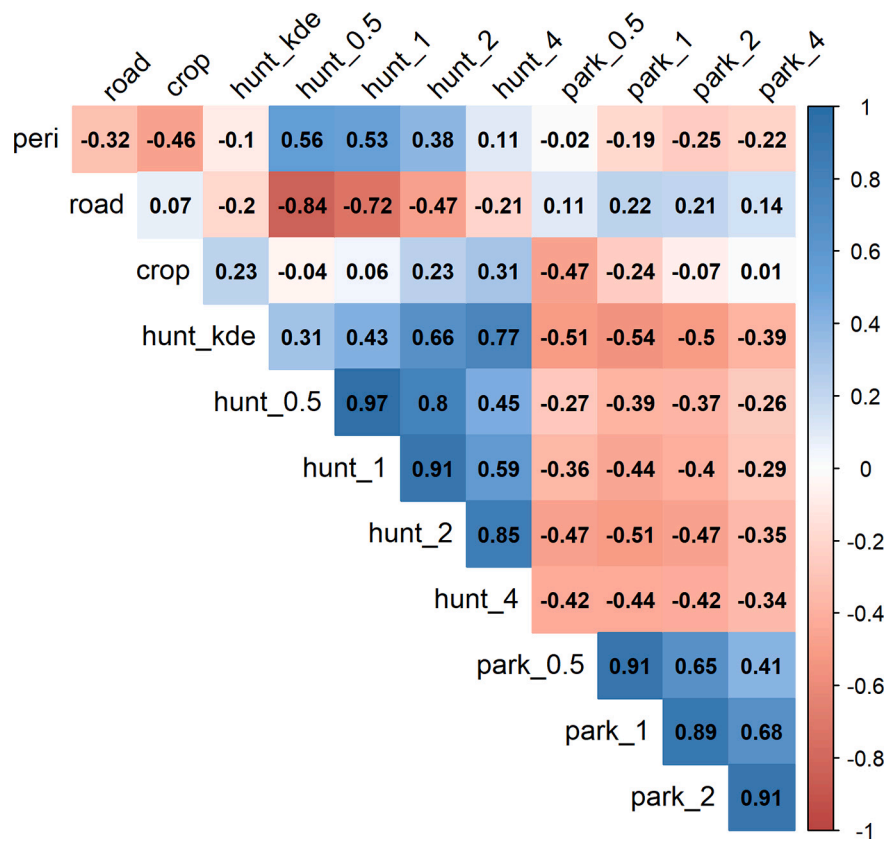


Fig. B4. Correlation matrix of candidate covariates, values represent correlation coefficients. Peri: distance to the forest edge; road: distance to the main road; crop: the proportion of cropland in a 1500 m buffer; hunt_kde: a map of hunting intensity based on 2d kernel density estimates; hunt_0.5–4: map of hunting intensity based on joint negative exponential decays with varying decay rates (0.5–4); park: a map of human disturbance based on joint negative exponential decays with varying decay rates (0.5–4).

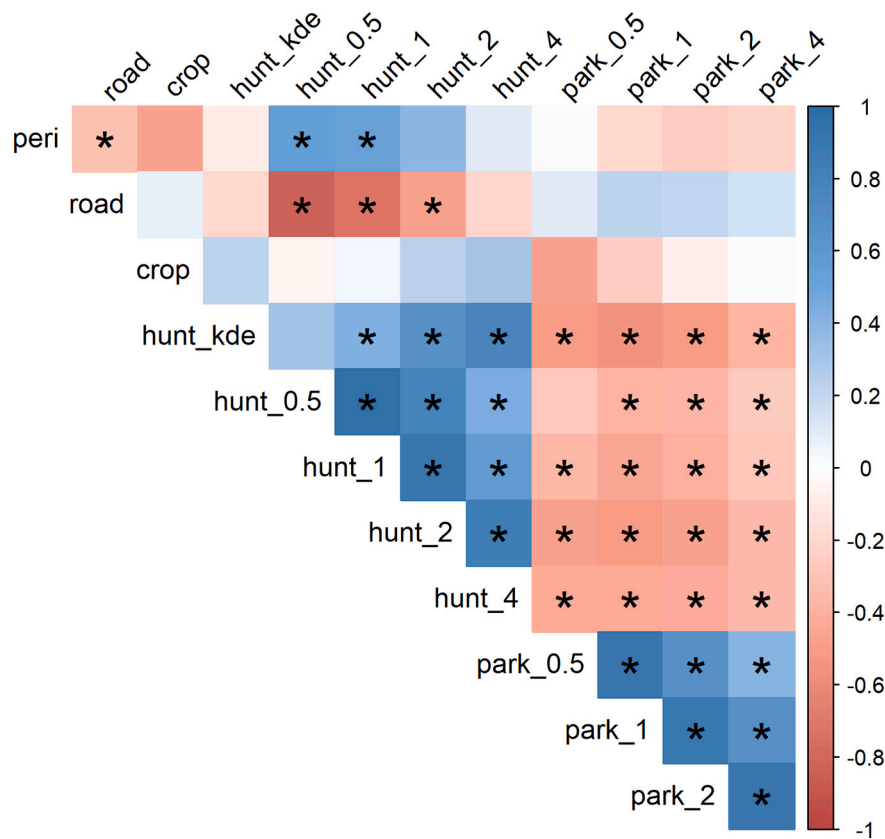


Fig. B5. Correlation matrix of candidate covariates, asterisks display pairs of covariates that are significantly correlated. Peri: distance to the forest edge; road: distance to the main road; crop: the proportion of cropland in a 1500 m buffer; hunt_kde: a map of hunting intensity based on 2d kernel density estimates; hunt_0.5–4: map of hunting intensity based on joint negative exponential decays with varying decay rates (0.5–4); park: a map of human disturbance based on joint negative exponential decays with varying decay rates (0.5–4).

Appendix C. Information on parking lots and hunting posts

Table C1
Parking lots in Meerdaal with the number of available spaces, and their assigned weights.

| ID | Name parking | No. spaces | Weights |
|----|----------------------|------------|---------|
| 1 | De Torenavalk | 130 | 0.3202 |
| 2 | De Spielberg | 58 | 0.1429 |
| 3 | Zoet Water | 183 | 0.4507 |
| 4 | Brise Tout | 20 | 0.0493 |
| 5 | St. Jorisweertstraat | 15 | 0.0369 |

Table C2
Hunting locations (ID) with their total effort in hours, their total number of shots, as well as their respective weights. Note that we do not include a table for yearly hunting weights.

| ID | Effort (h) | No. shots | Weights - effort | Weights - shot |
|----|------------|-----------|------------------|----------------|
| 1 | 2.25 | 0 | 0.0016 | 0.0000 |
| 2 | 2.42 | 0 | 0.0017 | 0.0000 |
| 3 | 3.25 | 0 | 0.0023 | 0.0000 |
| 4 | 2.50 | 0 | 0.0018 | 0.0000 |
| 5 | 2.50 | 0 | 0.0018 | 0.0000 |
| 6 | 2.42 | 0 | 0.0017 | 0.0000 |
| 7 | 4.40 | 0 | 0.0032 | 0.0000 |
| 8 | 3.58 | 0 | 0.0026 | 0.0000 |
| 9 | 6.58 | 0 | 0.0047 | 0.0000 |
| 10 | 16.60 | 1 | 0.0119 | 0.0156 |
| 11 | 0.87 | 0 | 0.0006 | 0.0000 |
| 12 | 2.58 | 0 | 0.0018 | 0.0000 |
| 13 | 2.83 | 0 | 0.0020 | 0.0000 |
| 14 | 2.00 | 0 | 0.0014 | 0.0000 |
| 15 | 3.58 | 0 | 0.0026 | 0.0000 |

(continued on next page)

Table C2 (continued)

| ID | Effort (h) | No. shots | Weights - effort | Weights - shot |
|----|------------|-----------|------------------|----------------|
| 16 | 1.58 | 0 | 0.0011 | 0.0000 |
| 17 | 3.75 | 0 | 0.0027 | 0.0000 |
| 18 | 48.50 | 2 | 0.0347 | 0.0313 |
| 19 | 22.33 | 0 | 0.0160 | 0.0000 |
| 20 | 15.62 | 1 | 0.0112 | 0.0156 |
| 21 | 23.72 | 2 | 0.0170 | 0.0313 |
| 22 | 25.98 | 3 | 0.0186 | 0.0469 |
| 23 | 15.50 | 1 | 0.0111 | 0.0156 |
| 24 | 47.78 | 3 | 0.0342 | 0.0469 |
| 25 | 2.08 | 0 | 0.0015 | 0.0000 |
| 26 | 78.29 | 2 | 0.0561 | 0.0313 |
| 27 | 17.42 | 1 | 0.0125 | 0.0156 |
| 28 | 26.58 | 1 | 0.0190 | 0.0156 |
| 29 | 54.92 | 5 | 0.0393 | 0.0781 |
| 30 | 9.50 | 2 | 0.0068 | 0.0313 |
| 31 | 35.25 | 0 | 0.0252 | 0.0000 |
| 32 | 12.50 | 0 | 0.0089 | 0.0000 |
| 33 | 25.50 | 2 | 0.0183 | 0.0313 |
| 34 | 1.67 | 0 | 0.0012 | 0.0000 |
| 35 | 22.30 | 0 | 0.0160 | 0.0000 |
| 36 | 94.63 | 8 | 0.0678 | 0.1250 |
| 37 | 35.03 | 1 | 0.0251 | 0.0156 |
| 38 | 1.75 | 0 | 0.0013 | 0.0000 |
| 39 | 27.08 | 2 | 0.0194 | 0.0313 |
| 40 | 1.67 | 0 | 0.0012 | 0.0000 |
| 41 | 72.03 | 4 | 0.0516 | 0.0625 |
| 42 | 12.85 | 1 | 0.0092 | 0.0156 |
| 43 | 70.22 | 1 | 0.0503 | 0.0156 |
| 44 | 40.62 | 2 | 0.0291 | 0.0313 |
| 45 | 50.27 | 2 | 0.0360 | 0.0313 |
| 46 | 53.43 | 2 | 0.0383 | 0.0313 |
| 47 | 41.25 | 3 | 0.0295 | 0.0469 |
| 48 | 2.25 | 0 | 0.0016 | 0.0000 |
| 49 | 16.57 | 0 | 0.0119 | 0.0000 |
| 50 | 31.02 | 0 | 0.0222 | 0.0000 |
| 51 | 22.92 | 1 | 0.0164 | 0.0156 |
| 52 | 12.75 | 1 | 0.0091 | 0.0156 |
| 53 | 51.61 | 2 | 0.0369 | 0.0313 |
| 54 | 34.75 | 0 | 0.0249 | 0.0000 |
| 55 | 1.25 | 0 | 0.0009 | 0.0000 |
| 56 | 9.92 | 1 | 0.0071 | 0.0156 |
| 57 | 58.83 | 0 | 0.0421 | 0.0000 |
| 58 | 32.56 | 3 | 0.0233 | 0.0469 |
| 59 | 5.13 | 2 | 0.0037 | 0.0313 |
| 60 | 67.22 | 2 | 0.0481 | 0.0313 |

Table C3

Number of hunting records, the total effort in hours and attempted shots registered during the summer (April – September) for each of the management zones in Meerdaal.

| Zone | Summer | No. records (% of annual total) | Effort in hours (% of annual total) | No. shots (% of annual total) |
|-----------------------|--------|------------------------------------|--|----------------------------------|
| Core | 2018 | 1 (0.68) | 12 (2.51) | 0 (0.00) |
| | 2019 | 2 (1.02) | 5 (1.03) | 0 (0.00) |
| | 2020 | 1 (0.48) | 3 (0.51) | 0 (0.00) |
| | 2021 | 0 (0.00) | 0 (0.00) | 0 (0.00) |
| Winter Hunting | 2018 | 2 (1.37) | 8 (1.67) | 0 (0.00) |
| | 2019 | 3 (1.53) | 5 (1.03) | 1 (3.12) |
| | 2020 | 2 (0.96) | 4 (0.67) | 0 (0.00) |
| Year-round Hunting | 2021 | 1 (0.65) | 1 (0.20) | 1 (3.57) |
| | 2018 | 143 (97.95) | 459 (95.82) | 20 (100) |
| | 2019 | 191 (97.45) | 477 (97.95) | 31 (96.88) |
| | 2020 | 205 (98.56) | 586 (98.82) | 29 (100) |
| | 2021 | 153 (99.35) | 492 (99.8) | 27 (96.43) |

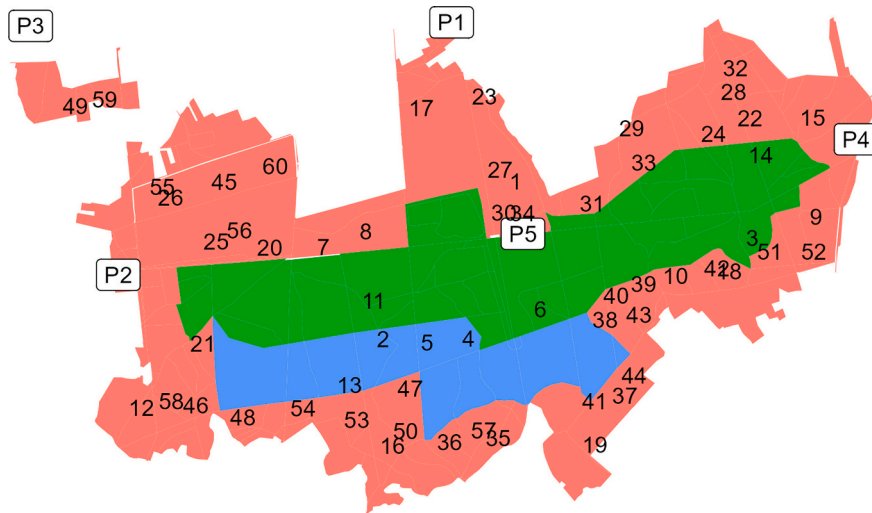


Fig. C1. Map of the study area, with references to the locations of parking lots and hunting posts.

References

- Amici, A., Serrani, F., Rossi, C.M., Primi, R., 2012. Increase in crop damage caused by wild boar (*Sus scrofa* L.): the “refuge effect”. *Agron. Sustain. Dev.* 32, 683–692. <https://doi.org/10.1007/s13593-011-0057-6>.
- Ballari, S.A., Barrios-García, M.N., 2014. Review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Rev.* 44, 124–134. <https://doi.org/10.1111/mam.12015>.
- Barker, R.J., Schofield, M.R., Link, W.A., Sauer, J.R., 2018. On the reliability of N-mixture models for count data. *Biometrics* 74, 369–377. <https://doi.org/10.1111/biom.12734>.
- Barrios-García, M.N., Ballari, S.A., 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biol. Invasions* 14, 2283–2300. <https://doi.org/10.1007/s10530-012-0229-6>.
- Bollen, M., Neyens, T., Fajenblat, M., De Waele, V., Licoppe, A., Manet, B., Casaer, J., Beenaerts, N., 2021. Managing African swine fever: assessing the potential of camera traps in monitoring wild boar occupancy trends in infected and non-infected zones, using spatio-temporal statistical models. *Front. Vet. Sci.* 8, 726117 <https://doi.org/10.3389/fvets.2021.726117>.
- Broggi, R., Grignolio, S., Brivio, F., Apollonio, M., 2020. Protected areas as refuges for pest species? The case of wild boar. *Glob. Ecol. Conserv.* 22, e00969 <https://doi.org/10.1016/j.gecco.2020.e00969>.
- Bubnicki, J.W., Churski, M., Schmidt, K., Diserens, T.A., Kuijper, D.P.J., 2019. Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. *eLife* 8, e44937. <https://doi.org/10.7554/eLife.44937>.
- Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., Riddell, A., 2017. Stan: a probabilistic programming language. *J. Stat. Softw.* 76, 32. <https://doi.org/10.18637/jss.v076.i01>.
- Castillo-Contreras, R., Carvalho, J., Serrano, E., Mentaberre, G., Fernández-Aguilar, X., Colom, A., González-Crespo, C., Lavín, S., López-Olvera, J.R., 2018. Urban wild boars prefer fragmented areas with food resources near natural corridors. *Sci. Total Environ.* 615, 282–288. <https://doi.org/10.1016/j.scitotenv.2017.09.277>.
- Castillo-Contreras, R., Mentaberre, G., Fernandez Aguilar, X., Conejero, C., Colom-Cadena, A., Ráez-Bravo, A., González-Crespo, C., Espunyes, J., Lavín, S., López-Olvera, J.R., 2021. Wild boar in the city: phenotypic responses to urbanisation. *Sci. Total Environ.* 773, 145593 <https://doi.org/10.1016/j.scitotenv.2021.145593>.
- Colomer, J., Rosell, C., Rodríguez-Tejedor, J.D., Massei, G., 2021. ‘Reserve effect’: an opportunity to mitigate human-wild boar conflicts. *Sci. Total Environ.* 795, 148721 <https://doi.org/10.1016/j.scitotenv.2021.148721>.
- Courbin, N., Garel, M., Marchand, P., Duparc, A., Debeffe, L., Börger, L., Loison, A., 2022. Interacting lethal and nonlethal human activities shape complex risk tolerance behaviors in a mountain herbivore. *Ecol. Appl.* 32, e2640 <https://doi.org/10.1002/eap.2640>.
- Fattebert, J., Baubert, E., Slotow, R., Fischer, C., 2017. Landscape effects on wild boar home range size under contrasting harvest regimes in a human-dominated agroecosystem. *Eur. J. Wildl. Res.* 63, 32. <https://doi.org/10.1007/s10344-017-1090-9>.
- Fernandez-De-Simon, J., Ferreres, J., Gortázar, C., 2023. The number of hunters and wild boar group size drive wild boar control efficacy in driven hunts. *Eur. J. Wildl. Res.* 69 <https://doi.org/10.1007/s10344-023-01661-7>.
- Fernández-López, J., Blanco-Aguilar, J.A., Vicente, J., Acevedo, P., 2022. Can we model distribution of population abundance from wildlife-vehicles collision data? *Ecography*. <https://doi.org/10.1111/ecog.06113>.
- Ferrer-Ferrando, D., Fernández-López, J., Triguero-Ocaña, R., Palencia, P., Vicente, J., Acevedo, P., 2023. The method matters. A comparative study of biologging and camera traps as data sources with which to describe wildlife habitat selection. *Sci. Total Environ.* 902, 166053 <https://doi.org/10.1016/j.scitotenv.2023.166053>.
- Fradin, G., Chamailé-Jammes, S., 2023. Hogs sleep like logs: wild boars reduce the risk of anthropic disturbance by adjusting where they rest. *Ecol. Evol.* 13 <https://doi.org/10.1002/ece3.10336>.
- Golding, N., Purse, B.V., 2016. Fast and flexible Bayesian species distribution modelling using Gaussian processes. *Methods Ecol. Evol.* 7, 598–608. <https://doi.org/10.1111/2041-210x.12523>.
- Grignolio, S., Merli, E., Bonghi, P., Ciuti, S., Apollonio, M., 2011. Effects of hunting with hounds on a non-target species living on the edge of a protected area. *Biol. Conserv.* 144, 641–649. <https://doi.org/10.1016/j.biocon.2010.10.022>.
- Guerrasio, T., Pelayo Acevedo, P., Apollonio, M., Arnón, A., Barroqueiro, C., Belova, O., Berdión, O., Blanco-Aguilar, J.A., Bijl, H., Bleier, N., Bučko, J., Elena Bužan, E., Carniato, D., Carro, F., Casaer, J., Carvalho, J., Csányi, S., Lucía Del Rio, L., Aliaga, H.D.V., Ertürk, A., Escribano, F., Duniš, L., Fernández-Lopez, J., Ferroglio, E., Fonseca, C., Gacici, D., Gavashelishvili, A., Giannakopoulos, A., Gómez-Molina, A., Gómez-Peris, C., Gruychev, G., Gutiérrez, I., Veith Häberlein, V., Hasan, S.M., Hillström, L., Hoxha, B., Iranzo, M., Mihael Janječić, M., Jansen, P., Illanas, S., Kashyap, B., Keuling, O., Laguna, E., Lefranc, H., Licoppe, A., Liefting, Y., Martínez-Carrasco, C., Mrdenović, D., Nežaj, M., Xosé Pardavila, X., Palencia, P., Pereira, G., Pereira, P., Pinto, N., Plhal, R., Plis, K., Podgórski, T., Pokorny, B., Preite, L., Radonjic, M., Marcus Rowcliffe, M., Ruiz-Rodríguez, C., Santos, J., Rodríguez, O., Scandura, M., Sebastián, M., Sereno, J., Šestovic, B., Shyti, I., Somoza, E., Soriguer, R., De La Torre, J.S., Soyumert, A., Šprem, N., Stoyanov, S., Smith, G.C., Sulce, M., Torres, R.T., Trajce, A., Urbaitis, G., Urbani, N., Uguzashvili, T., Vada, R., Zanet, S., Vicente, J., 2023. Wild Ungulate Density Data Generated by Camera Trapping in 37 European Areas: First Output of the European Observatory of Wildlife (EOW), 20. EFSA Supporting Publications. <https://doi.org/10.2903/sp.efsa.2023.en-7892>.
- Herrero, J., García-Serrano, A., Couto, S., Ortuño, V.M., García-González, R., 2006. Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. *Eur. J. Wildl. Res.* 52, 245–250. <https://doi.org/10.1007/s10344-006-0045-3>.
- Jägerbrand, A.K., Gren, I.-M., Sveriges, I., 2018. Consequences of increases in wild boar-vehicle accidents 2003–2016 in Sweden on personal injuries and costs. *Safety (Basel)* 4, 53. <https://doi.org/10.3390/safety4040053>.
- Johann, F., Handschuh, M., Linderth, P., Dormann, C.F., Arnold, J., 2020. Adaptation of wild boar (*Sus scrofa*) activity in a human-dominated landscape. *BMC Ecol.* 20, 1–14. <https://doi.org/10.1186/s12898-019-0271-7>.
- Joseph, L.N., Elkin, C., Martin, T.G., Possingham, H.P., 2009. Modeling abundance using N-mixture models: the importance of considering ecological mechanisms. *Ecol. Appl.* 19, 631–642. <https://doi.org/10.1890/07-2107.1>.
- Keever, A.C., McGowan, C.P., Ditchkoff, S.S., Acker, P.K., Grand, J.B., Newbolt, C.H., 2017. Efficacy of N-mixture models for surveying and monitoring white-tailed deer populations. *Mamm. Res.* 62, 413–422. <https://doi.org/10.1007/s13364-017-0319-z>.
- Kéry, M., 2018. Identifiability in N-mixture models: a large-scale screening test with bird data. *Ecology* 99, 281–288. <https://doi.org/10.1002/ecy.2093>.
- Kéry, M., Royle, J.A., 2016. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS*. Academic Press.
- Keuling, O., Stier, N., Roth, M., 2008. How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? *Eur. J. Wildl. Res.* 54, 729–737. <https://doi.org/10.1007/s10344-008-0204-9>.
- Keuling, O., Stier, N., Roth, M., 2009. Commuting, shifting or remaining?: different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during

- summer. *Mamm. Biol.* 74, 145–152. <https://doi.org/10.1016/j.mambio.2008.05.007>.
- Keuling, O., Baubet, E., Duscher, A., Ebert, C., Fischer, C., Monaco, A., Podgórski, T., Prevot, C., Ronnenberg, K., Sodeikat, G., Stier, N., Thurfjell, H., 2013. Mortality rates of wild boar *Sus scrofa* L. in central Europe. *Eur. J. Wildl. Res.* 59, 805–814. <https://doi.org/10.1007/s10344-013-0733-8>.
- Klimaatstatistiek van de Belgische gemeenten Oud-Heverlee (nis24086). https://www.meteo.be/resources/climatology/climateCity/pdf/climate_INS24086_9120_nl.pdf. (Accessed 25 May 2023).
- Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., P, J.W., Smith, D.W. & MacNulty, D.R., 2018. Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* 88, 638–652. <https://doi.org/10.1002/ecm.1313>.
- Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS One* 11, e0167259. <https://doi.org/10.1371/journal.pone.0167259>.
- Ledger, S., Rutherford, C., Benham, C., Burfield, I., Deinet, S., Eaton, M., Freeman, R., Puleston, H., Scott-Gatty, K., Staneva, A., 2022. *Wildlife Comeback in Europe: Opportunities and Challenges for Species Recovery. Final report to Rewilding Europe by the Zoological Society of London. BirdLife International and the European Bird Census Council.*
- Linderoth, P., 2010. *Schwarzwildprojekt Böblingen: Studie zum Reproduktionsstatus, zur Ernährung und zum jagdlichen Management einer Schwarzwildpopulation. Wildforschungsstelle des Landes Baden-Württemberg.*
- Mäkinen, J., Numminen, E., Niittynen, P., Luoto, M., Vanhatalo, J., 2022. Spatial confounding in Bayesian species distribution modeling. *Ecography* 2022. <https://doi.org/10.1111/ecog.06183>.
- Martin, J., Royle, J.A., Mackenzie, D.I., Edwards, H.H., Kéry, M., Gardner, B., 2011. Accounting for non-independent detection when estimating abundance of organisms with a Bayesian approach. *Methods Ecol. Evol.* 2, 595–601. <https://doi.org/10.1111/j.2041-210X.2011.00113.x>.
- Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Šprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozoliņš, J., Cellina, S., Podgórski, T., Fonseca, C., Markov, N., Pokorný, B., Rosell, C., Náhlik, A., 2015. Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Manag. Sci.* 71, 492–500. <https://doi.org/10.1002/ps.3965>.
- Mimnagh, N., Parnell, A., Prado, E., Moral, R.D.A., 2022. Bayesian multi-species N-mixture models for unmarked animal communities. *Environ. Ecol. Stat.* 29, 755–778. <https://doi.org/10.1007/s10651-022-00542-7>.
- Nakashima, Y., 2020. Potentiality and limitations of N-mixture and Royle-Nichols models to estimate animal abundance based on noninstantaneous point surveys. *Popul. Ecol.* 62, 151–157. <https://doi.org/10.1002/1438-390x.12028>.
- Ohashi, H., Saito, M., Horie, R., Tsunoda, H., Noba, H., Ishii, H., Kuwabara, T., Hiroshige, Y., Koike, S., Hoshino, Y., Toda, H., Kaji, K., 2013. Differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. *Eur. J. Wildl. Res.* 59, 167–177. <https://doi.org/10.1007/s10344-012-0661-z>.
- Podgórski, T., Baś, G., Jędrzejewska, B., Sönnichsen, L., Śniezko, S., Jędrzejewski, W., Okarma, H., 2013. Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *J. Mammal.* 94, 109–119. <https://doi.org/10.1644/12-mamm-a-038.1>.
- Quirós-Fernández, F., Marcos, J., Acevedo, P., Gortázar, C., 2017. Hunters serving the ecosystem: the contribution of recreational hunting to wild boar population control. *Eur. J. Wildl. Res.* 63. <https://doi.org/10.1007/s10344-017-1107-4>.
- Reinke, H., König, H.J., Keuling, O., Kuemmerle, T., Kiffner, C., 2021. Zoning has little impact on the seasonal diel activity and distribution patterns of wild boar (*Sus scrofa*) in an UNESCO Biosphere Reserve. *Ecol. Evol.* 11, 17091–17105. <https://doi.org/10.1002/ece3.8347>.
- Rowcliffe, J.M., Field, J., Turvey, S.T., Carbone, C., 2008. Estimating animal density using camera traps without the need for individual recognition. *J. Appl. Ecol.* 45, 1228–1236. <https://doi.org/10.1111/j.1365-2664.2008.01473.x>.
- Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60, 108–115. <https://doi.org/10.1111/j.0006-341X.2004.00142.x>.
- Royle, J.A., Chandler, R.B., Sollmann, R., Gardner, B., 2013. *Spatial capture-recapture.* Academic Press.
- Rutten, A., Casar, J., Swinnen, K.R.R., Herremans, M., Leirs, H., 2019. Future distribution of wild boar in a highly anthropogenic landscape: models combining hunting bag and citizen science data. *Ecol. Model.* 411, 108804. <https://doi.org/10.1016/j.ecolmodel.2019.108804>.
- Schley, L., Dufrene, M., Krier, A., Frantz, A.C., 2008. Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. *Eur. J. Wildl. Res.* 54, 589–599. <https://doi.org/10.1007/s10344-008-0183-x>.
- Solin, A., Särkkä, S., 2020. Hilbert space methods for reduced-rank Gaussian process regression. *Stat. Comput.* 30, 419–446. <https://doi.org/10.1007/s11222-019-09886-w>.
- Stillfried, M., Fickel, J., Börner, K., Wittstatt, U., Heddergott, M., Ortmann, S., Kramer-Schadt, S., Frantz, A.C., 2017a. Do cities represent sources, sinks or isolated islands for urban wild boar population structure? *J. Appl. Ecol.* 54, 272–281. <https://doi.org/10.1111/1365-2664.12756>.
- Stillfried, M., Gras, P., Börner, K., Göritz, F., Painer, J., Rölli, K., Wenzler, M., Hofer, H., Ortmann, S., Kramer-Schadt, S., 2017b. Secrets of success in a landscape of fear: urban wild boar adjust risk perception and tolerate disturbance. *Front. Ecol. Evol.* 5. <https://doi.org/10.3389/fevo.2017.00157>.
- Stillfried, M., Gras, P., Busch, M., Börner, K., Kramer-Schadt, S., Ortmann, S., 2017c. Wild inside: urban wild boar select natural, not anthropogenic food resources. *PLoS One* 12. <https://doi.org/10.1371/journal.pone.0175127>.
- Thurfjell, H., Ball, J.P., Åhlén, P.-A., Kornacher, P., Dettki, H., Sjöberg, K., 2009. Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): agricultural fields and edges. *Eur. J. Wildl. Res.* 55, 517–523. <https://doi.org/10.1007/s10344-009-0268-1>.
- Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C., Baubet, E., 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Can. J. Zool.* 87, 1129–1137. <https://doi.org/10.1139/Z09-101>.
- Triguero-Ocaña, R., Laguna, E., Jiménez-Ruiz, S., Fernández-López, J., García-Bocanegra, I., Barasona, J.Á., Rialde, M.Á., Montoro, V., Vicente, J., Acevedo, P., 2021. The wildlife-livestock interface on extensive free-ranging pig farms in central Spain during the “Montanera” period. *Transbound. Emerg. Dis.* 68, 2066–2078. <https://doi.org/10.1111/tbed.13854>.
- Tucker, M.A., Santini, L., Carbone, C., Mueller, T., 2021. Mammal population densities at a global scale are higher in human-modified areas. *Ecography* 44, 1–13. <https://doi.org/10.1111/ecog.05126>.
- Vajas, P., Calenge, C., Richard, E., Fattebert, J., Rousset, C., Saïd, S., Baubet, E., 2020. Many, large and early: hunting pressure on wild boar relates to simple metrics of hunting effort. *Sci. Total Environ.* 698, 134251. <https://doi.org/10.1016/j.scitotenv.2019.134251>.
- Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* 27, 1413–1432. <https://doi.org/10.1007/s11222-016-9696-4>.
- Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., Bürkner, P.-C., 2021. Rank-normalization, folding, and localization: an improved R for assessing convergence of MCMC. *Bayesian Anal.* 1, 1–28. <https://doi.org/10.1214/20-ba1221>.
- Vetter, S.G., Puskas, Z., Bieber, C., Ruf, T., 2020. How climate change and wildlife management affect population structure in wild boars. *Sci. Rep.* 10. <https://doi.org/10.1038/s41598-020-64216-9>.
- Wevers, J., Fattebert, J., Casar, J., Artois, T., Beenaerts, N., 2020. Trading fear for food in the Anthropocene: how ungulates cope with human disturbance in a multi-use, suburban ecosystem. *Sci. Total Environ.* 741, 140369. <https://doi.org/10.1016/j.scitotenv.2020.140369>.
- Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J., Musiani, M., 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. *J. Appl. Ecol.* 48, 1535–1542. <https://doi.org/10.1111/j.1365-2664.2011.02043.x>.