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The Chornobyl Exclusion Zone as a wildlife refuge: restricted human access shaped mammal recolonization

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Land-use changes and habitat degradation threaten biodiversity and ecosystem functions globally. Large terrestrial mammals are particularly vulnerable due to low reproductive rates, large spatial requirements and sensitivity to human disturbances. Increasing coverage and effectiveness of protected areas (PAs) is vital to conserve mammal species and their habitats. We used camera trapping to assess the impact of human activities and landscape characteristics on diversity, occupancy and detection probabilities of 11 terrestrial mammals in northern Ukraine in 2020–2021. We evaluated the impact of human stressors and landscape modifications on species diversity, occupancy and detection probabilities across the Ukrainian Chornobyl Exclusion Zone (CEZ), regional PAs and non-PAs. We implemented hierarchical Bayesian single-species single-season occupancy models to identify the covariates that described the occupancy (Ψ) and detection (p) probabilities for each species. Species diversity, occupancy and detection probabilities were significantly higher in the Ukrainian CEZ and neighbouring Drevlianskyi Nature Reserve (highest occupancy probabilities of Przewalski's horse, Eurasian lynx, moose and red deer) than in all other areas. PA coverage positively

influenced red deer, red fox and raccoon dog occupancies, while PA protection status showed mixed effects across species. Our results demonstrate that PAs are most effective when they are large, contiguous and human access restrictions are actively enforced.

1. Background

Land-use changes and resource exploitation result in habitat loss and degradation at regional and global scales and pose significant threats to biodiversity and ecosystem functions [1,2]. Biodiversity is the foundation of ecosystem resilience, supports ecosystem recovery from disturbances and provides essential ecosystem services [2]. Wildlife responses to human activities are modulated by the type and intensity of the activity, species life-history traits and behavioural plasticity [3]. Generalist species are behaviorally flexible and commonly show adaptive responses to human-altered conditions, while specialists generally have lower adaptability to changing conditions due to intrinsic traits and, thus, are more vulnerable and at higher risk of extinction [4]. Large terrestrial mammals are especially prone to population declines and extinction risks due to their low reproductive rates and large requirements for space, forage and prey, as well as to overexploitation by people [5,6]. Both lethal and non-lethal human disturbance can cause shifts from diurnal or crepuscular activity to nocturnal activity across various trophic levels [7]. Roads fragment wildlife habitats and channel lethal and non-lethal human disturbance affecting animal behaviours [8,9] such as movement, foraging and activity patterns [10,11].

The establishment of protected areas (PAs) is a key strategy to counter population declines of vulnerable species and secure long-term biodiversity conservation [11]. Such management interventions mitigate anthropogenic stressors and benefit biodiversity, particularly large species disproportionately affected by hunting, habitat loss and degradation [12]. PAs often serve as refuges for wildlife as they tend to have lower levels of human disturbance compared to areas without a protection status [13]. The need to expand PA coverage has been recognized as a major biodiversity conservation priority highlighted by the UN Biodiversity Conference, COP 15 [14]. Large PAs are more resilient to natural and anthropogenic stressors compared to small, fragmented PAs, support more diverse and abundant wildlife populations [15] and are also vital for conservation of far-ranging species [16]. However, in some cases, large PAs may only exist on maps as so-called 'paper parks' due to a lack of sound on-ground management and thus fail to foster biodiversity conservation [17,18].

The positive effects of PAs can be undermined by ineffective law enforcement, lack of personnel, illegal hunting and a lack of acceptance by local communities [19]. Non-consumptive recreation in PAs has become another conservation concern as it directly causes disturbance of wildlife [10] as well as habitat loss due to encroachment of recreational facilities and infrastructure within and along the PA edge [20,21]. Many PAs are designated in areas considered less valuable for agriculture and/or human development [22] or gain their conservation status because of contamination or armed conflict, such as the Chornobyl Exclusion Zone (CEZ) or the Korean Demilitarized Zone (the buffer zone between North and South Korea). These areas are dangerous and uninhabitable for people due to radioactive contamination and unexploded ordnance, yet they are important areas for wildlife recovery [23,24].

In addition to upsizing existing PAs, conservation management within PAs needs to be optimised to achieve conservation objectives [18]. Assessment of the PA effectiveness against anthropogenic stressors can be challenging due to methodological, political and logistical constraints [18,25]. The questionnaire-based PA management effectiveness (PAME) assessments are useful for evaluating the adaptive management of PAs but not for evaluating the effects of conservation interventions on habitats and species [12]. In-depth evaluation of the effectiveness of PAs relies on systematic, long-term biodiversity monitoring schemes and on spatial data on human activities inside and outside the PA that accurately reflect on-ground processes [17]. The general lack of systematic biodiversity data from non-PAs with environmental conditions similar to those of existing PAs also hampers the evaluation of species distributions in PAs [26].

Here, we analyse the effects of conservation status and the PA size on mammal diversity and occupancy. We used the Ukrainian part of the Chornobyl Exclusion Zone (hereafter, the Ukrainian CEZ), PAs, and non-PAs across northern Ukraine to assess the effects of human activities on species diversity, detection and occupancy probabilities. We considered the Ukrainian CEZ as a model PA wherein large contiguous PA size and stricter access enforcement than in other regional PAs allowed us to simultaneously test the effects of PA size and human access restriction. Understanding whether the terrestrial mammal occupancy is significantly higher in the large Ukrainian CEZ with its enforced human access restrictions compared to less restricted and smaller PAs and areas without a protection status is crucial for the improvement of conservation strategies [27]. We predicted that (i) large PAs have higher mammalian diversity, detection and occupancy probabilities compared to small PAs, and (ii) mammalian diversity, detection and occupancy probabilities decrease with increasing human activities, linear infrastructure (roads) and other landscape modifications.

2. Methods

(a) Study area

This study was conducted in the lowland Polissia Region, covering around 60 000 km^2 in northern Ukraine (figure 1). Altitudes are low, ranging from 100 to 150 m above sea level. The climate is continental, with mean temperatures ranging from −4 to −7°C in January and from +18 to +19°C in July. Annual precipitation is 550–650 mm. Polissia has a dense network of lakes and rivers

that repeatedly flood throughout the year (maximum submergence in late March–early April [28]). Polissia harbours a diverse mammal community which includes regionally red-listed and rare large carnivore species, such as brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), grey wolf (*Canis lupus*) and ungulates such as moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), European bison (*Bison bonasus*) and Przewalski's horse (*Equus f. przewalskii*) [24,29–33]. After the Chornobyl catastrophe in 1986, large carnivores have re-colonized both the Belarusian and Ukrainian parts of the CEZ [30,33–35]. In the 1990s, the European bison was reintroduced in the Belarusian part and Przewalski's horse in the Ukrainian part [29,31].

The study area comprised several PAs of various sizes and protection levels across the Ukrainian Polissia Region: (i) the Ukrainian CEZ, most of which was designated as the Chornobyl Radiation and Ecological Biosphere Reserve in 2016; (ii) four nature reserves: the Drevlianskyi, Polissia, Rivne and Cheremskyi Nature Reserves, all IUCN category Ia (strict nature reserve); (iii) two national nature parks—the Prypiat-Stokhid and Nobel National Nature Parks, IUCN category II (national park); and (iv) non-protected areas (non-PAs) bordering the Polissia, Rivne, Cheremskyi Nature Reserves and Prypiat-Stokhid and Nobel National Nature Parks (figure 1; electronic supplementary material, table S4). Within the PAs, secondary and unpaved roads dominate the road network, and hunting is prohibited. Logging is limited in national parks and prohibited in nature reserves. Tourism is permitted in national parks, prohibited in nature reserves and restricted access was possible in the Ukrainian CEZ until the Russian invasion in February 2022. Outside of PAs in the region, logging, livestock grazing, gathering non-timber resources (e.g. antler, berry and mushroom picking), illegal amber mining and hunting are among the main human activities likely to affect wildlife. Due to radioactive contamination after the Chornobyl catastrophe, access to the Ukrainian CEZ is highly restricted [36]. Similarly, the Drevlianskyi Nature Reserve (NR), which borders the Ukrainian CEZ, has analogous conservation management due to radioactive contamination. In comparison, the PAs to the west of the Ukrainian CEZ are similar in size, law enforcement and restrictions regarding human access. Therefore, we further categorized the aforementioned areas in the following way: the *Ukrainian CEZ*, *nature reserves* (Drevlianskyi, Polissia, Rivne, Cheremskyi Nature Reserves), *national parks* (Prypiat-Stokhid and Nobel National Nature Parks) and *non-PAs*, which border Polissia, Rivne, Cheremskyi Nature Reserves; Prypiat-Stokhid and Nobel National Nature Parks.

(b) Camera trapping and site data

We overlaid the study area with a 3.1 × 3.1 km grid to reduce spatial autocorrelation while ensuring sufficient spatial resolution to detect ecological variation. This grid size approximates or exceeds the home ranges of most large and medium-sized mammals within the study area [37–40]. We selected all cells covering the Ukrainian CEZ, PAs and non-PAs, and in these cells, we distributed remote meras at the central point of every other grid cell, within a 25 m buffer. Grid cells where central points were not accessible (e.g. a human settlement, swamp or water) were excluded and cameras were deployed in adjacent cells. We employed a crossed design, and the study period in most of the Ukrainian CEZ lasted from 20 July to 14 November 2020, and in the remaining western part of the Ukrainian CEZ, PAs and non-PAs in 2021 from 1 June to 18 October (electronic supplementary material, table S4). Cameras were deployed on the nearest tree with an unobstructed north-facing view within a 25 m buffer around the grid's central point. At locations (n = 16) where the 25 m buffer was inaccessible because of topographical features (swamps lacking solid ground), cameras were deployed at the closest position possible to the grid's central point within a 100 m buffer around the grid's central point. Cameras were installed at a height of approximately 50 cm and angled parallel to the ground. We used one unbaited camera per site (Cuddeback C2 and G2 models with black flashes and Ltl Acorn with infrared flashes) that operated in the field for at least 60 days without inspections. We used the software TRAPPER to record the presence of species [41], considered a day (24 h) as the time unit and defined a detection event as at least one photographic detection of a given species per day.

We characterized habitat at each camera trap site (n = 174) by assessing canopy cover, understory vegetation density and the forest development stage within a camera trap detection zone [42]. We assessed canopy cover and understory vegetation density around camera sites with digital photographs and the image manipulation software Gimp [43]. Canopy cover and understory vegetation densities were calculated from binary images by counting black (vegetation) and white (non-vegetation) pixels. The original seven categories of the forest development stage (0 = grassland, 1 = regeneration, 2 = dense thicket, 3 = dense forest stand, 4 = young mature forest, 5 = old mature forest, 6 = burned forest) were combined into three simplified categories for further analyses [44] (see details in electronic supplementary material, table S1). We extracted the Euclidean distance (in m) from each camera trap to the nearest road, river and edge of the nearest PA with Geographic Information Systems [45]. For sites located in non-PAs, the distance to the edge of the nearest PA was equal to 0, and all distance-related covariates were log-transformed.

(c) Occupancy modelling

We implemented Bayesian single-species single-season occupancy models [42,46] to estimate mammal occupancy and its determinants. Occupancy models are hierarchical models that usually consist of two sub-models, one sub-model for site occupancy status and one model for detection probability. We included covariates in both the occupancy probability and detection probability. We formulated the occupancy submodel as a Bernoulli process:

$$z_i \sim Bernoulli(\psi_i),$$

where ψ_i is the occupancy probability and z_i the latent occupancy state (0/1) at site $\mathbf{i}$. Occupancy probability can be modelled as the outcome of a logistic regression:

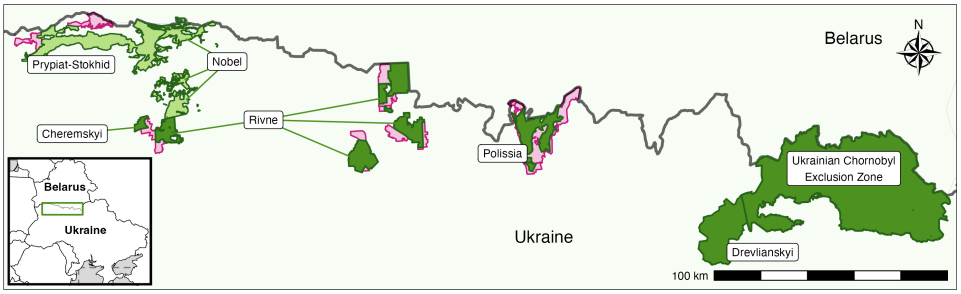

Figure 1. Study area in northern Ukraine. Masked areas indicate the Ukrainian CEZ, six protected areas and non-protected areas. Dark green colour shows IUCN category Ia (biosphere and strict nature reserves), light green shows IUCN category II (national parks) and pink shows non-protected areas sampled.

$$logit(\psi_i) = \beta_0 + \sum_k \times \beta_k x_{ik} + \beta_1(x_{ia} \times x_{ib}) + \beta_2(x_{ia} \times x_{ic}),$$

where β_0 is the species-specific intercept, β_k are main-effect coefficients for covariates x_{ik} and β_1, β_2 are coefficients for two interaction terms and x_{ik} is the value associated with kth covariate.

We formulated the detection submodel as another Bernoulli process:

$$y_{ij} \sim Bernoulli(z_i p_{ij}),$$

where y_{ij} is the actual detection (0/1) and p_{ij} the probability of detection at site i during occasion j, where 24 h were considered as one occasion. Detection ($y = 1$) of a species at a site during a given occasion is conditional on the site being occupied by that species. Whereas occupancy is assumed to be constant during the study period (closure assumption), detection probability can vary between occasions. Detection probability was modelled as:

$$logit(p_{ij}) = \beta_0 + \sum_k \times \beta_k p_{ijk}$$

where β_0 is the species-specific intercept, β_k are coefficients and p_{ijk} are covariates that may influence detection.

Our selection of covariates focused on spatial variation in species occurrence and how it was affected by environmental and anthropogenic variables (see electronic supplementary material, table S1, for further details). We included the specific protection status of each area (exclusion zone, nature reserve, national nature park and non-PA) as a covariate. There was insufficient variation in road density [47], PA and cropland coverages at 3.1 km scale as most of the camera traps (89%) were deployed within regional PAs and the 3.1 km scale did not capture differences around camera traps across the study area. To account for potentially differing intensities of human disturbances in large PAs compared to small PAs and non-PAs, we calculated the proportional coverage of protected areas [14] and cropland [48] within a 10 km buffer around each camera trap. Other landscape scale covariates such as tree cover [49] and land cover [50] were also calculated for the 10 km buffers around camera traps. For each 10 km buffer around a camera trap, we calculated the road density (m km^{-2}), the mean tree cover and determined the dominant land cover type. We estimated the intensity of human activity in the study area as the ratio of the number of days with human presence detected by camera traps and the total number of days each camera trap operated.

The same detection and occupancy covariates were used in all models for herbivores and mesocarnivores. We included the apparent presence/absence of roe deer (capreolusSite; electronic supplementary material, table S1), the main prey of lynx [51] as a species-specific detection and occupancy covariate for lynx, and ungulate diversity (ungDiversity_index; electronic supplementary material, table S1) as an occupancy and detection covariate for wolves, which prey on several species [52]. To account for changes in the occupancy status and detection probability at the camera sites in 2020 and 2021, we added the sampling year (equaling 0 when a camera trap was operating in 2020 and 1 when it was operating in 2021) as a covariate in the regressions with the detection and occupancy probabilities as the response variables. To account for the effect of an infrared camera trap flash on animal behaviour compared to a black flash [53] and consequently, the detection probability, we added a camera trap as a binary covariate (0 for camera traps with a black flash and 1 for camera traps with an infrared flash) in the regression with detection probability as the response variables (see electronic supplementary material, table S1, for further details). We did not find high correlations ($r > 0.7$) among numerical variables in the same model. All detection and occupancy covariates, along with their use in the species- and area-specific models, are described in electronic supplementary material, table S1. We considered both the additive effects and two interactions between covariates (PA area coverage × tree cover and PA coverage × road density).

(d) Model fitting and evaluation

Since the CEZ area and other areas are quite different in size, protection level and management, we wanted to allow independent estimation of all parameters, as well as independent covariate selection with the reversible jump Markov chain Monte Carlo (RJMCMC) [54] implemented in R v.4.3.2 [55] with the *NIMBLE* package [56]. Across all models, we used weakly informative priors to prevent extreme coefficient estimates with small datasets. Regression coefficients for detection and occupancy were assigned independent logistic distributions centred at zero with scale parameter 1 ($\beta \sim Logistic(0,1)$) with intercepts always included in the model. For covariate selection under RJMCMC, a binary indicator variable determined whether each covariate was included. We

reported posterior inclusion probabilities (PIPs) for each covariate as a measure of covariate importance. We applied a threshold of 0.5 to identify covariates with substantial support, i.e. those appearing in more than 50% of model iterations [57]. Covariates with the PIP ≥0.5 (the probability of variable inclusion ≥50%) as estimated through the RJMCMC were considered significant if the posterior probability of their beta coefficients did not overlap zero. We restricted interpretation to covariates with values above 0.5 and did not consider sub-threshold covariates as reliable predictors. The null model (intercept-only structure for either detection or occupancy) was used in the subsequent empirical analyses when all of the model covariates were estimated by the RJMCMC algorithm to have the PIP <0.5. We fitted our models in empirical analyses using Markov chain Monte Carlo (MCMC) and ran four chains, each 120 000 MCMC iterations and discarded the initial 30 000 iterations as burn-in. To reduce autocorrelation within a chain, we applied iteration thinning that selected every third sample from the MCMC chain. We visually assessed the convergence of the chains and verified it by calculating the Gelman–Rubin statistics for each covariate where R-hat values <1.1 indicated convergence [58]. We assessed the effect of covariates on detection and occupancy probabilities by using the mean of the posterior distribution and the associated Bayesian credible intervals (95% BCI) of each beta coefficient. We considered effects significant when the 95% BCI associated with a coefficient did not overlap zero.

3. Results

The sampling effort across the entire study area totalled 15 244 camera trap days. Cameras detected a total of 13 terrestrial mammal species, ranging from 13 in the Ukrainian CEZ to one in the Cheremskyi Nature Reserve, and including herbivores (n = 6), mesocarnivores (n = 4) and large carnivores (n = 3) (table 1). The Ukrainian CEZ had higher mammalian diversity and occupancy values than other PAs and non-PAs (figures 2 and 3; electronic supplementary material, table S2). At the same time, non-protected areas had species composition and occupancy values similar to small-sized PAs (figures 2 and 3; electronic supplementary material, S1–S4). The RJMCMC algorithm calculated covariate posterior inclusion probabilities (PIP) before model fitting, and only covariates with the probability of inclusion ≥50% (PIP = 0.5) were further selected (electronic supplementary material, table S3 and figures S5–S7). The RJMCMC revealed low PIP values (<0.5) for all covariates in the occupancy submodel for roe deer, European hare (*Lepus europaeus*) and wolf, as well as in the detection submodel for raccoon dog (*Nyctereutes procyonoides*), indicating these covariates were not important (electronic supplementary material, table S3 and figures S5–S7).

Increasing protected area coverage within a 10 km buffer was positively associated with the occupancy of red deer (β = 3.01, 95% BCI = 1.66, 4.55), red fox (*Vulpes vulpes*) (β = 0.82, 95% BCI = 0.38, 1.3) and raccoon dog (β = 1.09, 95% BCI = 0.49, 1.77). The PIP values for protected area coverage in the occupancy submodels for moose and lynx were ≥0.5 and showed a positive trend in species occupancy probabilities; however, the confidence intervals overlapped with zero. The PIP values were high for the categorical protection status in the occupancy submodels, but the 95% BCI overlapped zero, and there was no difference between any of the levels (reserve, national park or non-PA) and the baseline level (CEZ) (electronic supplementary material, figures S9–S11). Compared to the CEZ, detection probability was higher in the reserves for red fox (β = 0.58, 95% BCI = 0.09, 1.05) and lower for red deer (β = 1.3, 95% BCI = −1.73, –0.88), wild boar (β = 1.42, 95% BCI = −2.45, –0.49) and hare (β = −2.04, 95% BCI = −3.65, –0.68). Detection probability of roe deer was higher both in the national parks (β = 0.93, 95% BCI = 0.68, 1.17) and non-PAs (β = 0.38, 95% BCI = 0.13, 0.63), while detection probability of moose was higher only in national parks (β = 0.89, 95% BCI = 0.33, 1.45) and wild boar had lower detection probability in non-PAs compared to the Ukrainian CEZ (β = 1.64, 95% BCI = −3.59, –0.14). The proportion of cropland was positively related to moose, red deer and wild boar occupancies (β = 1.43, 95% BCI = 0.6, 2.58; β = 1.13, 95% BCI = 0.17, 2.28; and β = 1.07, 95% BCI = 0.37, 2.03, respectively; electronic supplementary material, table S4; figure 4).

Tree cover had a positive effect on moose occupancy (β = 1.81, 95% BCI = 0.67, 3.28) and the interaction between the protected area coverage and tree cover had a negative effect on badger (*Meles meles*) occupancy (β = −1.35, 95% BCI = −2.78, −0.16). Przewalski's horse and red deer detection probabilities were positively associated with burned forests (β = 2.18, 95% BCI = 0.76, 3.73; β = 0.67, 95% BCI = 0.46, 0.89) and wolf detection probability was negatively associated with open areas (grassland, thicket; β = −1.39, 95% BCI = −2.51, −0.32). Przewalski's horse and roe deer had lower detection probability in dense understory vegetation and thickets (β = −1.01, 95% BCI = −1.62, −0.43 and β = −0.17, 95% BCI = −0.26, -0.07). Przewalski's horse, hare and badger detection probabilities increased with decreasing distance to rivers (β = −0.79, 95% BCI = −1.15, −0.43; β = −0.52, 95% BCI = −0.79, −0.23 and β = −0.63, 95% BCI = −0.97, −0.3) while red deer and roe deer detection probabilities decreased in relation to distance to rivers (β = 0.37, 95% BCI = 0.27, 0.47 and β = 0.21, 95% BCI = 0.12, 0.3).

Wolf, lynx, Przewalski's horse and wild boar (*Sus scrofa*) detection probabilities decreased with increasing distance from roads (figure 4; electronic supplementary material, S8–S11 and table S4). Distance to the outer edge of the PA was positively associated with wolf, Przewalski's horse and badger detection probabilities (β = 1.39, 95% BCI = 0.87, 1.95; β = 2.05, 95% BCI = 0.69, 3.68 and β = 1.45, 95% BCI = 0.59, 2.34). Regarding the intensity of human pressure, the human ratio had a negative effect on moose detection probability (β = −1.59, 95% BCI = −2.9, −0.59). Moose and red deer detections were negatively related to sampling year (β = −0.77, 95% BCI = −1.23, −0.34 and β = −0.42, 95% BCI = −0.66, −0.2). Detection was not related to infrared camera trap flash for any species.

Occupancy probabilities varied among species, and the highest values were predicted for the most common herbivores (roe deer and moose). Roe deer, moose and wild boar had the highest occupancy across protection status categories (figure 2; electronic supplementary material, S1–S2 and table S2). Wild boar had intermediate values across the study area, while hare and Przewalski's horse had the lowest values compared to other herbivorous species. Red deer occupancy was similarly high to that of other herbivores (roe deer, moose) in the Ukrainian CEZ and the Drevlyanskyi NR but lower in other PAs and non-PAs. Przewalski's horse had low occupancy even within the Ukrainian CEZ (mean occupancy = 0.3; 95% BCI = 0.23, 0.36). Red fox occupancy was the

Table 1. Species composition, number of camera trap photos and sites with species detected in the Ukrainian CEZ, Drevlyanskyi, Polissia, Rivne and Cheremskyi Nature Reserves; Nobel and Prypiat-Stokhid National Nature Parks and adjacent non-protected areas. Species listed in bold ($n = 11$) had enough observations for modelling detection and occupancy probabilities.

	red deer, *Cervus elaphus*	roe deer, *Capreolus capreolus*	moose, *Alces alces*	Przewalski's horse, *Equus ferus przewalskii*	wild boar, *Sus scrofa*	European hare, *Lepus europaeus*	red fox, *Vulpes vulpes*	raccoon dog, *Nyctereutes procyonoides*	European badger, *Meles meles*	marten species (*Martes* sp.)	grey wolf, *Canis lupus*	Eurasian lynx, *Lynx lynx*	brown bear, *Ursus arctos*	livestock, *Bos taurus* and *Equus caballus*	domestic dog, *Canis lupus familiaris*	people	total
no. camera trap photos																	
Ukrainian CEZ	11 719	2907	2665	1054	501	124	263	171	96	25	102	37	12	113*	23	20	19 832
Drevlianskyi	554	852	231	0	45	0	116	28	4	0	9	3	0	0	2	229	2073
Polissia	0	139	44	0	3	4	4	0	0	0	2	0	0	0	3	200	399
Rivne	0	81	3	0	0	0	0	0	0	0	0	0	0	336	5	751	1176
Cheremskyi	0	172	0	0	0	0	0	0	0	0	0	0	0	0	0	72	244
Prypiat-Stokhid	0	747	384	0	21	0	19	0	0	2	0	0	0	1533	19	1226	3951
Nobel	0	1021	50	0	13	6	0	0	0	0	0	0	0	44	10	1051	2195
non-PAs	0	811	268	0	3	0	18	0	0	5	0	0	0	48	17	160	1330
total	12 273	6730	3654	1054	586	134	420	199	100	32	113	40	12	2074	79	3709	31 200
no. camera trap sites with photos																	
Ukrainian CEZ	66	65	71	13	24	16	23	16	11	5	17	8	2	1	0	3	87
Drevlianskyi	12	16	8	0	3	0	5	4	2	0	3	1	0	0	2	13	17
Polissia	0	6	3	0	3	2	1	0	0	0	1	0	0	0	1	6	10
Rivne	0	7	1	0	0	0	0	0	0	0	0	0	0	2	2	11	12
Cheremskyi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Prypiat-Stokhid	0	11	6	0	2	0	3	0	0	1	0	0	0	3	3	7	16
Nobel	0	10	3	0	3	2	0	0	0	0	0	0	0	1	3	9	12
non-PAs	7	17	0	0	1	0	3	0	0	2	0	0	0	1	0	10	19
total	85 (49%)	133 (76%)	92 (53%)	13 (8%)	36 (21%)	20 (12%)	35 (20%)	20 (12%)	13 (8%)	8 (5%)	21 (12%)	9 (5%)	2 (1%)	8 (5%)	11 (6%)	60 (35%)	174 (100%)

Note: *Feral domestic cattle

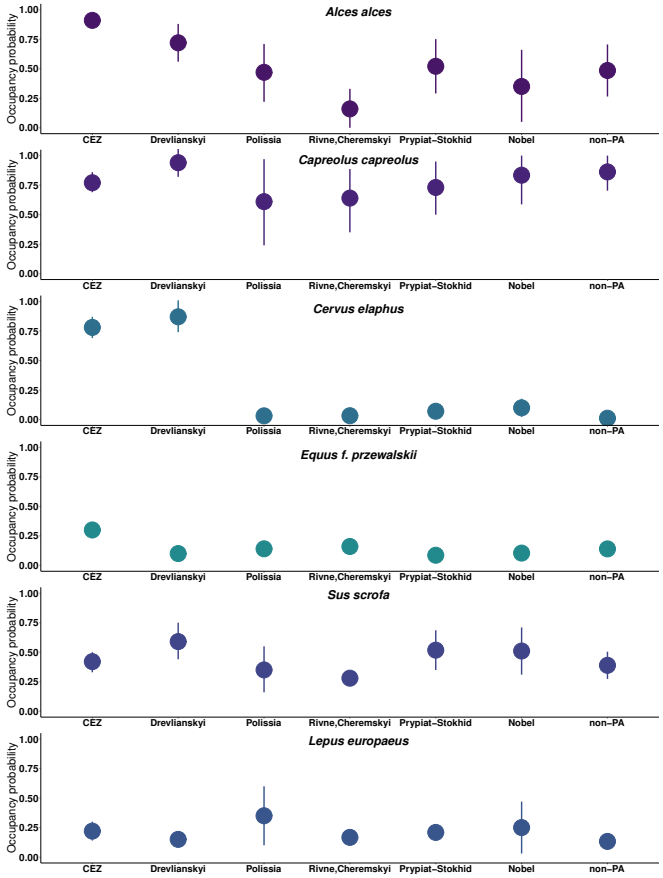

Figure 2. Moose (*Alces alces*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), Przewalski's horse (*Equus f. przewalskii*), wild boar (*Sus scrofa*) and brown hare (*Lepus europaeus*) occupancy probabilities in the Ukrainian CEZ, six protected areas (Drevlianskyi, Polissia, Rivne and Cheremskyi Nature Reserves, Prypiat-Stokhid and Nobel National Nature Parks) and non-protected areas.

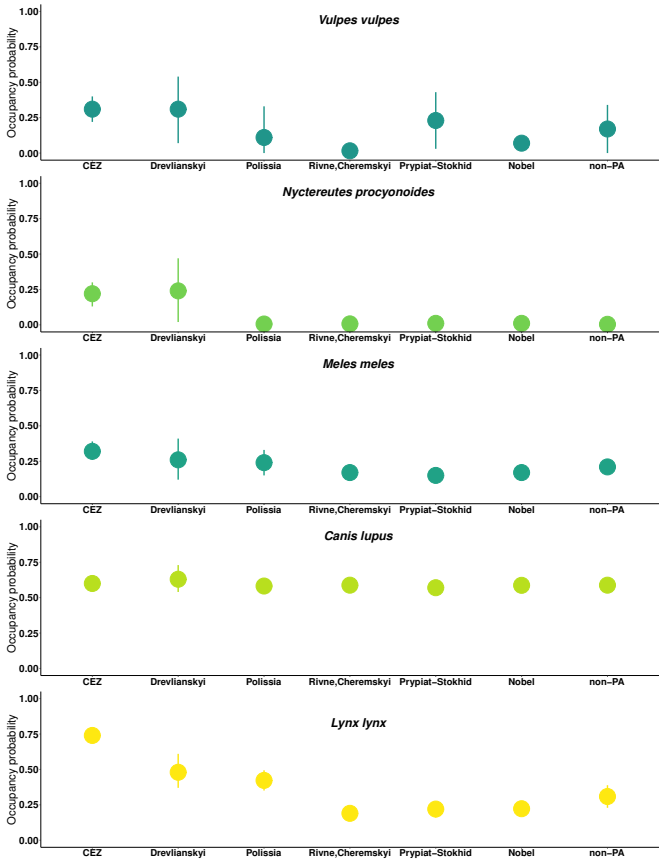

Figure 3. Red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), European badger (*Meles meles*), grey wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) occupancy probabilities in the Ukrainian CEZ, six protected areas (Drevlianskyi, Polissia, Rivne and Cheremskyi Nature Reserves, Prypiat-Stokhid and Nobel National Nature Parks) and non-protected areas.

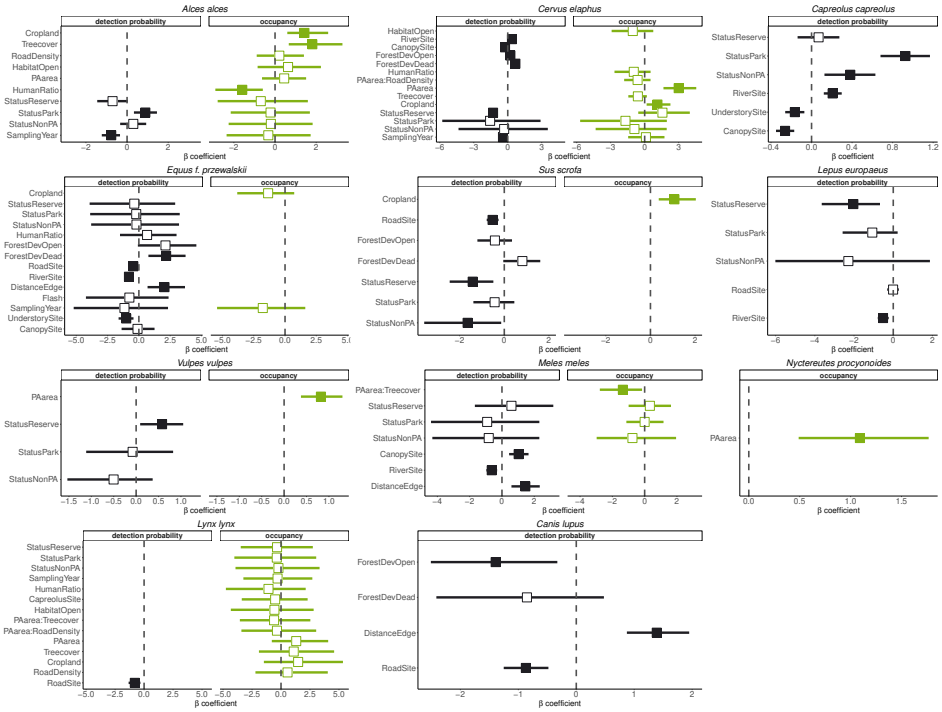

Figure 4. Effect of site- and landscape-specific covariates (with the posterior inclusion probability ≥0.5) on detection and occupancy probabilities. Plots include mean standardized β coefficients and 95% Bayesian credible intervals (95% BCI) for all covariates and the two area categories—the CEZ area (green bars) and other areas (black bars). Boxes are coloured when the 95% BCI did not overlap zero (dashed vertical line).

lowest in the Rivne and Cheremskyi NRs combined (mean occupancy = 0.02, 95% BCI = 0.01, 0.02) and the highest in the Ukrainian CEZ (mean occupancy = 0.31, 95% BCI = 0.22, 0.39) and the Drevlianskyi NR (mean occupancy = 0.31, 95% BCI = 0.07, 0.54; figure 3; electronic supplementary material, S2). Wolf occupancy was the lowest in the Prypiat-Stokhid NNP (mean occupancy = 0.57, 95% BCI = 0.54, 0.6) and the highest in the Ukrainian CEZ and the Drevlianskyi NR (mean occupancy = 0.63, 95% BCI = 0.54, 0.73), while lynx occupancy was the lowest in the Rivne and Cheremskyi NRs combined (mean occupancy = 0.19, 95% BCI = 0.15, 0.23) and the highest in the Ukrainian CEZ (mean occupancy = 0.74, 95% BCI = 0.7, 0.77).

4. Discussion

Our results revealed that larger and less human-disturbed PAs—the Ukrainian CEZ and adjacent Drevlianskyi NR—showed higher mammalian diversity, occupancy and detection probabilities than smaller PAs (support prediction 1). These two areas form a continuous landscape with high forest cover and less pronounced edge effects than in other regional PAs of smaller size. Less intensive anthropogenic disturbance in the Ukrainian CEZ and likely more efficient enforcement of restrictions on human access could positively impact the diversity, occupancy and detection probabilities of ungulates and large carnivores (prediction 2). We also found that non-PAs had similar diversity and occupancy values to neighbouring small PAs, indicating less efficient conservation management in other regional PAs compared to the larger CEZ and Drevlianskyi, which are strictly regulated human access. Smaller and more fragmented regional PAs may merely be too small to sustain permanent abundant populations of species with extensive home ranges (e.g. large carnivores).

Patterns in mammal detection probabilities generally followed occupancy patterns, and anthropogenic disturbance had mixed effects on detection probabilities of terrestrial mammals. Overall, all species had the highest occupancy in the Ukrainian CEZ, while occupancy probabilities were lower in smaller PAs and non-protected areas. Our study thus provides support for previous findings on the importance of large size and low intensity of anthropogenic stressors in PAs for the conservation of large mammals [13,59]. The proportion of PA coverage within a 10 km buffer around the camera traps was a positive predictor of occupancy for red deer, red fox and raccoon dog, potentially because of higher human disturbance near the PA edge and hunting in the adjacent areas. PA status (reserve, park or non-PA) did not have a significant effect on species occupancy probabilities, whereas detection probabilities of red deer, wild boar and brown hare were lower in other PAs than in the Ukrainian CEZ. In addition, the detection probabilities for Przewalski's horse, badger and wolf increased further away from the PA edge. These results might be explained by the greater susceptibility of these species to anthropogenic disturbance compared to species that may better cope with such stressors. Higher moose and roe deer detection probabilities in national parks, as well as a positive effect of cropland on moose and wild boar occupancies, may indicate species selection of good foraging habitats in human-modified landscapes [60,61]. Higher fox detection probability in nature reserves may be linked to abundant prey and/or food availability from human waste within or in the vicinity of smaller and fragmented regional PAs [62,63].

As in other areas experiencing recolonization patterns, highly adaptable generalists showed the highest occupancy in the CEZ area [64]. Occupancy patterns for common species (roe deer, moose, wild boar, red fox) were comparable across northern Ukraine—roe deer and moose had the highest occupancy in the Ukrainian CEZ, Drevlianskyi NR, Prypiat-Stokhid NNP,

Nobel NNP and non-PAs (figure 2; electronic supplementary material, S1–S3). Occupancy patterns for regionally rare species (wolf, lynx, badger, Przewalski's horse, moose) were area-specific, with the Ukrainian CEZ and the neighbouring Drevlianskyi NR having the highest occupancy probabilities. Overall low red fox occupancy values across northern Ukraine may indicate anthropogenic factors such as rabies, poorly regulated yet widespread use of rodenticides, and fox poaching that were not included in the model [65,66]. In Western Europe, red fox populations increased after oral rabies vaccination campaigns [67], which are still in the early stages in Ukraine, and comprehensive vaccination coverage may not be ensured [68]. Few correlations between red fox and raccoon dog occupancies and model covariates may reflect species' adaptations to diverse habitats [69,70]. A higher detection probability of badgers in forested areas aligns with previous studies on badger habitat preferences [71,72]. However, lower badger occupancy in forests farther from the PA edge and lower raccoon dog occupancy in the Ukrainian CEZ might be linked to the effect of large carnivore predation on these mesocarnivore species [73,74]. The low occupancy of Przewalski's horse in the Ukrainian CEZ is probably explained by the species's low population numbers—around 120 individuals in 2021 [32] as well as the species's habitat selection [75]. Released in 1998–1999, Przewalski's horses (n = 23) acclimatized to the new environment [29], began reproducing and dispersed from the release site to Belarus and across the Prypiat River [76]. This suggests that horses in the Ukrainian CEZ no longer exhibit post-release site fidelity but instead select habitats farther from the CEZ edge, potentially for their higher forage quality [77].

The detection probability of Przewalski's horse was lower at sites with increasing understory density. Przewalski's horse is a species adapted to open landscapes with sparse vegetation, which facilitates visibility and movement [78]. Higher detection probabilities of the Przewalski's horse near rivers could be explained by the species's high water consumption and thus preferences to stay close to water sources surrounded by lush riparian vegetation [78,79]. Absent correlations between roe deer occupancy and model covariates might be explained by roe deer's high adaptability and flexibility [80,81]. Red deer and Przewalski's horse had higher detection in low canopy cover and understory density, respectively, but detection probabilities for both species were also positively associated with burned forests. This association could be explained by the period when camera traps operated in the Ukrainian CEZ—monitoring was conducted after the large forest fires in spring 2020 [36]. Forest fires in 2020 were caused by illegal stubble grass burning outside the Ukrainian CEZ near the south-western border [82]. Whereas forest fires predominantly have adverse effects on less mobile species, medium- and large-sized mammals are highly mobile and therefore less susceptible to fires [36]. Moreover, post-fire understory and ground vegetation recovery may provide abundant fodder and thus constitute highly suitable habitats for herbivores [83,84].

The anthropogenic disturbance was negatively associated with both moose occupancy and the sampling year (2021), which had a negative effect on moose and red deer detections. The more fragmented western part of the Ukrainian CEZ and the smaller PAs sampled in 2021 likely had lower habitat quality and suitability and more intensive anthropogenic stressors compared to less disturbed central parts in the Ukrainian CEZ sampled in 2020. In contrast to our prediction, road density was not a limitation to the occurrence of mammals either as an additive covariate or in an interaction with protection status and might be linked to low traffic or low mammal occurrences along the road density gradient. Moreover, detection of Przewalski's horse, wild boar, lynx and wolf was higher closer to roads. This is in accordance with other research that found carnivores selecting linear infrastructure with low vehicular traffic for hunting and movement [85,86].

(a) Management and conservation implications

Accurate estimates of species abundance are crucial for wildlife research and management [87]. Hunters commonly advocate carnivore control to reduce predation pressure on game species [88]. Reliance on annual counts by hunters [89] has been shown to be inaccurate as they do not rely on scientific or standardized methods and provide rather deficient and biased outputs either to support or disprove arguments about currently abundant wildlife populations in Ukraine. The use of remote cameras, acoustic surveys, eDNA and snow tracking allows the collection of data suitable for occupancy modelling and estimates of species distribution, habitat use and relative abundance to guide wildlife management decisions [90]. However, the reliability of detection rate and site occupancy as indices of species abundance and density is highly dependent on the match between the sampling design and the ecology of the monitored species [91], habitat similarity of the compared sites over large spatial scales as well as sampling and analytical refinements (e.g. random sampling and index calibration) [92].

Radiation exposure can have negative health effects and reduce survival and reproduction in animal populations [93,94]. However, we did not assess the contribution of radiation to overall results as previous camera studies reported that wildlife abundance and distribution within the CEZ in Belarus were unaffected by ^{137}Cs contamination densities [95]. The gradual exodus of people within the CEZ due to the Chornobyl disaster in 1986 was followed by restrictions on human activities and the designation of PAs— first in Belarus (the Polesie State Radioecological Reserve, 1988) and then Ukraine (the Chornobyl Radiation and Ecological Biosphere Reserve, 2016) [96]. The absence of people has been accompanied by recolonization patterns which, in turn, have resulted in increased wildlife abundances and the recolonization by species that were locally extinct before the disaster, such as large carnivores [30,33–35]. This highlights that PAs are most effective when human intervention is minimal, supporting the argument for human access enforcement as an essential measure for wildlife conservation. In addition, other regional PAs remain smaller and fragmented, and their long-term conservation potential could be enhanced by area expansion that aligns with the Kunming–Montreal Global Biodiversity Network, thereby emphasising the enlargement and connectivity of PAs to protect biodiversity [97]. However, all PAs evaluated in this study are located along the Belarus–Ukrainian border where military activities, including inside the PAs in both countries, have sharply increased since the Russian full-scale invasion in February 2022 and will remain high as long as the war continues. At the same time, civilian access, monitoring and research activities have been significantly restricted across the state border zone. For example, hunting has been

banned nationwide since February 2022. Given the dynamic geopolitical and ecological conditions, continued monitoring of PAs in northern Ukraine is essential not only to estimate biodiversity but also to assess the feasibility of expanding PAs and the impact of armed conflict on long-term conservation in the region.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Covariate data, camera trap data in a tabular format and the R script to reproduce the analyses have been archived on Figshare repository [98].

Supplementary material is available online [99].

Declaration of AI use. AI used as a 'search engine' to aid identification and adjustment of R code for data visualization.

Authors' contributions. S.K.: conceptualization, data curation, formal analysis, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; R.B.: formal analysis, methodology, software, validation, writing—review and editing; A.Z.: supervision, writing—review and editing; O.B.: data curation, writing—review and editing; C.F.: data curation, writing—review and editing; A.F.S.: conceptualization, data curation, writing—review and editing; A.V.: data curation, writing—review and editing; S.D.: data curation, writing—review and editing; N.B.: data curation, writing—review and editing; I.Z.: data curation, writing—review and editing; V.D.: data curation, writing—review and editing; N.S.: supervision, writing—review and editing; M.H.: conceptualization, data curation, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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