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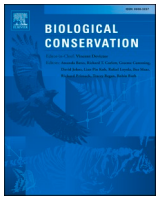

Space use of a diverse megafauna community in a rewilding area in the southwestern Carpathians

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ABSTRACT

Most landscapes today have lost much of their historical biodiversity, particularly the largest animals (megafauna). Yet, in some regions declining human pressure and stronger conservation policies allow megafauna to return, and rewilding efforts sometimes seek to amplify these trends through reintroductions. Megafauna, however, return to landscapes still inhabited and used by people, making it crucial to understand how they adapt to such shared landscapes. Here, we studied the space use of a uniquely diverse megafauna community, including recently reintroduced European bison, in a rewilding area in the Romanian Carpathians. We conducted extensive sign surveys (2688 km) to monitor eight large mammals in 2022 and 2023. We then applied Bayesian occupancy models to understand the space use of our target species. Our results show that landscape composition is important for allowing a diverse megafauna community to share space with people. Many species (e.g., red deer, roe deer, grey wolf, brown bear) used different forms of refuge habitat (i.e., topographically complex areas, dense forest) to avoid people. Only one species, the European bison, appeared to be negatively affected by direct human pressure (i.e., active logging). Conversely, land-use legacies such as forest gaps and abandoned pastures were selected by most species (i.e., European bison, red deer, roe deer, wild boar, brown bear). Our study shows that diverse megafauna, including the largest species, can share space with people in mosaic landscapes. These landscapes, especially if human pressure is declining, offer major opportunities to protect megafauna and restore their ecological roles, in Europe and elsewhere.

1. Introduction

The expansion of the human enterprise has resulted in the widespread degradation of biodiversity, jeopardizing nature's contributions to human societies and potentially undermining the basic functioning of the earth system (Díaz et al., 2019). Two major groups of drivers are responsible for this. First, the expansion and the intensification of land use have caused widespread habitat loss, fragmentation, and degradation (Tilman et al., 2017). While land use has a long history, habitat destruction has accelerated particularly strongly recently (Ellis et al., 2021). Second, overexploitation, for instance, in the form of hunting, threatens many species and has likewise accelerated recently (Sales et al., 2022). Additionally, climate change, pollution, invasive species and disease are major extinction drivers, particularly if they act in concert with habitat destruction and overexploitation (Maxwell et al., 2016). How to safeguard and restore biodiversity in the face of these intensifying threats is thus a major challenge (Jaureguiberry et al., 2022).

Large animals (hereafter: megafauna) have been particularly strongly affected by human pressures (Svenning et al., 2024; Lemoine et al., 2023). These species carry high intrinsic risk (e.g., low reproductive rates, high energy demands), require large home ranges, and are the preferred prey of hunters, from the late Quaternary to now (Young et al., 2016). At the same time, megafauna play pivotal roles in

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ecosystem functioning, such as through shaping forest structure, facilitating seed dispersal, or recycling nutrients (Ripple et al., 2015). Their loss might thus trigger cascading effects in ecosystems (Malhi et al., 2016). Halting, and where possible reversing megafauna extinction risk are therefore central conservation goals (Pettorelli and Bullock, 2023).

Encouragingly, several recent trends now provide opportunities for achieving these goals. First, rural outmigration, structural change in agriculture and a global redistribution of agricultural production have led to declining land-use pressure and farmland abandonment in many landscapes (Kuemmerle et al., 2016). Second, after centuries of relentless hunting and persecution of megafauna, attitudes towards them have shifted recently, including stronger protection (Lécuyer et al., 2022). Third, protected areas have been expanding in recent times, and although not all of them are effective, many protected areas have become strongholds for megafauna (Wolf and Ripple, 2018). This expansion of protected area networks will continue given recent strong commitments under the Kunming-Montreal Global Biodiversity Framework, which foresees the conservation of 30 % of land, waters, and seas (CBD COP, 2022). Lastly, acknowledging the widespread degradation of ecosystems and biodiversity (Pettorelli and Bullock, 2023), restoration has become a central policy goal, as exemplified through the UN Decade of Restoration (United Nations Environmental Agency, 2019), the European Green Deal and Nature Restoration Law (Hering et al., 2023) or the recently agreed-upon goal to restore 30 % of all degraded lands globally (CBD COP, 2022).

As a result, remarkable megafauna returns are starting to happen in Europe but the landscapes into which megafauna return remain inhabited by people and are influenced by their activities (Linnell et al., 2020). These landscapes often entail novel conditions for megafauna (Kuijper et al., 2024), with human pressure sometimes a stronger determinant of space use and behavior of megafauna than environmental factors (Cretois et al., 2021). Adaptations of megafauna space use in human-dominated landscapes include temporal avoidance of people or human-dominated areas by wildlife, for instance of roe deer (*Capreolus capreolus*) use open areas during night while avoiding them during day (Bonnot et al., 2013). Similarly, species such as lynx (*Lynx lynx*) and grey wolf (*Canis lupus*) can more easily coexist with people in landscapes that provide refuge habitats, such as topographically complex landscapes or forests (Gaynor et al., 2018; Oeser et al., 2023). Existing work has either focused on single species, regions with impoverished megafauna communities (Cretois et al., 2021), or have on strictly protected areas (Bubnicki et al., 2019), whereas there is a paucity of studies of megafauna-rich communities in human-dominated landscapes. Although Europe currently hosts 18 wild herbivores and four large carnivores, merely 1 % of its land contains more than five species (Linnell et al., 2020; Ripple et al., 2015). Understanding how megafauna navigate shared landscapes in places where megafauna communities are rich is therefore crucial to inform conservation and restoration efforts aimed at increasing megafauna diversity.

The Carpathian Mountains provide a unique opportunity in this context. The region has long served as a critical stronghold for megafauna, and thanks to declining human pressure in many areas, the region today remains a hotspot for large mammals (Rozylowicz et al., 2011; Kuemmerle et al., 2016). For instance, the Carpathians contain large populations of brown bear (*Ursus arctos*), grey wolf, and Eurasian lynx over the past centuries thanks to their remoteness (Chapron et al., 2014). Large ungulates such as red deer (*Cervus elaphus*), roe deer, wild boar (*Sus scrofa*), chamois (*Rupicapra rupicapra*) are also abundant in the Carpathian range, although their populations have waxed and waned locally (Niedziałkowska et al., 2011, 2024; Plis et al., 2022). Likewise, after disappearing from the Carpathian region in the 18th century, European bison (*Bison bonasus*) have been reintroduced in the Polish, Slovak, Ukrainian and Romanian Carpathians (Krasińska and Krasiński, 2013). This provides unique opportunities to study megafauna communities that could theoretically be restored over much of Europe and how they share space with people but we know of no study that has done so.

Here, we investigated the influence of different human pressures on the spatial use patterns of megafauna in the Carpathians of Romania. The region presents a truly unique assemblage of large mammals including the recently reintroduced European bison, the largest surviving European terrestrial mammal. Specifically, we addressed the research question: *How do human pressures and landscape composition shape the space use of large mammals?* We pursued two main objectives: (1) to examine species-specific effects of human pressure and landscape variables, and (ii) to predict the occupancy probability in the study area for each species.

2. Methods

2.1. Study area

Our study area is situated in the Tarcu Mountains (586 km^2) in the southwestern Romanian Carpathians (Fig. 1). The region encompasses temperate continental and alpine climates in a topographically complex landscape, with elevations ranging from about 380 m to nearly 2200 m a.s.l. Average annual temperature varies from 0.2 °C at higher elevations to 9.8 °C at lower elevations. Annual precipitation varies from approximately 1200 mm to <700 mm. The landscape is predominantly forested (74 %), consisting of broadleaved and mixed forests with European beech (*Fagus sylvatica*) dominating at lower elevation, and Norway spruce (*Picea abies*) dominating at higher elevation. Additionally, there are small meadows interspersed within forest and, at higher elevations, extensive alpine grasslands. Human settlements and cropland account for <1 % of the Tarcu Mountains (Boscaiu, 1971).

The area is partially designated as a Natura2000 protected site (IUCN category IV), recognized for its importance as ecological corridor connecting five protected areas, three of which are national parks (NP; IUCN category II), namely Retezat NP (381 km^2), Domogled-Valea Cernei NP (612 km^2) and Cheile Nerei Beusnita NP (367 km^2). The study area encompasses a multi-use landscape with diverse human activities.

Logging operations, mainly consisting of selective logging, are overseen by local forestry authorities, and involve heavy machinery, sometimes requiring road development to reach remote areas. Regulated hunting of ungulates is permitted, with wild boar and roe deer as the main species but chamois and red deer are also hunted in smaller numbers. European bison and large carnivores are protected year-round. Moreover, livestock grazing is widespread, mainly consisting of sheep as well as rarely by cattle. During the growing period, sheep flocks (>500 individuals) graze on grasslands during the day, accompanied by shepherds and guarding dogs, and are sheltered at night. Lastly, agriculture (e.g., crops and orchards) occurs in the vicinity of villages at the border of the study region but remnants of abandoned orchards are present inside the region.

Our study area features one of the richest large mammal assemblages in Europe (Linnell et al., 2020), including the European bison, red deer, roe deer, wild boar, chamois, grey wolf, Eurasian lynx, and brown bear (Rozylowicz et al., 2011). European bison were recently reintroduced to the area and have grown to a sizeable population (estimated at 155 individuals; WWF Romania, *unpublished data*) after initial reintroductions of 80 individuals between 2016 and 2021. Importantly, the Tarcu herd of European bison is among the least-managed free-ranging European bison herds, not receiving supplementary feed during winter, in contrast to most other wild herds (Kuemmerle et al., 2018).

2.2. Study design and datasets used

We defined our study area as the convex polygon around all European bison occurrences registered from GPS collar data since their release between 2016 and 2022 (~300 km^2). We then divided the study site to a grid system of 2 × 2 km^2 to equally distribute the survey effort (Fig. 1). This cell size was chosen to approximately resemble the daily

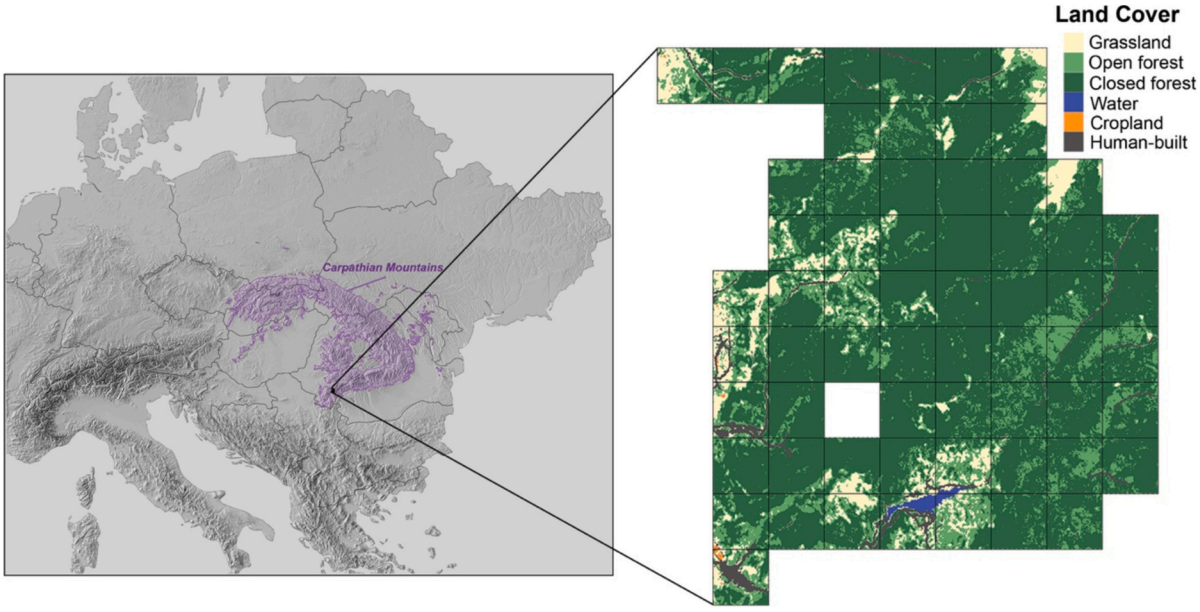

Fig. 1. The location of the study region in Europe and the Carpathian Mountains. The cells (2×2 km^2, $n = 63$) represent sampling units. The study area is dominated by closed forest but contains open forests with smaller openings connected to past clear-cutting and ongoing selective logging.

displacement patterns of most species within our mammal community (Pop et al., 2018; Dyck et al., 2022, WWF, *unpublished data*). Next, we removed cells that were inaccessible due to topographic or logistical constraints. We then allocated survey trails averaging 2 km in each cell, considering accessibility and ensuring to cover all main land-cover types encountered in a cell such as grasslands and forest. The trails were primarily established along old forest roads originally developed for logging operations, which are now accessible only by foot due to vegetation growth and fallen trees. The study design led to 15 longer trails (range = 8–20 km) covering the entire study area.

We systematically surveyed all trails every month from October 2022 to September 2023 (12 surveys). During the surveys, five teams, each composed of one trained and highly experienced ranger and a student, recorded all fresh signs (i.e., tracks, scats, resting places) of large mammal occurrences (i.e., approximately less than a week old) and direct sightings using handheld GPS devices. Occupancy analysis require species' presence in a binary format (i.e., 1 and 0), therefore we recorded consecutive tracks of the same species maintaining a minimum distance of 200 m to mimize double overcounting the same individual within a single cell (Karanth et al., 2011). All teams conducted fieldwork simultaneously in different parts of the study region to ensure logistical efficiency (i.e., fewer car trips required). Signs that could not be confidently identified were excluded. While red deer and European bison tracks are easily distinguishable, cattle and European bison tracks can appear similar. Hence, in areas of overlap between the two species, we recorded signs only when additional evidence (i.e., scats, hair) confirmed the species' presence. The same applied to distinguish grey wolf and dog tracks, although the presence of dogs in the study area is minimal. Rangers had 10+ years of experience in wildlife monitoring and tracking in the study region. All rangers originate from the study region, having grown up in nearby villages and having engaged in a wide range of outdoor activities such as livestock herding, forestry, or ecotourism guiding for decades.

To capture human pressures, we used both, observations in the field and land-use data provided by local institutions. For active logging, we recorded signs of timber exploitation (e.g., presence of workers, tractor tracks) and obtained data on timber volumes harvested from the local forestry districts as the volume of wood exploited per cell per month. We obtained livestock grazing data in two ways: (1) recorded encounter rates of livestock (e.g., fresh tracks, scats) along survey trails; (2) obtained data on the presence of sheep flocks on grassland patches and the respective time use of the area during the year from the local municipalities, as livestock owners are required to declare the number of animals and grazing periods due to grasslands being state property. Additionally, we considered roads, which in our study area are mainly inaccessible to the public and are only used by hunters, foresters and (few) private landowners.

To capture landscape composition, we derived data from available land-cover/use maps at 30 m resolution (Potapov et al., 2022). We did not consider forest extent because all the cells in the study area had a high share of forests, largely consisting of broadleaved forest. However, forests in the study area are managed and experience natural disturbances, and therefore, vary in structure. For this reason, we used high-resolution (10 m) tree cover from the Tree Cover Density 2018 datasets (Copernicus, European Environment Agency, 2023) to calculate the mean coverage (%) per each grid cell. We derived grassland extent (km^2) from an existing land-cover map (Potapov et al., 2022), selected after visually evaluating various candidate land-cover products. Forest gaps exist in the area and are mainly associated with past logging. We derived the extent of past disturbances (km^2) extracted from existing satellite-based forest disturbance maps that capture disturbances for the period 2010–2020 (Senf and Seidl, 2021). Finally, we extracted elevation from the Shuttle Radar Topography Mission (SRTM) at 30 m resolution (NASA Shuttle Radar Topography Mission SRTM, 2013). Elevation is a proxy for both, terrain complexity and the distance from human settlements and activities (usually taking place in the valleys), and therefore acts as a proxy for refuge habitats for many species (Milanesi et al., 2017). All calculations were conducted through the r package "*raster*" (Hijmans, 2024).

2.3. Data analyses

To assess the space use of our target species in the study area, and evaluate the importance of different human pressures, we used single-season Bayesian occupancy models. Occupancy models are a type of hierarchical models, which take binary response data, consisting of two sub-models: (1) an occupancy probability (ψ) sub-model; and (2) the observation process sub-model governed by detection (p) probability (Royle and Kéry, 2007). We consider occupancy as the use of a spatial unit by a species over a defined time period (MacKenzie, 2005).

The true occupancy status of species at a site *i*, *Zi* is modelled as: $Z_i \sim$ Bernoulli(ψ_i) where Z_i is a random variable drawn from Bernoulli's distribution and has two possible states 'occupied' ($Z = 1$) or 'unoccupied' ($Z = 0$; Royle and Kéry, 2007). Thus, the underlying latent (un- or partially observed) occupancy state at site *i*, Z_{ij}, is modelled as:

$$Z_i \sim \text{Bernoulli}\ (\psi_i) \tag{1}$$

and the observations/detections during each of the *J* replicates at site *i*, $y_{ij,\ 1,\ 2,\ 3,\ \ldots,\ 63}$ are modelled as conditional on Z_i.

$$y_{i,j} \mid Z_i \sim Bernoulli\left(Z_i \times p_{i,j}\right) \tag{2}$$

To evaluate whether the occupancy (ψ) of our study species is influenced by the anthropogenic pressures andor landscape characteristics, we considered a set of hypotheses (see in Table 1). To define the influence of detection (p), we considered the sampling effort (i.e., distance walked on trails). As we conducted sign surveys, we gathered data regarding meteorological conditions (i.e., snow, rainfall) data for the day preceding each survey. Given that we surveyed most trails on mud-based substrates, weather conditions were expected to influence soil moisture levels, and define the substrate type (e.g., snow, dry, wet surfaces). Lastly, we collected monthly precipitation data from the Tarcu Mountain Meteorological station.

Table 1
Predictor variables, units, and associated hypotheses for modelling occupancy of large mammals in the Carpathians Mountains, Romania.

Variable	Unit	Hypothesis
Occupancy		
Elevation	*meters*	*Elevation positively influences large mammal space use by reducing human accessibility, thus serving as a refuge while also providing less disturbed habitats* (Milanesi et al., 2017)
Tree Cover	*Percentage of tree cover per cell*	*Denser forests positively influence large mammal space use by offering refuge for the largest species, as well as for species that are more sensitive to human pressures* (Hofman-Kamińska et al., 2019).
Grassland	*Grassland extent per cell (km^2)*	*Grasslands provide food resources for grazers or intermediate feeders, such as European bison, red deer and roe deer* (Hofmann, 1989; Bubnicki et al., 2019).
Forest gaps	*Extent of forest gaps per cell (km^2)l*	*Forest gaps positively influence the space use of the ungulates due to abundance of foraging resources* (Kuijper et al., 2009)
Road length	*Road length per cell (km)*	*Road length positively influences space use by large mammals, as increased accessibility reduces the energetic costs associated with foraging* (Hill et al., 2021).
Livestock intensity	*Livestock presence divided by number of visits*	*Livestock intensity negatively affects large mammals' space use due to competition for foraging resources and the presence of shepherds and livestock guarding dogs* (Soofi et al., 2018).
Logging intensity	*Harvested volume per cell (m^3)*	*Logging influences the space use of large mammals negatively due to noise of heavy machinery and workers' presence*
Detection		
Effort	*Distance walked per cell*	*Effort influences detection positively* (Mackenzie and Andrew Royle, 2005; MacKenzie et al., 2002).
Weather	*Weather conditions the day before conducting the surveys (sun, rain, snow)*	*Weather conditions preceding a sign survey can influence track detectability and influence scat deterioration* (McHenry et al., 2016; Lyra-Jorge et al., 2008).
Rainfall	*Average monthly precipitation per cell (mm)*	*Precipitations provide wet soil conditions, which can positively influence species detection, as increased soil moisture enhances the visibility of tracks* (Fahimi et al., 2024)

We summarized all landscape and human pressure predictors at a 0.5×0.5 km^2 resolution to avoid potential spatial pseudo-replication, and to better characterize the influence of the predictor variables at the trail level due to the topographically complex nature of the landscape (Lombardi et al., 2017; Dyck et al., 2022). We extracted the response variable (detection and non-detection) directly from the 2×2 km^2 cells for all species individually. We recorded species detection (1) and non-detection (0) data for 12 months for each species, except for brown bear. For bear, we considered data only for nine months, as the species hibernates during winter (January–March), which could have influenced occupancy estimates for brown bear (Popescu et al., 2017).

We checked for multicollinearity among predictor variables using Spearman's correlation coefficient test with a cut-off of |rho>0.7| (Fig. S1; Dormann et al., 2013). In our Bayesian framework, we consider substantial evidence to reject a hypothesis if the credible interval at the 95 % level does not or only slightly overlap with 0 and is in the expected direction, and if the intervals overlap with 0 slightly, we considered as less substantial, otherwise non-substantial (Benjamin et al., 2018).

To build our Bayesian occupancy models, we used the '*ubms*' package (Kellner et al., 2022) in Stan (Carpenter et al., 2017) via R version 4.2.3 interface (R Core Team, 2024). We ran each model with 2000 iterations (1000 burn-in) and three chains using Markov Chain Monte Carlo (MCMC; Kellner et al., 2022). First, we fitted a null model for each species where we assumed all parameters to be constant. Next, we added the linear effects of survey covariates (i.e., effort, weather conditions, rainfall) on the detection (p) sub-model while keeping the occupancy parameter constant. Then, we added linear effects of site covariates on the occupancy (ψ) sub-model, while keeping the relevant variables for the detection parameter (MacKenzie et al., 2002). We subsequently included multiple combinations of covariates in the occupancy (ψ), considering interactions between variables, as well as variables' quadratic terms, maintaining detection (p) as defined in the previous steps (MacKenzie et al., 2002). While building models, we assessed whether covariates had substantial effects, and if so, we kept the variable and added new variables in the following model. We ranked our models using the leave-one-out cross-validation (LOO) method with the '*fitList*' function (Fiske and Chandler, 2011) to determine the best-fitting model (Sivula et al., 2023). We assessed the convergence of our best-fitting models by visually observing the MCMC trace plots and by plotting the binned residuals (see from Fig. S4). Finally, we evaluated the goodness-of-fit of our best-fitting models with the MacKenzie-Bailey Chi-square test (Table S1; Kellner et al., 2022). This involves Bayesian posterior predictive checks, also known as discrepancy tests, a common test statistic that quantifies the distance between the observed and the expected data under. To implement this, we selected 1000 posterior draws for the best-fitting model (Kellner et al., 2022). For each draw, the Mackenzie-Bailey statistic (MacKenzie and Bailey, 2004) was computed for both the actual dataset (detection and non-detections) and a simulated dataset. We then measured the discrepancy using a Chi-square statistic, defined as the sum of $(\text{observed}-\text{expected})^2/\text{expected}$ as a posterior predictive check (Kéry and Royle, 2016). If the model fits well, the proportion of posterior draws where the simulated statistic exceeds the actual statistic should be approximately 0.5 (Kellner et al., 2022). A test statistic value close to 0 or 1 indicates a low goodness of fit.

Our full model specifications for each species were thus:

$$\text{logit}\,(\psi_i) = \beta_0 + \beta_1.X_{\text{livestock,i}} + \beta_2.X_{\text{active_logging,i}} + \beta_3.X_{\text{road,i}} + \beta_4.X_{\text{grasslands,i}} + \beta_5.X_{\text{forest.gaps,i}} + \beta_6.X_{\text{elevation,i}} + \beta_6.X_{\text{tree_cover,i}} \quad (3)$$

and

$$\text{logit}\left(p_{ij}\right) = \alpha_0 + \beta_1.X_{\text{effort},i,j} + \beta_2.X_{\text{weather},i,j} \quad (4)$$

3. Results

We walked a total of 2,688 km of transects during 36 field days, which led to the detection of 2,677 independent signs of our eight megafauna species. The predominant signs of presence were tracks (n = 1786), followed by scats (509), direct observations (109), debarking (119), digging (90), resting sites (37) and hair (27). The most frequent species were the recently reintroduced European bison (n = 900 signs), followed by red deer (804), roe deer (459), brown bear (212), wild boar (211), wolf (84), chamois (4) and lynx (3). We excluded chamois and lynx due to lack of data. Species' signs recorded the lowest number of occurrences in February attributed to the lower survey effort (we surveyed only 6 out of 15 transects due to inaccessibility after heavy snowfall).

All models demonstrated good convergence and goodness-of-fit (i.e., MacKenzie–Bailey chi-square test), with the exception of the wild boar (Table S1). For red deer and brown bear, model fit was somewhat lower, with test values was closer to 1 and to 0, respectively (Table S1; Fig. S3). Our detection model (Fig. 2) indicated that survey effort had a substantial positive effect for red deer (β = 0.62, 95 % Bayesian Credible Interval = 0.46 to 0.80), grey wolf (β = 0.57, 95 % BCI = 0.30 to 0.84), roe deer (β = 0.56, 95 % BCI = 0.39 to 0.75), European bison (β = 0.51, 95 % BCI = 0.33 to 0.70), wild boar (β = 0.49, 95 % BCI = 0.26 to 0.65), and slightly positive effect for brown bear (β = 0.22, 95 % BCI = 0 to 0.44). Weather conditions were included in the best-fitting model for all species except brown bear. Specifically, snow had a substantial positive effect on the detection of red deer (β = 0.72, 95 % BCI = 0.23 to 1.20), roe deer (β = 0.53, 95 % BCI = 0.06 to 0.99), and a substantially negative effect on wild boar detection (β = −0.80, 95 % BCI = −1.39 to −0.20). Precipitation had a substantial positive effect on grey wolf detection (β = 0.53, 95 % BCI = 0.22 to 0.87) and slightly positive effect on red deer detection (β = 0.17, 95 % BCI = 0 to 0.36).

The occupancy parts of our models showed that landscape composition variables were most important in determining the space use of our megafauna species, while human pressure variables were relatively unimportant (Fig. 2). Among landscape composition variables, elevation had a substantial positive effect on space use of brown bear (β = 2.33 to 95 % BCI = 0.98 to 4.17), European bison (β = 1.30 to 95 % BCI = 0.48 to 2.26) and red deer (β = 1.20 to 95 % BCI = 0.32 to 2.29). Tree cover had a substantial positive impact on the space use of European bison (β = 2.43 to 95 % BCI = 1.07 to 4.05) and roe deer (β = 1.27 to 95 % BCI = 0.19 to 2.43), and a positive but non-substantial effect on grey wolf. Grassland extent had a substantial positive effect for European bison (β = 2.18 to 95 % BCI = 0.74 to 3.86) and roe deer (β = 1.50 to 95 % BCI = 0.20 to 2.97). Additionally, forest gaps had a substantial positive effect for red deer (β = 1.53 to 95 % BCI = 0.04 to 3.50), roe deer (β = 1.48 to 95 % BCI = 0.14 to 3.39) and brown bear (β = 1.48 to 95 % BCI = 0.18 to 3.23), and a positive but non-substantial effect on wild boar. Among human pressure variables, only the European bison appears to be affected by human activities, with active logging having a substantial negative effect on European bison space use (β = −1.01, 95 % BCI = −1.84 to −0.24). Road length appeared in the best-fitting models for red deer and grey wolf, with a positive but non-substantial effect (the quadratic term for road length had a substantial effect on red deer space

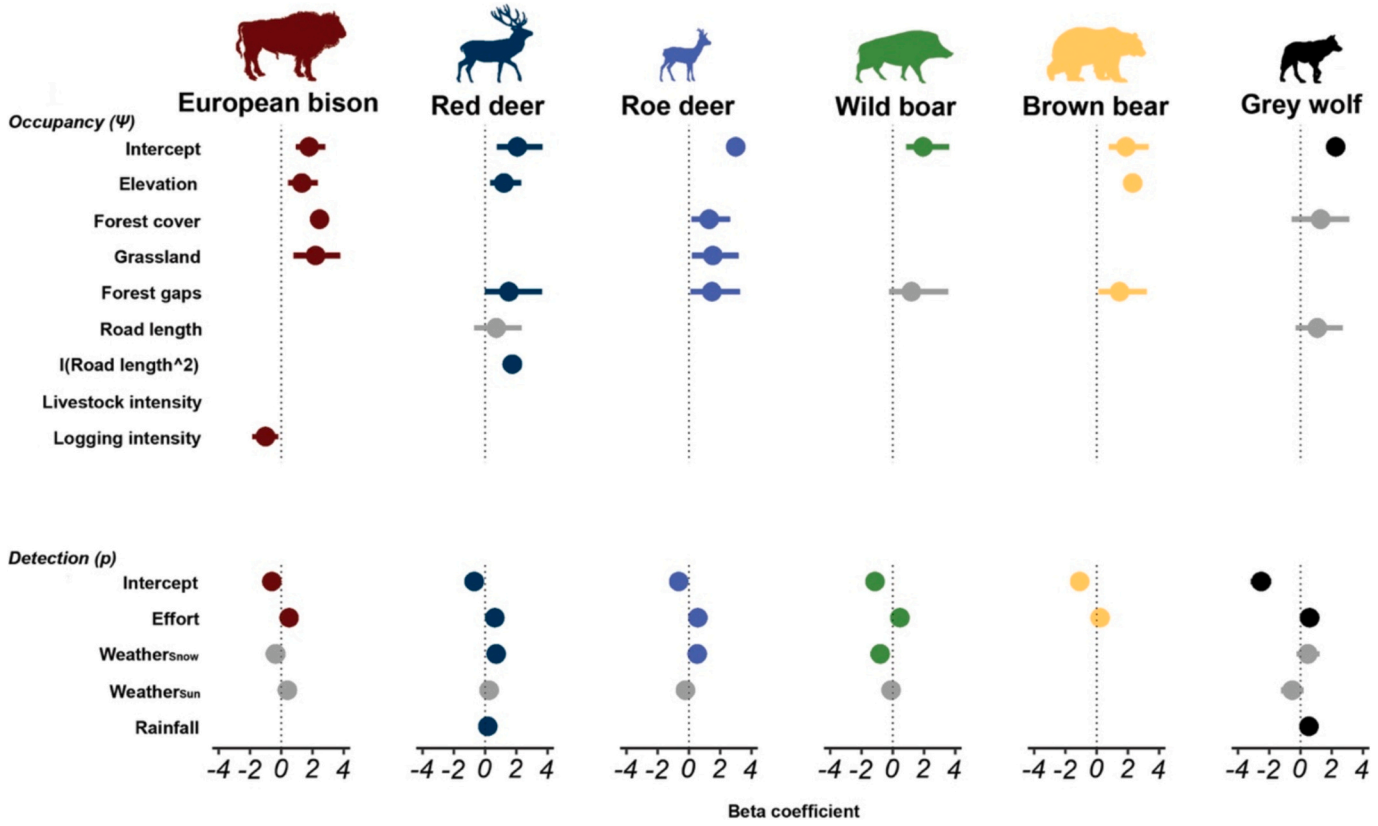

Fig. 2. Effect size of variables determining the occupancy (ψ) and detection (p) of megafauna in the southwestern Carpathians, Romania. The figure shows standardized mean effect sizes (circles) and their credible intervals (rounded lines). Colour signals predictors with substantial effects (non-substantial effects = light grey). Predictors that are not shown were not part of the best-fitting model.

use).

Variable importance varied significantly among species and over the range of variables (Fig. S2). Notably, active logging led to a drastic decline in European bison occupancy probability, decreasing from 0.85 in the absence of logging to nearly zero at timber harvesting levels exceeding 3000 m^3 per cell. Conversely, road length was associated with increased occupancy of red deer, although only at higher road length (>3000 m). Similarly, elevation had a marked effect on the occupancy of European bison, roe deer and brown bear above 1000 m. Tree cover increased European bison occupancy to 0.50 when cover was higher than 60 %, while roe deer occupancy was higher at lower (<40 %) tree cover. Grassland extent increased European bison occupancy substantially when the extent was >0.1 km^2, and roe deer occupancy when the extent was >0.02 km^2. Forest gaps had a similar effect on red deer and roe deer and brown bear, with occupancy increasing proportionally to forest gaps size.

Our occupancy models predicted reasonable, yet varied space use patterns among species (Fig. 3). All species had a higher predicted occupancy in the east of the study area compared to the west. Roe deer had the highest predicted occupancy probability ($\psi = 0.87$, 95 % BCI = 0.70 to 0.97), followed by red deer ($\psi = 0.82$, 95 % BCI = 0.64 to 0.93), wild boar ($\psi = 0.81$, 95 % BCI = 0.63 to 0.92), grey wolf ($\psi = 0.78$, 95 % BCI = 0.52 to 0.99), European bison ($\psi = 0.74$, 95 % BCI = 0.56 to 0.89) and brown bear ($\psi = 0.67$, 95 % BCI = 0.52 to 0.80). The latter two species had particularly low occupancy over much of the northwestern and southwestern study region but with high occupancy predicted for the eastern study area (Fig. 3).

4. Discussion

Restoring megafauna within their historical ranges is a conservation priority, yet our understanding of how megafauna communities fare in landscapes shared with people remains overall weak. A main reason for this gap is that diverse megafauna communities are rare outside strictly protected areas, especially in regions with long land-use histories such as Europe. Here, we focussed on a unique rewilding area in the Romanian Carpathians, containing most of the surviving Europe's megafauna, including the recently reintroduced European bison, in a landscape with comparatively low human pressure compared to other areas in Europe. Using an extensive sign survey and Bayesian occupancy modelling, we show different ways how human pressures and landscape composition mediate megafauna space use allowing them to share the landscape with people. First, megafauna likely avoided human encounters through selecting for refuge habitat (e.g., topographically complex terrain, dense forest). Second, all species except for the most recently reintroduced European bison were unaffected by ongoing human disturbances (e.g., logging, pastoralism). Third, most species benefitted from the legacies of past human pressures in the form of open areas from historical logging and pastoralism, and selected for such areas. Overall, the influence of people shapes megafauna space use even in sparsely populated landscapes, yet megafauna communities manage to adapt and successfully navigate such shared landscapes.

Our occupancy models underlined the importance of refuge habitat to avoid human pressures (Fig. 2), with the space use of many species positively linked to complex terrain (i.e., European bison, red deer and brown bear) and dense forests (e.g., European bison and roe deer). Such landscape characteristics constrain some human activities (e.g. crop farming) and allow wildlife to avoid people at fine scales, rendering such

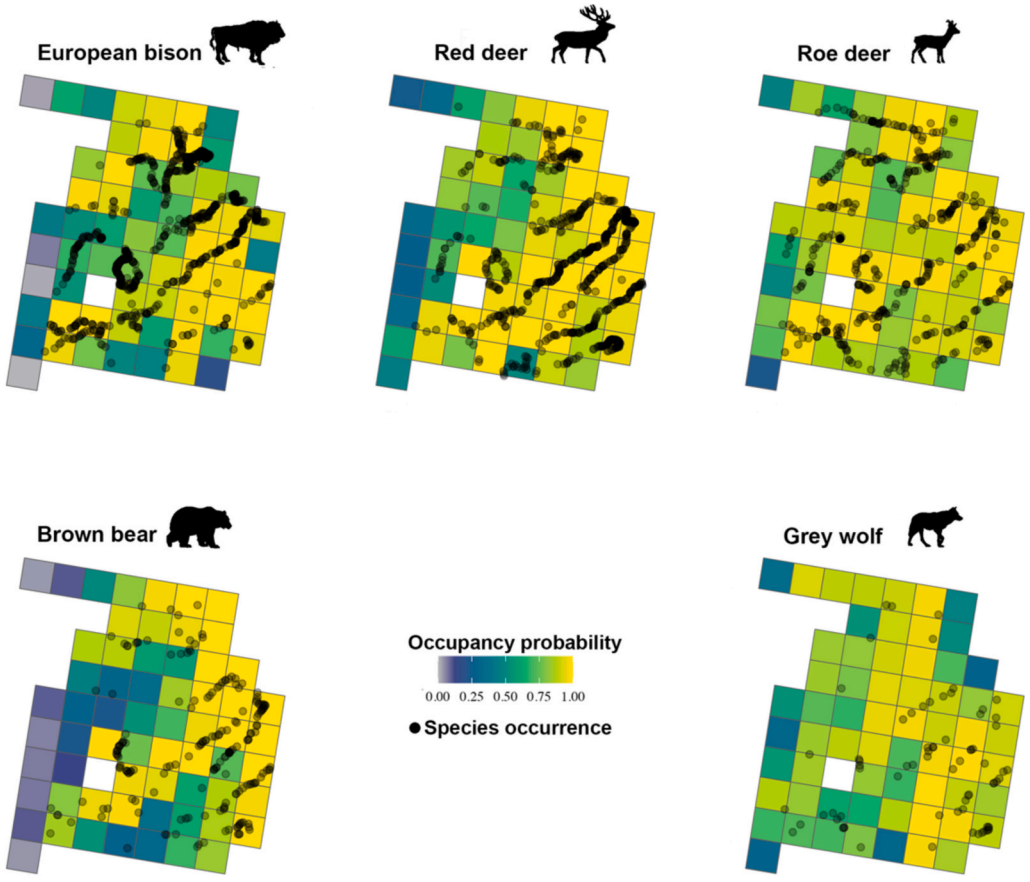

Fig. 3. Predicted occupancy probability for each species per cell (actual species occurrences on transects indicated by dots) in the study area. Wild boar was excluded from the figure as the best-fitting model included only one variable for the occupancy part, resulting in a low predictive performance.

areas refuge habitats (Oeser et al., 2023). For our study region, the mosaic of closed and open habitats linked to low-intensity land use appears to provide a balance between foraging resources, shelter, and refuges for avoiding encounters with people. This finding is broadly in line with other recent studies highlighting the importance of refuge habitats (Cristescu et al., 2019; Oeser et al., 2023). For instance, wolves used former military training grounds as refuges during their westward range expansion (Planillo et al., 2024), lynx use complex terrain and dense forests more in landscapes with higher human pressure (Oeser et al., 2023), European bison use dense forest as refuge and for movement (Hofman-Kamińska et al., 2019) or roe deer use dense forests to reduce predation risk from hunting (Müller et al., 2017). From a conservation and restoration perspective, this suggests that landscapes with complex topography, larger forest complexes, and or areas that people avoid offer potential for rewilding (Cretois et al., 2021). Such areas (e.g., mountains, remote areas) are also experiencing the strongest trends in depopulation and farmland abandonment in parts of the world (Kuemmerle et al., 2016), likely reinforcing their value for megafauna restoration.

Ongoing human disturbance, measured at relatively coarse grain, did not appreciably influence megafauna space use in our analyses, indicating a high adaptive capacity to temporary disturbances like logging and pastoralism. In our case, roe deer, red deer, and wild boar showed the overall highest occupancy (Fig. 3), reflecting their generalist ecology and higher densities (Bubnicki et al., 2019; Hofmann, 1989). Grey wolves had high-to-moderate occupancy, likely due to the availability of extensive and connected forests and refuge habitat (Dyck et al., 2022). Conversely, brown bears had the lowest occupancy. European bison had high-moderate occupancy but were the only species affected by human activity, likely due to the short time since reintroduction or their large size, limiting hiding. Overall, this suggests that occupancy, at a relatively coarse scale, is mainly determined by biophysical conditions (Cretois et al., 2021), along with temporal avoidance of people for the newly reintroduced species, allowing megafauna to persist in shared landscapes with low-intensity management if refuges are available.

A third finding from our study was that historical land use has left lasting impacts (Foster et al., 2003), and through this influences contemporary megafauna space use. Specifically, forest gaps and grasslands, derived and shaped by past historical clearcutting, selective logging and pastoralism, emerged as important habitats for most of our species (Fig. 2), many of which are at least partially grazers (Hofmann, 1989; Kuijper et al., 2009). This underscores land use deintensification as a critical factor enhancing habitat suitability for megafauna (Davoli et al., 2024). However, recent trends in Europe include agricultural intensification of grasslands on the one hand, as well as abandonment and forest encroachment of these grassland on the other (Kuemmerle et al., 2016). Without sufficient levels of natural herbivory, or low-intensity land use replacing natural grazing and browsing, these landscapes might thus become less suitable for megafauna in the long run. Trophic rewilding could contribute to restoring herbivory pressure by wildlife, although this could entail considerable conflict potential, particularly where large herbivores, such as European bison, attain high densities, our study indicates that megafauna restoration and low-intensity land use can be aligned in mosaic-type landscapes such as ours.

Our sign survey in the Carpathians, an understudied region of high conservation value (Popescu et al., 2016), yielded robust and plausible occupancy models, though several limitations should be noted. First, ungulate detection rates correlated with body mass, suggesting a detection bias against smaller and elusive species (i.e., chamois and Eurasian lynx). Second, wild boar was found at low densities due to a recent African Swine Fever outbreak, explaining insignificant occupancy results. Third, we were unable to map some food sources, such as stacked hay, fruit orchards, wildlife feeding sites, as well as hunting intensity, which may have influenced megafauna space use, although we expect these factors to play a role. Fourth, while our field teams were highly skilled wildlife trackers, we cannot fully rule out the missing or misidentification of tracks (e.g. due to recent rainfall or confusion between bison/cattle and wolf/dogs). For most species, we had large numbers of tracks, but missed tracks or signs could impact models for the most elusive species (i.e., Eurasian lynx and grey wolf). Fifth, the red deer and brown bear models performed slightly less well than the other models, potentially related to under- or over-dispersion (Gelman et al., 2013). This may indicate that the model slightly underestimates the variability in the observed data, possibly related to the high density of red deer and the low density of brown bears in our mammal community. Higher species abundance increases the probability of detection, whereas lower abundance reduces it (MacKenzie and Bailey, 2004). Lastly, camera trapping was not feasible due to objections from local hunting associations. Future use of camera traps could be valuable for understanding the spatiotemporal patterns of megafauna interactions, especially through multi-species dynamic occupancy models. These models are not possible with sign survey data, as it is unclear if species detected at the same site avoid each other temporally.

Megafauna have been lost in many parts of the world but recent socio-economic trends, as well as conservation and restoration commitments, provide hope that these species can return to contemporary landscapes (Davoli and Svenning, 2024). Yet, much of our understanding of their ecology derives from studying them in remote places void of people and without land use, such as large protected areas. Most landscapes today remain human-dominated to varying degrees (Kennedy et al., 2019), typically consisting of a mosaic of more and less natural habitats (Ellis et al., 2021). Here, we highlight how such landscapes offer considerable potential for restoring diverse megafauna communities, including the largest-bodied species such as the European bison. Our study highlights the importance of refuge habitat (e.g., dense forests or topographically complex terrain), that species can adapt to human pressures, and might even benefit from low-to-moderate human pressures (e.g., logging), and their landscape legacies (e.g., more open landscapes). This provides a hopeful message for restoring diverse megafauna communities and the key ecological functions they provide in places where they have been lost historically, even if these landscapes today are human-dominated.

CRediT authorship contribution statement

Gabriele Retez: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mahmood Soofi:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Arash Ghoddousi:** Writing – review & editing, Writing – original draft, Conceptualization. **Julian Oeser:** Writing – review & editing, Writing – original draft. **Adrian Grancea:** Project administration, Funding acquisition. **Tobias Kuemmerle:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors used ChatGPT to improve the readability of the work. The authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.110977.

Data availability

Data will be made available on request.

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