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Research article

Ecological dynamics and coexistence patterns of wild and domestic mammals in an abandoned landscape

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The issue of agricultural land abandonment in southern Europe has raised concerns about its impact on biodiversity. While abandoned areas can lead to positive developments like creating new habitats and restoring native vegetation, they can also result in human–wildlife conflicts, particularly in areas with extensive farming and free-ranging livestock. To understand habitat selection and use of livestock and wild ungulates, it is essential to study their spatial and temporal distribution patterns. In this context, we conducted a long-term large mammal monitoring project using camera traps in the Peneda-Gerês National Park in northern Portugal. Our primary focus was on exploring habitat preferences, occupancy dynamics, and potential spatial use correlations between domestic and wild species, utilizing dynamic occupancy models. Most wild species exhibited stable area use patterns, while domestic species experienced marginal declines, and the Iberian ibex displayed signs of repopulation. We observed distinct effects of habitat variables on occupancy, colonization, and extinction, revealing species-specific patterns of habitat utilization. Human disturbance had a notable impact on domestic species but did not affect wild ones. Camera sensitivity emerged as a critical factor, enhancing detection probability for all species. Additionally, habitat and weather variables exerted varying effects on detection probabilities, underscoring the necessity of accounting for these factors in modeling the detection process. We found shared habitat preferences between cattle and horses, both positively correlated with wolves, suggesting potential human–wildlife conflicts. Despite extensive spatial overlap, domestic and wild species seem to exhibit ecological independence possibly due to distinct strategies and low predation pressure. Overall, the study emphasizes the multifaceted factors influencing habitat use. The observed species associations contribute to understanding ecological relationships and potential resource competition, emphasizing the importance of considering environmental variables for effective wildlife conservation and management.

Keywords: camera traps, dynamic occupancy models, long-term monitoring, mammals, Portugal

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Introduction

The issue of agricultural land abandonment has become increasingly prominent in southern Europe during the past 60 years (Nunes et al. 2010, Gabarrón-Galeote et al. 2015, Pereira and Navarro 2015). This can have varying effects on biodiversity, depending on the region and the extent of abandonment (Navarro and Pereira 2012). Potential positive outcomes may include the creation of more heterogeneous habitats or the restoration of native vegetation (Navarro and Pereira 2012). Additionally, certain species, such as forest species or large mammals, may benefit from the return of natural vegetation and reduced human disturbances in abandoned areas, opening opportunities for the expansion or even recolonization of species (Boitani and Linnell 2015). Yet, while this transformation can impact local biodiversity positively, it can also give rise to human–wildlife conflicts, particularly affecting low-intensity farming operations, such as the breeding of free-ranging domestic herbivores like cattle or horses (Chirichella et al. 2014, Putman and Apollonio 2014, Boitani and Linnell 2015). Especially in Mediterranean Europe extensive pastoral systems have a long-standing history with a high relevance of ecological and cultural importance (Rebollo et al. 1993).

However, livestock predation by wolves can lead to conflicts with rural communities where livestock is a significant source of income (Torres and Fonseca 2016). Studies found a notable dietary preference for horses and cattle, constituting more than 60% of the wolf's diet in northern Portugal, and this trend has seen recent increases (Llaneza and López-Bao 2015, Pimenta et al. 2017). In contrast, wild species such as roe deer and wild boar contribute to a mere 5% of their diet (Llaneza and López-Bao 2015). This amount of livestock predation is unlikely to stem from high numbers of wolves or low densities of wild species; instead, it can be ascribed predominantly to the free-ranging husbandry practices prevalent in the region, where livestock is permitted to roam unguarded within the mountainous terrain (Pimenta et al. 2017). Despite strict legal protection for wolves in Portugal dating back to 1988 and the implementation of compensation programs for livestock owners, illegal persecution in the form of shooting, poisoning, or trapping of wolves still persists (Torres and Fonseca 2016).

On the other hand, livestock, particularly in forest habitats, have been hypothesized to pose a threat to wildlife, causing habitat degradation, seedling and understory destruction, and resource competition (Carter et al. 2014, Zhang et al. 2017). Free-ranging livestock might compete with wild ungulates for habitat and resources, altering wildlife habitat use patterns, reducing densities, and leading to possible exclusion from heavily grazed areas (Rebollo et al. 1993, Putman and Apollonio 2014). Resource competition might be especially strong between cattle and horses, which are preferential grazers, and native wildlife species that rely on bulk-feeding strategies (Putman and Apollonio 2014). Additionally, several studies also found negative impacts of livestock grazing on the activity of ungulates, resulting in a reduced probability of shared habitat use by temporal avoidance (Feng et al. 2021). In addition to direct competition, spatial overlap between wild and domestic species might also lead to indirect competition through the modification of habitats, which can lead to a reduction in environmental quality for wild species (Putman and Apollonio 2014).

To date, there is still limited knowledge about livestock–wild species interactions in European landscapes. While some studies have shown significant negative impacts of livestock on wildlife in regions where free-ranging practices are prevalent (Chirichella et al. 2014, Putman and Apollonio 2014, Horcajada-Sánchez et al. 2019, Feng et al. 2021, Roberts et al. 2021, Dahal et al. 2023), patterns of habitat use and partitioning between domesticated and wild ungulate species in abandoned European landscapes remain poorly understood (Apollonio et al. 2010). Particularly in areas with extensive grazing, increasing wild species populations may result in unforeseen patterns of habitat use and species interactions for both domestic and wild animals. It is therefore necessary to investigate the spatial and temporal distributional patterns of animals to understand their ecological drivers.

In both long-term monitoring and metapopulation studies, estimating the proportion of sites occupied by target species holds great importance. Site occupancy probabilities serve as a metric reflecting the current population state, and can further be used to estimate local extinction and colonization probabilities (MacKenzie et al. 2003). This can be achieved by applying dynamic occupancy models. Dynamic occupancy models estimate occupancy across multiple seasons, shedding light on underlying population dynamics that drive changes in site occupancy, potentially yielding a process-based understanding of human and other impacts on wild populations. By incorporating survey- and site-specific covariates, such as habitat and climatic conditions, these models can provide unbiased estimates of local colonization and extinction rates while accounting for imperfect detection (MacKenzie et al. 2003).

To assess the impacts of land abandonment and low-intensity livestock breeding, we conducted a long-term large mammal monitoring project using camera traps in the Peneda-Gerês National Park in northern Portugal – an area that experienced rural depopulation and agricultural abandonment and underwent great land-use changes in the past 60 years (van der Zanden et al. 2018). In this region, it is still a common practice to breed free-ranging cattle and horses, offering an exceptional opportunity to study potential interactions between livestock and wildlife in abandoned landscapes with otherwise very low levels of human disturbance (Moço et al. 2014).

Our study aimed to explore habitat preferences of both domestic and wild species in the area and assess dynamics and trends throughout the study period. We investigate the environmental factors influencing area use, as well as local colonization and extinction probabilities. Last, we explored the existence of spatial use correlations between domestic livestock and wild species.

Material and methods

Study area

The study was conducted in the parishes of Castro Laboreiro and Lamas de Mouro in the Peneda-Gerês National Park in northern Portugal (Fig. 1). The area's elevation ranges from 300 to 1340 m a.s.l. It is situated at the transition between the Mediterranean and Atlantic biogeographic zones and features a temperate Mediterranean climate with cold and rainy winters and warm summers (van der Zanden et al. 2018). Following land abandonment and natural succession, the region now sustains various habitats, encompassing small agricultural fields in the valley, shrublands, oak forest patches on the hillside, and pastures for livestock along with agricultural fields on the plateau (Rodrigues 2010). It further contains a diverse trophic network comprising various species. Among the domestic species, cattle *Bos taurus* and horses *Equus caballus* primarily roam freely, although some cattle can return to the stables during the night or in winter, while goats *Capra aegagrus hircus* and sheep *Ovis aries* are guarded during grazing and return to the villages at night (Moço et al. 2014). Additionally, the area is home to various wild ungulates, including European roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, Iberian ibex *Capra pyrenaica*, and red deer *Cervus elaphus*. Several mesopredators, such as red fox *Vulpes vulpes*, Eurasian badger *Meles meles*, stone marten *Martes foina*, and common genet *Genetta genetta* can be observed. Furthermore, the study area supports a stable population of Iberian gray wolf *Canis lupus*. Hunting in the national park is officially prohibited for all species except for the wild boar, but illegal hunting of roe deer or wolf might still occur.

Study design

Within the study area, we established a long-term monitoring program using camera traps (Fig. 1). The program was initiated in 2015 and, since then, we have consistently deployed camera traps annually during the summer months from April to October. We deployed 64 camera traps in a 16 km^2 grid with an average of 500 m between camera trap locations southwest of the Castro Laboreiro village. Cameras were mounted at approximately 50–100 cm from the ground depending on the terrain and vegetation to maximize field of view. While most camera locations remained the same over the years, we occasionally had to make small adjustments due to changes in vegetation, fire incidents, or instances of theft. For further information on the study area and the specifics of the study design see Zuleger et al. (2023). The original study design did not specifically target occupancy analysis, potentially affecting the grid size's suitability for species with large home ranges, such as wolves. However, our primary objective is to examine habitat use patterns rather than solely focusing on species presence or absence. Using an occupancy framework, we aim to investigate how these species interact with specific habitat characteristics.

Dynamic occupancy models

To do so, we employed a multi-season occupancy model framework, first introduced by MacKenzie et al. (2003) to estimate initial site occupancy (ψ), colonization (Υ), extinction (ε), and probability of detection (p). The framework accommodates the possibility of sites transitioning between occupied and unoccupied states across seasons (Fig. 2), treating dynamic changes as a first-order Markov process (MacKenzie et al. 2003, 2006). The probability of occupancy for each site at time t, ψ_t, was calculated by:

$$\psi_t = \psi_{t-1}\left(1-\varepsilon_{t-1}\right)+\left(1-\psi_{t-1}\right)\Upsilon_{t-1} \tag{1}$$

The models provide insights into general occupancy trends over the study duration for each species, enabling us to

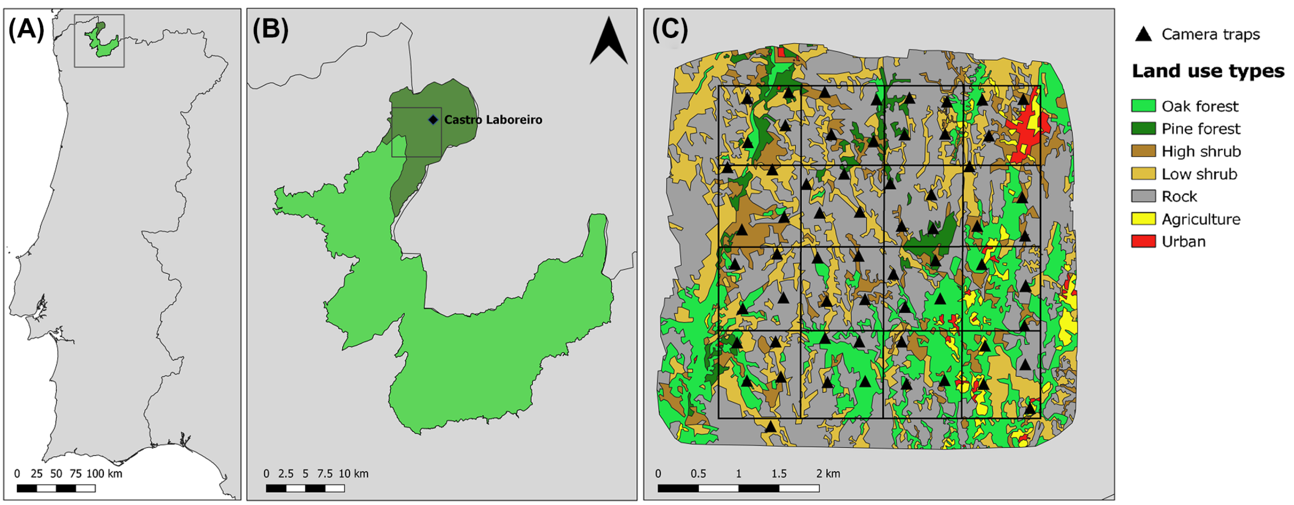

Figure 1. (A)–(B) Study location in the Peneda-Gerês National Park in northern Portugal. (C) Camera-trap locations and land-use types within the survey area. Cameras were placed randomly with regard to animal density and activity, but the locations were chosen in a way to represent the different land-use types in the area relative to their overall occurrence (Zuleger et al. 2023).

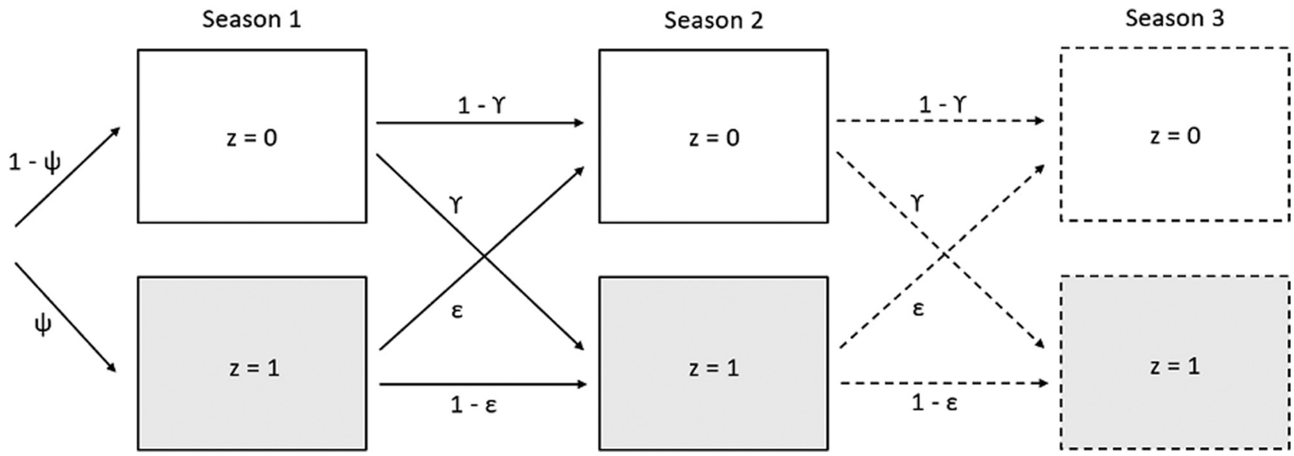

Figure 2. Dynamic site-occupancy model. z is true occupancy (0 or 1) of a site, ψ is occupancy probability, γ is local colonization probability, 1 − γ is the probability that the site stays unoccupied, ε is local extinction probability, and ε – 1 is the probability that the site stays occupied.

observe how site usage fluctuated over time. Additionally, we introduced covariates on the parameters to account for variations across seasons or sites and to investigate habitat use of the study species. Suitable covariates for occupancy, colonization, and extinction probabilities may vary by site and primary sampling period (e.g. habitat characteristics). These covariates along with variables that vary by secondary sampling periods, such as precipitation or temperature, can also affect detection probabilities (MacKenzie et al. 2003). The relationship between covariates and the parameter of interest (Θ) can be estimated following:

$$\theta = \frac{\exp(Y\beta)}{1+\exp(Y\beta)} \tag{2}$$

where Y is the matrix of covariate information and ß is the vector of logistic model coefficients.

By incorporating these covariates, we were able to identify specific habitat features that influence occupancy, colonization, and extinction probabilities, thus providing a deeper understanding of habitat use and preferences of the study species. This approach allowed us to make more informed inferences about species distribution and habitat requirements throughout the study period.

Data

For the analysis, we used data collected from 2015 to 2022, focusing on the period between 10 May and 29 August of each year, as we assumed habitat overlap to be greatest during the summer months (Girard et al. 2013). Additionally, this time frame allowed us to maximize the overlap of sampling periods between years, ensuring robust and consistent results.

To reduce temporal autocorrelation, we defined a sampling occasion as seven consecutive camera-trap nights, resulting in a binary presence–absence dataset for each species, covering 16 weeks (secondary sampling periods). To reduce spatial autocorrelation, we created a 1 × 1 km grid on top of our sampling area and grouped camera traps into 16 grid cells which were considered sampling locations (Fig. 1).

The selection of variables for our analysis was guided by literature research, aiming to capture key ecological factors known to influence species habitat use (Table 1). For occupancy this entails covariates such as elevation, land-use types (oak forest, pine forest, shrublands, rock, agriculture, and urban) and human disturbance indicators (distance to roads and distance to urban). The information on land-use types was obtained from remote sensing data collected in 2020. The distance to paved roads was evaluated by calculating the cost distance according to Naismith's rule, accounting for different travel times depending on the terrain (Naismith 1892). We used a digital elevation model to estimate the effect of elevation and ruggedness on distance and used the mean of the distances for each camera included in a grid cell for analysis. For detection probabilities, we tested for an effect of the different land-use types, as well as camera trap sensitivity setting and weather variables (temperature, solar radiation, and precipitation). Weather covariates were obtained from a local weather station and averaged across sampling occasions.

Before proceeding with the analysis, all covariates were checked for pairwise correlation using a Spearman rank test, and any highly correlated variables with a $|r| > 0.7$ were removed from the analysis to avoid redundancy and ensure the robustness of the results. This left us with eight covariates, which were incorporated in the final analysis (Table 1). The distance to paved roads was highly correlated with elevation and the area covered by rock in the study area, therefore, it also represents a measure of those two variables.

Model fitting

All continuous covariates were scaled to a mean of 0 and a SD of 1 prior to the analyses.

Given the large number of variables potentially impacting each model parameter, we employed a model selection approach that integrated theoretical considerations

Table 1. Explanation of variables used in the model selection for initial occupancy (ψ), colonization (ϒ), extinction (ε), and detection (p) probabilities.

Variable		Parameter	References
CostDist_road	Cost distance to paved roads estimated with digital elevation models (mean across all cameras per grid cell)	ψ, ϒ, ε	Torres et al. (2011) Bonnot et al. (2013) Meisingset et al. (2013) Lopes de Oliveira (2018) Rio-Maior et al. (2019) Ripari et al. (2022) Mayer et al. (2023)
Shrub	Area covered by shrub (high shrub and low shrub combined) within the 1 × 1 km grid cell [ha]	ψ, ϒ, ε, p	Abaigar et al. (1994) Morellet et al. (2011)
OakForest	Area covered by oak forest within the 1 × 1 km grid cell [ha]	ψ, ϒ, ε, p	Pereira et al. (2012)
PineForest	Area covered by pine forest within the 1 × 1 km grid cell [ha]	ψ, ϒ, ε, p	Hofmeester et al. (2019)
Urban_agri	Area covered by urban infrastructure and agricultural pastures combined within the 1 × 1 km grid cell [ha]	ψ, ϒ, ε, p	Rio-Maior et al. (2019) Gaudiano et al. (2021) Oliveira (2021)
Sensitivity	Sensitivity setting of the camera trap (mean across all cameras per grid cell)	p	Meek et al. (2014) Hofmeester et al. (2019)
Temp_min	Minimum temperature [°C] per day, averaged across weeks (secondary periods)	p	Meek et al. (2014) Hofmeester et al. (2019) Madsen et al. (2020)
Rad_max	Maximum radiation [W/m²] per day, averaged across weeks (secondary periods)	p	Hofmeester et al. (2019)

from existing studies with a stepwise regression method. Specifically, we utilized backward elimination to refine the set of variables for each species and model parameter. We started by fitting a global model including all variables that were not highly correlated with each other. The first parameter we focused on was the detection probability (p), as accurate modeling of the detection process is critical for reliable estimation of other parameters and for making robust inferences about occupancy, colonization, and extinction. Subsequently, we reduced the variables for the initial occupancy (ψ), which provides the baseline for estimating colonization and extinction processes, followed by variable reduction for colonization (ϒ) and finally for extinction (ε). In each step, we removed the least significant variable iteratively until only variables with a p-value ≤ 0.157, as recommended by Heinze and Dunkler (2017), remained. All models were fitted using the *colext* function from the R package 'unmarked' (Fiske and Chandler 2011).

Spatial use correlations

Additionally, we aimed to investigate potential spatial use correlations between the domestic and wild species, as well as between predator and prey species. For this, we used the occupancy estimates obtained from the final models at both the grid cell and annual levels as an indicator of species occurrence. We fitted a linear regression model for each study species separately using the occupancy probability of the other species as predictor variables.

Results

We obtained a sufficient number of observations to fit dynamic occupancy models to seven species. Among these, roe deer *Capreolus capreolus* and wild boar *Sus scrofa* exhibited the widest distribution, being observed at an average of 35 [min. 24–max. 50] and 26 [13–42] camera trap locations per year, respectively. The domestic species, cattle *Bos taurus* and horses *Equus caballus* were present at 19 [13–28] and 24 [8–37] camera trap locations, respectively. The remaining species were less common, with occurrences ranging from an average of 2 [0–5] camera locations for the Iberian ibex *Capra pyrenaica* to 11 [1–22] for the red fox *Vulpes vulpes* per year. Wolves *Canis lupus* were observed at 5 [2–8] locations per year.

Occupancy trends

For the wild species, European roe deer showed the highest initial occupancy estimates (1.00 ± 0.00 SE), followed by wild boar (0.82 ± 0.10, Fig. 3, Supporting information). The domestic species also demonstrated high initial occupancies: 0.95 (± 0.10) for cattle and 0.91 (± 0.08) for horses (Fig. 3, Supporting information). Red foxes had an initial occupancy of 0.46 (± 0.13), while gray wolves exhibited 0.51 (± 0.17, Fig. 3, Supporting information). The Iberian ibex had the lowest estimate, with 0.00 (± 0.07), reflecting no detections in 2015 (Fig. 3, Supporting information). Red fox and wild boar had the highest colonization probability estimates (1.00 ± 0.00 and 0.88 ± 0.13, respectively), while the Iberian ibex had the lowest (0.06 ± 0.03, Fig. 3, Supporting information). Other species demonstrated intermediate probabilities. Extinction probabilities varied across species, with the highest for gray wolf (0.49 ± 0.15) and the lowest for the Iberian ibex (0.00 ± 0.00) and European roe deer (0.02 ± 0.02, Fig. 3, Supporting information). Detection probabilities were highest for European roe deer at 0.39 (± 0.01) and lowest for the Iberian ibex (0.01 ± 0.01, Fig. 3, Supporting information). Smoothed occupancy estimates revealed a decline in the area

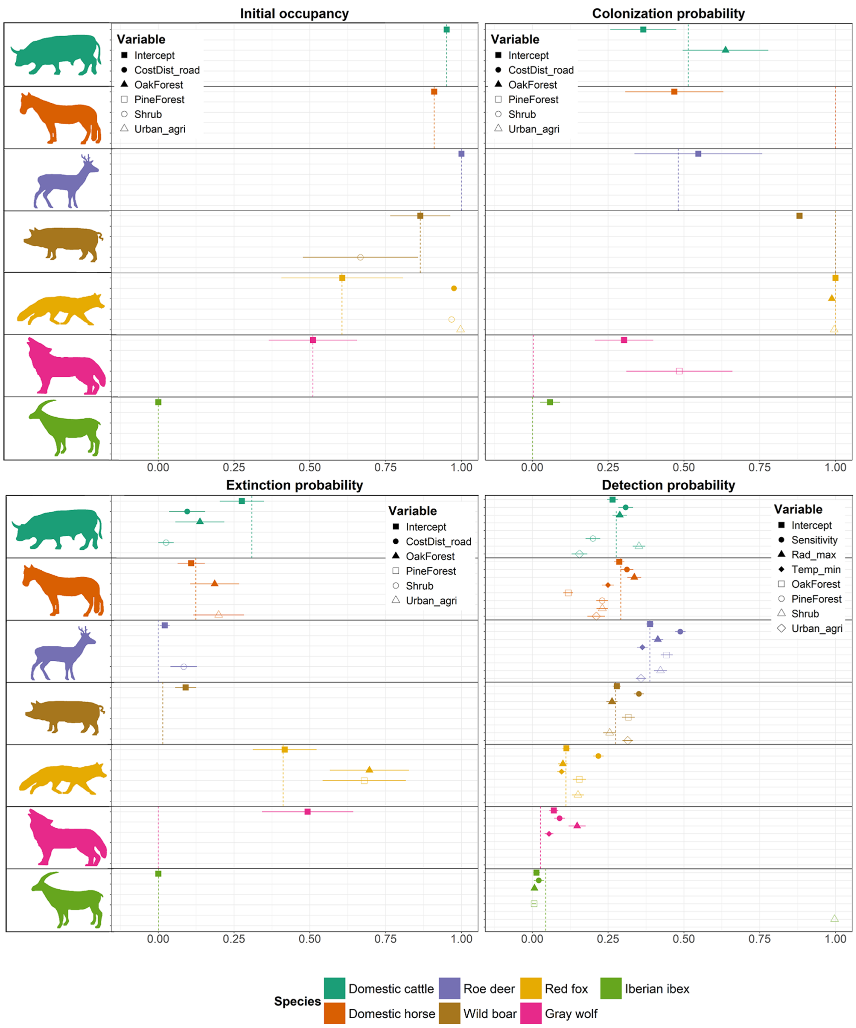

Figure 3. Effect sizes of the variables influencing initial occupancy, as well as colonization, extinction, and detection probability according to the best model following backwards elimination (p > 0.157). The intercept was estimated keeping all variable effects at their mean (0). Since continuous covariates were scaled to a mean of 0 and an SD of 1, effect sizes of each variable are estimated based on a change in one SD from the mean, while keeping the intercept constant (1) and all remaining variables at their mean (0). All estimates are back-transformed from the logit scale to the original scale.

utilized by domestic cattle from 95.14 ± 9.53% in 2015 to 49.14 ± 12.04% in 2022 (ß = −0.04, p = 0.09, R^2 = 0.30, F(1,6) = 3.97, p = 0.09, Fig. 4). Horses also exhibited a slight decrease from 91.00 ± 8.03% in 2015 to 74.45 ± 9.38% in 2022 (ß = -0.03, p = 0.06; R^2 = 0.39, F(1,6) = 5.45, p = 0.06; Fig. 4). In contrast, wild species generally showed stable occupancy trends, with the Iberian ibex indicating a significant increase in area use from 0.01 ± 6.54% in 2015 to 33.53 ± 18.48% in 2022 (ß = 0.05, p = 0.00; R^2 = 0.96, F(1,6) = 149.5, p = 0.00; Fig. 4).

Factors influencing habitat use and detection

Except for wild boar and red fox, no variables affecting initial occupancy (ψ) were identified across the various species. For wild boar, an increase in shrub cover resulted in decreased initial occupancy; while for red fox, increasing distance to roads, shrub cover, and the area covered by urban infrastructure and agricultural lands positively impacted initial occupancy (Fig. 3, Supporting information). Site-specific colonization probability (ϒ) was positively impacted by the amount of oak forest for domestic cattle, while red fox colonization probability slightly decreased with increasing oak forest cover as well as urban and agricultural areas (Fig. 3, Supporting information). Additionally, the colonization probability of gray wolves was positively affected by pine forest cover (Fig. 3, Supporting information). For extinction probabilities, species-specific effects were observed: oak forest cover increased extinction probabilities of domestic horses and red foxes, but decreased them for domestic cattle (Fig. 3, Supporting information). Similarly, shrub cover negatively affected the extinction probability of domestic cattle, but positively impacted roe deer extinction probabilities (Fig. 3, Supporting information). We also observed an increase in

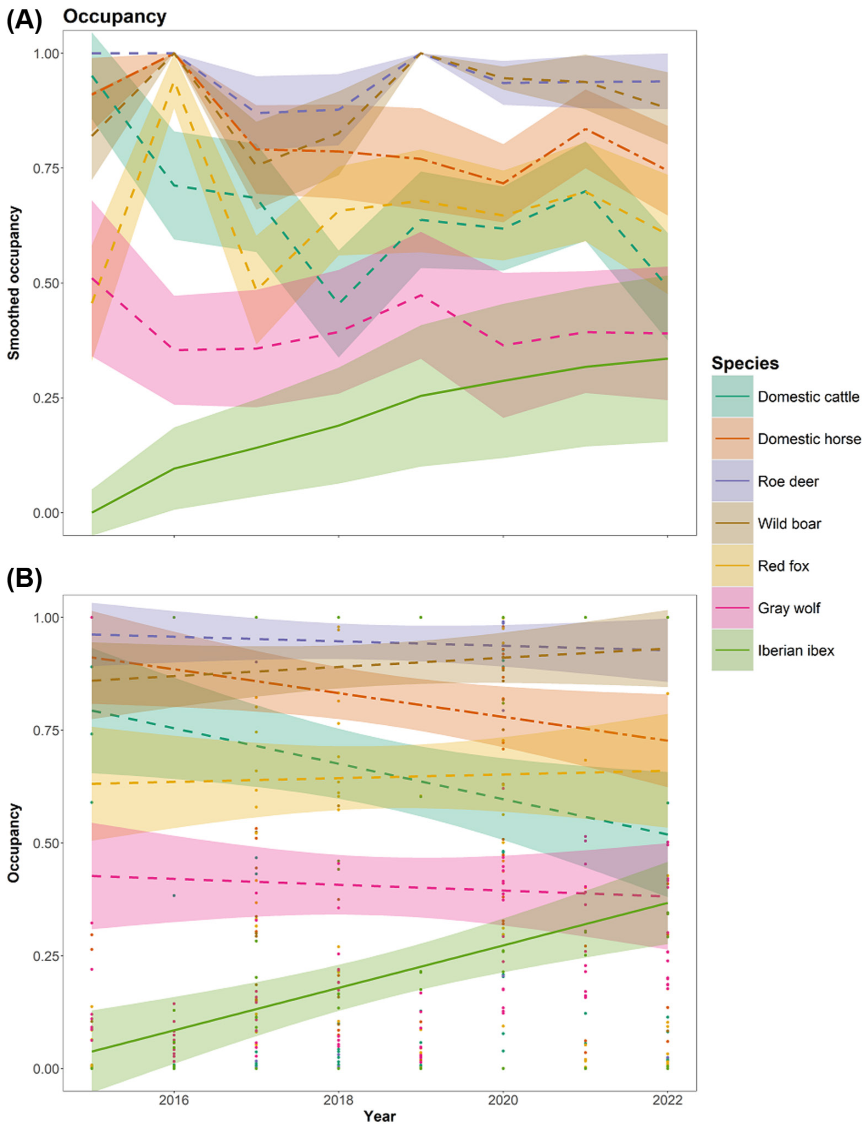

Figure 4. Occupancy trends of the study species across years based on the final model obtained. (A) Smoothed occupancy estimates and standard errors for the entire study area per year obtained from nonparametric bootstrapping with 1000 iterations. (B) Occupancy trends based on a linear regression fitted to smoothed site-specific occupancy estimates obtained from non-parametric bootstrapping with 1000 iterations. Solid lines indicate significant trends ($p < 0.05$), two-dashed lines indicate marginally significant trends ($p < 0.10$), and dashed lines indicate no significance.

extinction probability with increasing pine forest cover for red foxes (Fig. 3, Supporting information). Human disturbance indicators only affected the two domestic species: urban infrastructure and agricultural pastures increased the extinction probability of horses, while increasing distance to roads decreased it for cattle (Fig. 3, Supporting information).

Regarding detection probabilities (p), a higher camera sensitivity setting positively influenced detectability for all species, with the most pronounced effects for European roe deer and red fox (Fig. 3, Supporting information). Solar radiation positively impacted the detection probability of cattle, horses, roe deer, and wolves, but negatively impacted wild boar, red fox, and Iberian ibex detectability (Fig. 3, Supporting information). Additionally, detection probabilities of horses, roe deer, red fox, and wolf decreased with increasing temperatures (Fig. 3, Supporting information). Habitat covariates displayed diverse effects on detection probabilities depending on the species: oak forest cover positively affected the detection probability of roe deer, wild boar, and foxes, but yielded a negative effect for horses and ibex (Fig. 3, Supporting information). Pine forest negatively affected detectability of the two domestic species, but had no effect on wild species (Fig. 3, Supporting information). Shrub cover positively impacted the detectability of cattle, roe deer, red fox, and Iberian ibex, but negatively affected horse and wild boar detectability (Fig. 3, Supporting information). Finally, urban and agricultural areas decreased detectability of cattle, horses, and roe deer, but increased it for wild boar (Fig. 3, Supporting information).

Spatial use correlations

We observed positive spatial use correlations between cattle and horses (ß = 0.11, p = 0.37) and cattle and wolves (ß = 0.15, p = 0.19), as well as a potential negative relationship between the site usage of cattle and roe deer (ß = −0.24, p = 0.19; Fig. 5). However, none of these correlations was statistically significant ($R^2 = 0.00$, $F(6,121) = 0.91$, $p = 0.49$). Horses showed a positive relationship with the presence of red fox (ß = 0.18, p = 0.01) and wolves (ß = 0.22, p = 0.00; $R^2 = 0.09$, $F(6,121) = 2.97$, $p = 0.01$), while roe deer exhibited a slightly positive relationship with the occurrence of wild boar (ß = 0.10, p = 0.18; $R^2 = 0.00$, $F(6,121) = 0.93$, $p = 0.48$). Additionally, we found a positive relationship between the occurrence of foxes and Iberian ibex (ß = 0.23, p = 0.04; $R^2 = 0.05$, $F(6,121) = 2.15$, $p = 0.05$). However, given the limited predictive power of the models, it is crucial to approach their interpretations and conclusions with caution. Model summaries for each species are provided in the Supporting information.

Discussion

We employed dynamic occupancy models (MacKenzie et al. 2003) to conduct an eight-year evaluation of large mammal habitat use within the Peneda-Gerês National Park in northern Portugal. These models, previously used for wildlife monitoring using camera traps (Wearn and Glover-Kapfer 2017, Gould et al. 2019), improve the understanding of the dynamics of species occupancy (MacKenzie et al. 2003). Our study, conducted on a relatively small scale covering only 16 km², offers insights into local habitat preferences and ecological interactions, extending beyond mere occupancy assessments. Here, the parameters serve as valuable metrics for habitat use, revealing local conditions and resource availability (MacKenzie et al. 2006).

General trends and covariates influencing habitat use

We observed high overall site use by European roe deer and wild boar, with generally stable trends across most species. Colonization rates exceeded extinction rates for all species except for gray wolf, signaling positive trends in site usage. However, domestic species showed a decline in area use, likely because their initial populations were above equilibrium levels.

Equilibrium occupancy refers to the habitat proportion occupied by a species when the population is stable over time, balancing colonization and extinction. Solving Eq. (1) for equilibrium ($\psi_t = \psi_{t-1}$), we estimated equilibrium occupancy for cattle to be approximately 0.57 and for horses to be 0.81. Our observations suggests that their populations initially were above equilibrium, leading to a decline in site use over time. Conversely, wild species maintained their site use, indicating that their populations are likely closer to or at equilibrium occupancy levels, with favorable conditions supporting their stability in the region. The Iberian ibex is a notable exception to this trend. Once extinct in Portugal, it shows signs of repopulation, indicating a positive response to land abandonment and rewilding. The repopulation originates from a reintroduction initiative of the western Spanish ibex *Capra pyrenaica victoriae* on the Spanish side of the border (Moço et al. 2006, Fonseca et al. 2017). Ongoing expansion is expected due to favorable habitat conditions in the National Park (Moço et al. 2006).

Our investigation into habitat preferences revealed that oak forest and pine forest coverage positively influenced cattle habitat use, indicating favorable conditions and food availability within oak forests, aligning with prior studies associating cattle with temperate woodlands with intermediate vegetation cover (Gaudiano et al. 2021, Oliveira 2021). The positive association with pine forest is likely influenced by landscape characteristics, particularly the presence of a major

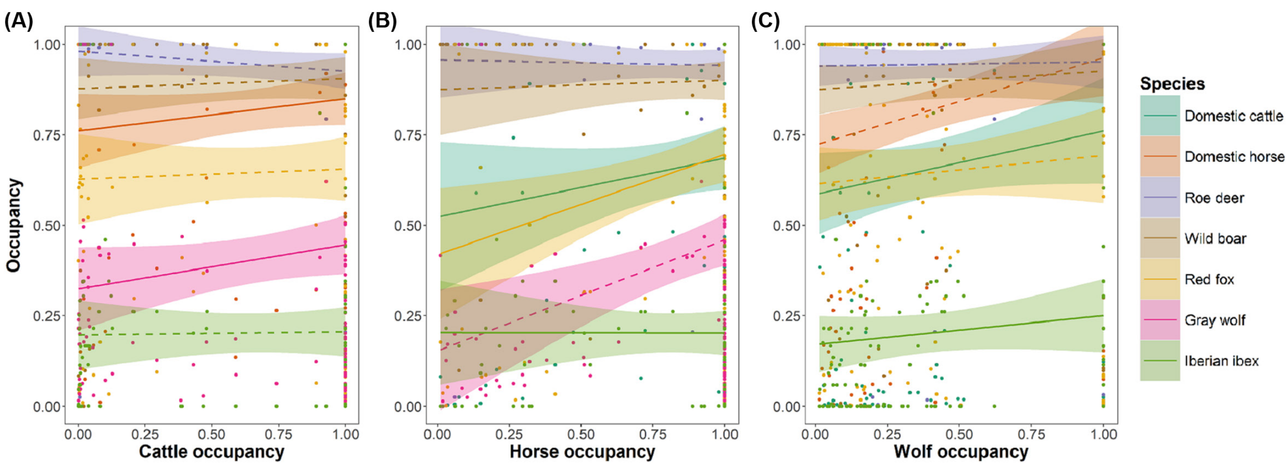

Figure 5. Effect of the occurrence of (A) domestic cattle, (B) domestic horses, and (C) wolf on the occupancy of the study species obtained from a linear regression based on occupancy estimates per sampling location and year obtained from the final models. Solid lines indicate significant correlation (p < 0.05), two-dashed lines indicate marginally significant correlation (p < 0.10), and dashed lines indicate no significance.

stable located within this habitat type. Conversely, horses exhibited a negative effect of oak forests on colonization probability, indicating their preference for open shrublands as supported by Oliveira (2021), who verifies the more frequent use of shrublands over oak forests by horses in northern Portugal. Shrub cover negatively affected wild boar and roe deer occurrence, suggesting unfavorable conditions. This corresponds with observed habitat preferences of both species, favoring forest habitats over shrublands (Virgós and Tellería 1998, Barros et al. 2020, Çoğal and Sözen 2020, Gaudiano et al. 2021, Oliveira 2021, Dagtekin et al. 2023), although studies have indicated selection of areas with higher shrub cover in northern Portugal for roe deer and wild boar, respectively (Torres et al. 2011, Oliveira 2021). However, the wide distribution of both species in our study area complicates the assessment of habitat variables' influence on a fine spatial scale.

Conversely, cattle and red fox exhibited a positive response to shrub cover, indicating a higher likelihood of persistence in areas with abundant shrub. Since both high and low shrublands were grouped into one category for analysis, the results might also suggest a preference for open spaces that signify resource abundance and potential predator detection. Gray wolves' habitat selection is likely driven by prey availability rather than specific environmental characteristics (Nakamura et al. 2023). Given the abundance of livestock and wild prey species across our study area, coupled with relatively little human infrastructure, habitat suitability is likely uniformly high throughout the region, rendering habitat effects negligible. Moreover, the limited spatial coverage of our study area (16 km^2) may have precluded the observation of habitat effects on wolf area use, given the wide variation in their home ranges, ranging from 100 to 1000 km^2 (Macdonald and Barrett 1993, Aulagnier et al. 2008).

Notably, we found that human disturbance only impacted the habitat use of the domestic species, with cattle showing reduced extinction probabilities with greater distances to roads, and horses displaying an increased local extinction probability near urban areas. This indicates a tendency to avoid locations with higher human disturbance, supporting previous studies that emphasize the negative impact of human infrastructure on the habitat use of domestic species (Gaudiano et al. 2021, Oliveira 2021). Free-ranging cattle, especially during summer, may prefer higher-altitude feeding grounds to minimize human disturbance and resource competition with other domestic livestock in closer proximity to urban settlements, such as goats or sheep (Moço et al. 2014). Despite the introduced and managed origin of horses in the area, many adopting a feral lifestyle may employ habitat selection to reduce human disturbance. Foxes displayed diverse effects to human disturbance variables, with urban and agricultural areas having a positive effect on initial occupancy, but a slightly negative one on colonization probability. This potentially suggests that, during the initial sampling period in 2015, there was a disproportionally high number of fox observations in urban or agricultural areas, which could be due to temporal or spatial biases inherent to the sampling protocol or environmental conditions of that specific year, or possibly to random variation. Despite this, we did not observe any effects of human disturbance covariates on wild species, suggesting varying degrees of resilience or adaptability to urban environments. It is, however, important to note that the level of human disturbance in our study area is very low, marked by low human population densities (only 4.7 inhabitats km^{-2} in 2021 compared to an average population density of 109 inhabitants km^{-2} in the EU and 113 inhabitants km^{-2} in Portugal; Instituto Nacional de Estatística 2021, Eurostat 2023) and predominantly undisturbed wild areas. Tourism primarily comprises low-level recreational activities. Moreover, we did not analyze habitat use at different circadian periods and the impact of human disturbance on wild species might be higher during the daytime, forcing animals to use areas in close proximity to urban infrastructure mostly during nighttime hours (Bonnot et al. 2013, Rio-Maior et al. 2019).

While our study offers insights into immediate habitat use, it may not fully encompass a species' complete occupancy pattern or broader ecological processes. The small study area and sparse data, especially for wolves and ibex, limit generalizability (Welsh et al. 2013) and emphasize caution when applying these findings to other systems.

Detection probabilities

Detection probabilities in our study were affected by several covariates. Notably, camera trap sensitivity positively influenced detectability across species, with the effect being most pronounced for species with smaller body sizes such as roe deer or red fox. This highlights the importance of optimizing camera trap configurations in the field and considering them as covariates in subsequent data analysis (Hofmeester et al. 2019, Palencia et al. 2021).

Integrating weather-related variables, such as temperature and precipitation, further enhanced detectability estimations with solar radiation positively influencing the detectability of certain species and higher temperatures negatively affecting several species. Although discerning whether these differences arise from changes in visibility or activity levels during diverse weather conditions is challenging, our results underscore the necessity of incorporating them in the models (O'Connell et al. 2011, Hofmeester et al. 2019, Madsen et al. 2020). Likewise, habitat covariates played a crucial role, indicating the importance of vegetation structure on detectability in camera trap surveys. Oak forest coverage had contrasting effects, positively influencing detectability for roe deer, wild boar, and foxes while negatively affecting horses and ibex. Additionally, we noted a decrease in detectability with pine forest coverage for cattle and horses, and diverse effects of shrub cover and urban areas on the different study species. These outcomes potentially reflect species-specific behaviors and habitat use rather than true detectability indicators. However, they underscore the multifaceted factors influencing detection probabilities, including camera settings, weather conditions, and habitat characteristics. Incorporating these insights into monitoring strategies and optimizing camera trap deployments in diverse ecological settings is crucial for accurate ecological assessments (Hofmeester et al. 2019).

Spatial use correlations

Species occurrences in our study area reveal insightful association patterns, suggesting potential ecological relationships. The slightly positive correlation between cattle and horses indicates shared habitat preferences and coexistence, consistent with findings in the Rocky Mountains (Girard et al. 2013). This relationship is likely influenced by ecological factors such as vegetation types that support grazing and the availability of grazing resources. The correlation between cattle presence and wolf occurrences highlights the role of livestock in the wolf's diet in northern Portugal, potentially leading to human–wildlife conflicts due to livestock's economic significance (Llaneza and López-Bao 2015, Torres and Fonseca 2016). Additionally, the positive relationship observed between horse site usage and gray wolf occurrence highlights this ecological interaction. After cattle, horses are reported as the second primary prey of wolves in various studies, underscoring their critical role in the predator–prey dynamics of the region (Freitas and Álvares 2021).

In contrast, we observed a very slight negative relationship between cattle and roe deer, suggesting potential avoidance or differing habitat preferences likely due to differences in diet preference and foraging behavior. Roe deer typically prefer forested habitats or areas with dense vegetation where they can browse on shrubs and trees (Macdonald and Barrett 1993, Virgós and Tellería 1998, Oliveira 2021), whereas cattle are more adapted to open grasslands or pasturelands where they graze on grasses and forbs (Gaudiano et al. 2021, Oliveira 2021). This habitat differentiation might lead to spatial segregation rather than active avoidance between the two species. Additionally, evidence of shared habitat use between roe deer and wild boar implies common habitat preferences, particularly in forested areas and mixed woodlands. While roe deer and wild boar may share common habitat and feeding preferences, the abundant resources in the study area are likely to reduce competitive pressures between them. Contrary to co-occurrence patterns observed nearby (Oliveira 2021), our findings indicate a degree of ecological independence or lack of direct interactions between domestic and wild species in terms of space utilization. Despite extensive spatial overlap, distinct feeding strategies, resource abundance, and low hunting and predation pressure likely mitigate resource competition and facilitate stable coexistence (Roberts et al. 2021). However, studies suggest that livestock effects on wild species might be contingent on abundance rather than mere occurrence (Acevedo et al. 2007, Moço et al. 2014, Feng et al. 2021, Roberts et al. 2021). For example, Feng et al. (2021) demonstrated that considering cattle encounter rates refines habitat use models, showing that studied ungulate species reduce habitat use or avoid areas in response to cattle grazing. Negative impacts of livestock presence on the relative abundance of the Iberian ibex were also reported (Acevedo et al. 2007, Moço et al. 2014). The context-dependent nature of livestock effects highlights the importance of factors such as habitat quality, food availability, and species' abundances. Although the free-ranging behavior of livestock may influence wild ungulate habitat utilization, relatively low numbers of livestock may have limited our availability to detect such effects. Compared to the EU averages (0.7 to 0.9 total livestock per hectare), livestock densities in the study area are considerably lower (0.2 to 0.4 individuals per hectare; Instituto Nacional de Estatística 2019, Zuleger et al. 2023), possibly affecting the magnitude of their influence.

Despite being considered a low-level human disturbance, livestock grazing can exert both positive and negative effects on wildlife (Rebollo et al. 1993, Moço et al. 2014, Barros et al. 2020, Feng et al. 2021, Roberts et al. 2021). Hence, a comprehensive understanding of fine-scale behavioral patterns and diet composition, as well as complex interactions between livestock and wildlife, becomes essential for effective wildlife conservation and management (Rebollo et al. 1993, Moço et al. 2014, Zhang et al. 2017). Enhancing our capacity to formulate informed assumptions regarding potential competition within our study area also requires considering densities, seasonal variations, resource use overlap, and ecological carrying capacities (Moço et al. 2014, Barros et al. 2020, Dagtekin et al. 2023, Nakamura et al. 2023).

In summary, our study provides significant insights into the impacts of domestic livestock on the habitat utilization of wild species in the Peneda-Gerês National Park, Portugal. By documenting a decrease in the area occupied by domestic species and its potential implications for wild ungulates, we highlight a critical conservation issue. Our findings emphasize the potential of co-existence between domestic and wild species, but also highlights the need for further research to comprehensively understand the dynamics of these interactions and their long-term consequences.

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Author contributions

Annika M. Zuleger: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Visualization (lead); Writing – original draft (lead). **Andrea Perino**: Conceptualization (equal); Investigation (equal); Writing – review and editing (equal). **Henrique M. Pereira**: Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data are available from the Zenodo Repository: https://doi.org/10.5281/zenodo.13270728 (Zuleger et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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