



Spatiotemporal patterns of livestock predation across contrasting farming systems in an expanding grey wolf population

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ABSTRACT

Livestock predation by large carnivores, particularly the grey wolf (*Canis lupus*), threatens rural livelihoods and often triggers retaliatory killing, compromising wolf conservation. Identifying the drivers of livestock attacks is essential for locating conflict hotspots and improving prevention strategies. We analyzed wolf depredation in two recolonization areas of southwestern Europe with contrasting livestock systems (sheep - La Rioja - and cattle - Guadalajara). Using official damage records from 2016 to 2024, we modeled depredation risk at two spatial scales: municipal (damage occurrence per municipality per year) and local (attack locations). Models incorporated ecological, topographic, and management variables, including distance to wolf breeding areas, livestock and wild prey density, land use, and landscape features. Risk maps were generated for both scales. At the municipal scale, in La Rioja, depredation risk increased with habitats used by wolves as scrubland and forest cover, livestock density, and proximity to breeding areas. In Guadalajara, elevation, water availability and breeding sites were the main predictors. At the local scale, risk was consistently associated with proximity to breeding areas and grasslands, increasing with grassland cover and decreasing in anthropogenic landscapes. In Guadalajara, elevations also increased risk. These results demonstrate that depredation drivers vary between regions and spatial scales, emphasizing the need for locally adapted mitigation strategies. Combining municipal and local models provides a robust framework for identifying high-risk areas during wolf range expansion and prioritizing preventive measures according to livestock systems and landscape characteristics. This multi-scale approach offers practical guidance for improving human-wolf coexistence and supporting evidence-based conservation and conflict management in expanding wolf populations.

1. Introduction

In recent decades, large carnivore populations have increased, recolonizing areas in Europe from which they had previously disappeared (Boitani et al., 2022). This recovery has been facilitated by changes in human population density (Chapron et al., 2014; Cimatti et al., 2021), rural land abandonment (Bürgi et al., 2017), growing social tolerance toward wildlife (Pereira and Navarro, 2015), and legal protection of the species (Boitani, 2003). However, the socio-political conflicts generated by the presence of large carnivores and the damage they inflict on human property have remained as the primary conservation concern (Chapron et al., 2025). These conflicts are often exacerbated in the case of the wolf (*Canis lupus*), as public perceptions regarding wolves can be more negative than for other large carnivores,

regardless of the intensity and frequency of their interactions with humans (Dressel et al., 2015; Olson et al., 2015; Fernández-Gil et al., 2016; Bautista et al., 2019).

In recent years, wolf conservation policies have undergone substantial changes (Ramírez-Loza et al., 2026). In the Iberian Peninsula, the species has been legally protected since 1988 in Portugal (Law No. 90/88), with subsequent revisions and updates, most notably in 2016 (Decree-Law N°. 54/2016) and 2025 (Decree-Law N°. 64/2025), none of which involved a reduction in its level of protection. By contrast, wolves in Spain have not historically received the same degree of legal protection. North of the Duero river, wolf populations were subject to regulated, quota-based hunting, whereas south of the Duero river the species has been fully protected since 1992 under Annex IV of the EU Habitats Directive (Ordiz et al., 2022). In 2021, the Spanish government

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extended full protection to wolves across the entire country by including the species in the List of Wild Species under Special Protection (LESRPE in Spanish). However, in March 2025, the Spanish parliament approved the removal of wolves from the LESRPE in areas north of the Duero river, thereby lifting full protection in that region and reinstating their status as a game species subject to regulated quotas. Furthermore, the Iberian wolf population remains practically isolated from the rest of the European grey wolf populations, limiting natural gene flow and demographic connectivity.

Since the lowest population estimate in the 1980s, the wolf population in the Iberian Peninsula has reoccupied some of its previous distribution range (Torres and Fonseca, 2016). Today, wolves occupy the north-western region of the peninsula, with only sporadic occurrences in the east (MITERD, 2025; Ordiz et al., 2022). During this expansion, livestock depredation may increase as dispersing wolves, particularly young and inexperienced individuals, colonize new areas before stable territories and breeding packs become established (Imbert et al., 2016; Mayer et al., 2022; Sells et al., 2022). Consequently, wolves in recently recolonized areas often occur at lower densities and in less established social groups than those in long-established populations (Quevedo et al., 2019). Sheep and cattle are the main livestock species raised under extensive production in Spain, and they constitute the main domestic prey species targeted by wolves in expansion areas (Imbert et al., 2016; Linnell et al., 2001). Negative attitudes toward wolves can be particularly prevalent in regions where the species has been absent for long periods and subsequently recolonized (Gosling et al., 2019). In such areas, long-standing practices of coexistence with large predators, including the use of traditional livestock protection measures, have often been lost (Carter and Linnell, 2016; Durá-Alemañ et al., 2024; Olson et al., 2015), which results in intense social conflict related to the wolf management and conservation, especially in areas experiencing higher numbers of wolf damage (Del Río et al., 2026; Redpath et al., 2017). Consequently, livestock losses and the financial burden associated with preventive measures tend to be higher in these areas (Bautista et al., 2019; Mech, 2017). Over time, however, conflict levels may decline as local communities gradually adapt to coexistence with the species (Zimmermann and Wabakken, 2014).

Isolated wolf populations, such as the Iberian one, remain at risk, and their long-term viability depends on the implementation of effective conservation measures due to their high susceptibility to extinction (López-Bao et al., 2015). Consequently, regional governments face the challenge of balancing livestock protection with conservation objectives of integrating these predators into human-dominated landscapes (Pettersson et al., 2021; van Eeden et al., 2018). Conflict mitigation can be achieved through compensation programs, which pay for damage-related losses and aim to enhance local tolerance toward large carnivores among stakeholders (Bautista et al., 2019; Boitani et al., 2010). Another conflict mitigation strategy is to identify areas with high probability of damage to livestock with ecological modeling. Some of the factors often related to livestock damage are the abundance of wild prey (Meier et al., 2024), livestock availability, land use characteristics (Treves et al., 2004) and the implementation of preventive measures (Pimenta et al., 2017). These models may also be used to forecast the risk in unoccupied areas likely to be recolonized by the wolf in the future (Jedrzejewski et al., 2008; Marucco and McIntire, 2010). Anticipating where damage-related conflicts are likely to expand is critical for the successful conservation and management of wolf populations (Eriksson and Dalerum, 2018).

The aim of this study was to evaluate the spatiotemporal patterns of damage incidents across multiple scales. Specifically, focusing on two contrasting livestock systems (sheep and cattle) in recently recolonized areas of Spain, we assessed how prey density, orographic features, anthropogenic factors, distance to key landscape elements, and natural landscape variables influence damage patterns. We further aimed to: (i) assess temporal trends in damage incidents in each system, (ii) evaluate the probability of damage and its drivers at municipal and local scales,

and (iii) compare both systems to propose context-specific management recommendations.

2. Material and methods

2.1. Study area

The study was conducted in two wolf recolonization areas, La Rioja and Guadalajara, which differ in topography, land cover, grazing practices, seasonal use of pastures, livestock management, and livestock protection measures. These ecological and management differences provided the rationale for analysing the two regions separately. Although livestock densities in the wolf-inhabited areas are broadly similar, the composition of wolf damage differs between regions, with sheep accounting for most damage in La Rioja and cattle representing the largest proportion of damage in Guadalajara (Fig. 1). Moreover, the regions also differ substantially in ecological and management characteristics. La Rioja is characterized by rugged mountain terrain where cattle remain on pasture year-round, whereas sheep use mountain pastures mainly during summer and are housed at night during winter, typically under the protection of livestock guardian dogs. In contrast, Guadalajara has gentler terrain, cattle are moved seasonally between summer and winter grazing areas, and sheep are generally housed every night and are not always accompanied by livestock guardian dogs.

La Rioja province (5045 km²) is located in northern Spain and encompasses a wide range of ecological and topographical conditions. The region exhibits a marked contrast between the agricultural plains and vineyard-dominated landscapes of the north, and the mountainous southwestern sector, which is characterized by forests, scrubland, and higher livestock densities. Mountain grasslands play a key role in summer grazing (SIOSE, 2020). Wolf-livestock interactions are concentrated in the southwestern part of the province, where the mountainous landscape is defined by rugged terrain, narrow valleys, and mid-to-high-elevation summits, some exceeding 2000 m. Vegetation is dominated by mixed forests of oak (*Quercus pyrenaica*, *Q. faginea*), beech (*Fagus sylvatica*), and Scots pine (*Pinus sylvestris*), interspersed with shrub communities such as heather (*Calluna vulgaris*) and common broom (*Cytisus scoparius*) (Fernández-Aldana, 2015). Extensive livestock grazing is widespread in the area, with higher densities of cattle and sheep in the mountainous zones compared to those in the northern agricultural plains (Government of La Rioja, 2023). The predominant management system consists of extensive cattle farming throughout the year and seasonal extensive grazing of sheep on summer pastures. During the winter, livestock remains close to the farm and is kept indoors at night. Extensive livestock grazing is widespread, with cattle (5.89 ind/km²) and sheep (12.62 ind/km²) densities in the mountains, known as “Sierras de la Demanda, Urbión y Cebollera”, higher than in the agricultural plains of the north, cattle density is (0.85 ind/km²) and sheep density is (7.65 ind/km²) (Government of La Rioja, 2023). However, 94% of wolf damage involves sheep. Wild ungulates, including red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), and roe deer (*Capreolus capreolus*), are also abundant. No other large predator species are present in the study area. The Iberian wolf (*Canis lupus signatus*) recolonized this area in the 1990's, with up to five packs recently recorded, three of them shared with neighboring provinces (MITERD, 2025). In this area, located north of the Duero river, the species was subjected to regulated hunting, except during the period between September 2021 and March 2025, when it was granted full protection in Spain (Fig. 1).

Guadalajara province (12,167 km²) is located in central Spain within the region of Castilla-La Mancha (Fig. 1). Land use is heterogeneous: extensive croplands dominate the western and southern parts of the province, whereas the northern and eastern mountainous sectors are covered by broadleaved and coniferous forests, scrublands, and grasslands. Wolf-livestock interactions are restricted to the northwestern mountainous area, where the landscape consists of a mosaic of oak, Scots pine and Spanish juniper (*Juniperus thurifera*) forests interspersed with

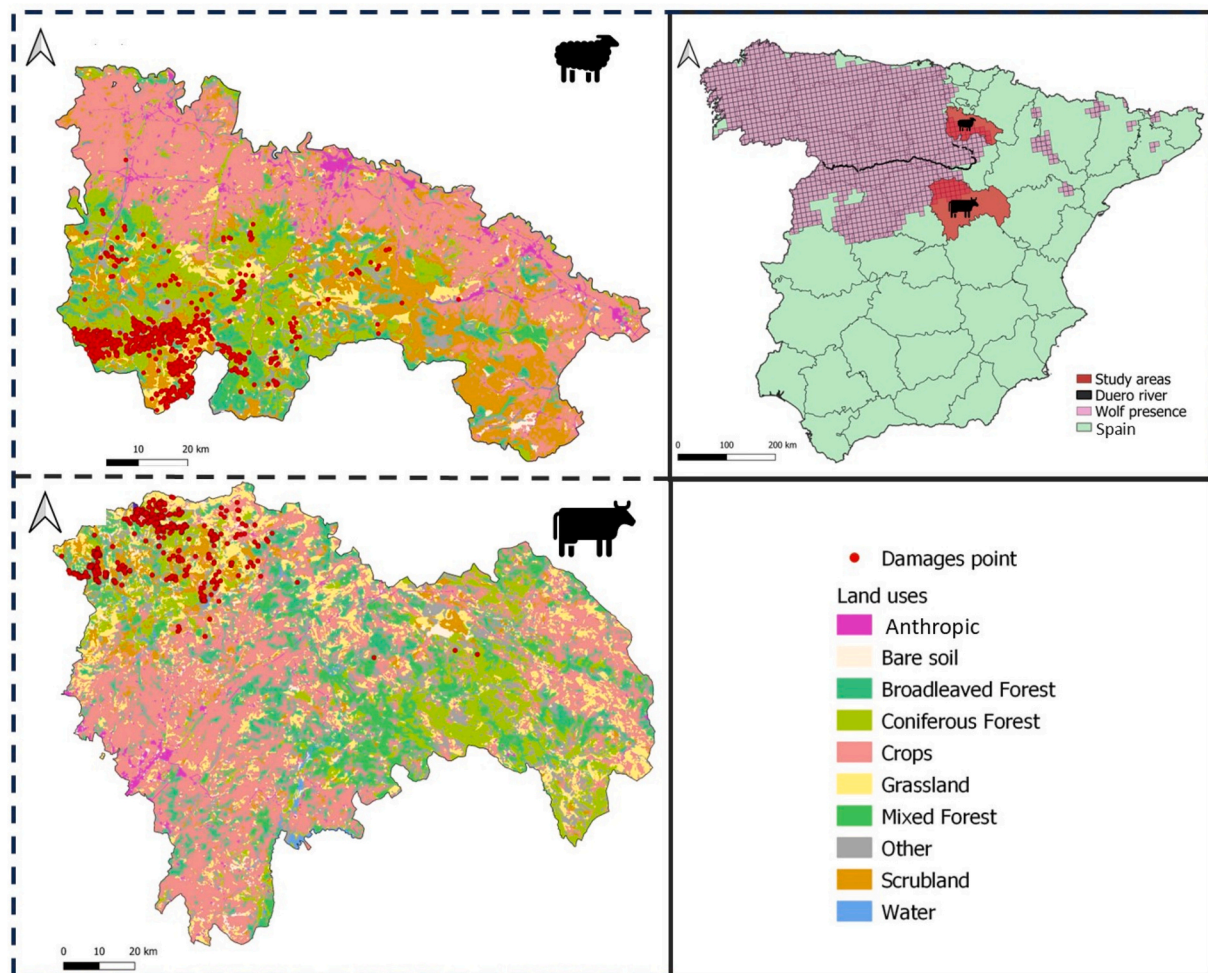


Fig. 1. Study area showing La Rioja, Spain (top left) and Guadalajara, Castilla-La Mancha, Spain (bottom left) in wolf expansion areas, with land use (SIOSE, 2020) and damage locations (red dots) from 2016 to 2024. The upper right map shows the distribution area of the Iberian wolf (purple) in Spain between 2021 and 2024 in a 10×10 km grid (MITERD, 2025). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

scrubland communities such as heaths (*Erica* spp.), common broom and thorny broom (*Genista* spp.), and grasslands that support extensive sheep and cattle grazing (Sánchez-Mata et al., 2017). The dominant management system consists of year-round extensive cattle grazing and sheep husbandry under daily supervision, with animals being enclosed at night. Extensive livestock grazing is widespread, with cattle (7.09 ind./km²) and sheep (11.02 ind./km²) in the Sierra Norte Natural Park (Government of Castilla – La Mancha, 2024). The main wild ungulates present in this area are wild boar and roe deer. No other large predator species are present in the study area. The Iberian wolf recolonized this area in the 2000's, with up to four packs recently recorded, two of them shared with neighboring provinces (MITERD, 2025). In this area, located south of the Duero river, the wolf has not been hunted since 1992 (Fig. 1).

2.2. Data collection

Data on livestock damage were obtained from official wolf damage compensation records collected between 2016 and 2024 by the regional Governments of La Rioja and Castilla - La Mancha. For each damage attributed to wolves, we recorded geographic coordinates (when available), the date of occurrence, and the number and type of livestock killed. For La Rioja, data from 2016 to 2018 were available only at the municipality scale (coordinates were not recorded).

We obtained livestock abundance data (cattle and sheep) for La Rioja for the period from 2016 to 2024 (RIOJASTAT, 2025; Table S1) and for

Guadalajara for the years 2017, 2021 and 2024 (INE, 2020; Table S1). Hunting yield data for wild ungulates (red deer, roe deer and wild boar) from both regions were obtained for the period 2016–2024 (ENETWILD-consortium et al., 2022; Table S1). For each municipality, we calculated annual densities of domestic and wild ungulates species. We also obtained human population data from 2016 to 2024 at the municipality level (INE, 2025; Table S1) and calculated human population density for each municipality. Orographic variables (altitude, slope, aspect and terrain roughness) were derived from a digital elevation model with a spatial resolution of 200 m (IGN, 2025; Table S1). Land-use information was extracted from the Spanish Land Cover and Land Use Information System SIOSE (SIOSE, 2025; Table S1) and reclassified into ten categories: Broadleaved forest, Coniferous forest, Mixed forest, Grassland, Scrubland, Anthropogenic, Crops, Bare soil, Water and Other. The proportion of each category was calculated at the municipality scale. For the local scale (damage locations) models, we additionally calculated the proportion of each land-use class within a 500-m circular buffer surrounding each registered damage location. Euclidean distances were computed to various ecological and anthropogenic features, including paved roads, pathways, water bodies (rivers or reservoirs), grassland, forests, scrublands, urban areas and wolf pack breeding centers identified in 2022. These data also included information on wolf breeding groups in 2022, primarily detected during the pup-rearing period (summer) through territorial marking, howling surveys, field observations, and camera-trap monitoring. Land-use variables were transformed using ArcSin ($\sqrt{\text{Sqrt}(x)}$), and all variables were scaled (mean = 0 and SD

= 1) prior to analysis.

2.3. Statistical analysis

2.3.1. Regional scale

We assessed temporal trends in wolf damage for each livestock system using a Generalized Linear Model (GLM) with a Poisson error distribution and a log-link function. The response variable was the annual number of damage events per region, with year included as a predictor. In addition, we applied the Mann-Kendall trend test, a non-parametric method for detecting monotonic trends in time series, to municipalities with stable wolf presence (≥ 5 years within the nine-year study period), analyzed separately for each livestock system.

2.3.2. Municipality scale

To develop the spatial-temporal model at the municipality scale, we used the number of wolf damage records from 2016 to 2024. We fitted a binomial Generalized Linear Mixed Model (GLMM) with a logit-link function, where the response variable was the presence or absence of wolf damage in each municipality per year; one observation per municipality each year. The municipality was included as a random effect to account for repeated yearly observations. We considered all municipalities that had experienced at least one damage during this period or were located within a 9000-m buffer around the nearest recorded damage. This 9000 m buffer delineated areas of potential wolf presence based on the daily mean movement range of wolves from their activity centers in La Rioja province (Jiménez et al., 2023). All municipalities intersecting this buffer were included in the analysis. The final dataset included 124 municipalities for La Rioja model and 151 municipalities for Guadalajara model. We incorporated as predictors the annual prey density estimated at the municipality scale, including sheep, cattle, red deer, roe deer and wild boar. Human population density was also included as an annual municipality-level variable. Additional fixed predictors included the distance from each municipality to the nearest known wolf breeding site (pack center) identified in 2022, as well as municipal averages of aspect, slope, altitude and terrain roughness. Aspect was derived from the DEM and reclassified into four cardinal categories (North: 315–45°, East: 45–135°, South: 135–225°, and West: 225–315°). Also, the proportional cover of different land-use categories. For the cattle model, univariate models were fitted separately for cattle and sheep density because livestock data for these municipalities were available for only three of the nine years. All continuous predictor variables were scaled before analysis. We assessed multicollinearity among predictors using the Variance Inflation Factor (VIF), retaining only variables with $VIF < 3$ (Zuur et al., 2010). In La Rioja, variables related to altitude, slope and roughness were excluded due to collinearity. In Guadalajara, slope, roughness, coniferous forest cover and crop cover were excluded for the same reason.

2.3.3. Local scale

We developed a species distribution model (SDM) using presence and pseudo-absence data derived from wolf damage incidents locations recorded between 2018 and 2024 (Figs. S1, S2). Specifically, we used the coordinates of these incidents to perform a two-dimensional Kernel Density Estimation (KDE) on a 100×100 m cells, generating a continuous surface representing the spatial density of damage. To identify core areas of wolf activity, we selected grids comprising 80% of the cumulative probability of damage occurrence (Vander Wal and Rodgers, 2012). A binary raster was then generated to retain only the areas with the highest damage densities. We applied a 9000 m buffer around this core area to include further places that could potentially host a damage. To avoid excluding peripheral damage, we additionally identified events falling outside this buffer. Each of these points was buffered by 9000 m, and all the resulting polygons were merged to produce a complementary area. This procedure ensured that both central and isolated damage zones were represented in the final study area. Pseudo-

absence points were generated randomly in equal number to presence points, maintaining a minimum distance of 1000 m from any presence location points to reduce spatial bias. Temporal consistency was ensured by selecting pseudo-absences within the same temporal window as the corresponding presence records. For each presence and pseudo-absence point, we calculated environmental predictors including orographic variables (slope, elevation, aspect, and roughness), distances to wolf breeding centers, and distances to ecological and anthropogenic features. Additionally, land-cover composition within a 500 m buffer was calculated for each point. All variables were scaled, as well as transformed buffer-based ratios. Collinearity among predictors was assessed using the “car” package (Fox and Weisberg, 2018), and variables with high multicollinearity ($VIF > 3$) were removed (Zuur et al., 2010). In La Rioja model, roughness, slope and crop cover were excluded; in Guadalajara model, roughness, distance to roads and population density were removed. To address spatial autocorrelation, we applied spatial thinning with a minimum distance of 500 m between points. The dataset was randomly partitioned into training (70%) and testing (30%) subsets. We fitted GLMM with binomial error distribution and a logit link using the “glmmTMB” package (Brooks et al., 2017), including municipality as a random factor.

2.4. Model selection and validation

Final models were obtained using a forward stepwise selection based on the Akaike Information Criterion (AIC) (Burnham and Anderson, 2004). The model with the lowest AIC was considered the most parsimonious, and models within two AIC units were regarded as having comparable support. Residuals and their distributions were examined using the R package “DHARMa” (Hartig and Hartig, 2017). Spatial independence of residuals was evaluated using Moran's I, and temporal autocorrelation was assessed using an Autoregressive Integrated Moving Average (ARIMA) model and the autocorrelation function (ACF) of the residuals. No significant spatial structure was detected. Model performance was assessed on a 30% holdout test set using ROC curves computed with the “pROC” package (Robin et al., 2011). The optimal classification threshold was selected by maximizing the sum of sensitivity and specificity (Youden's Index). All analyses were performed in R 4.2.1 (R Core Team, 2021).

Lastly, the selected municipality-scale model was fitted using the municipalities included in the analyses. The fitted model was then applied only to the selected municipalities identified as being at risk of wolf attack within each study region to predict the probability of wolf damage based on the corresponding environmental predictor values, thereby generating regional risk maps. Municipalities outside this selected set were not included in the model projection. Finally, to produce a spatial risk map at the local scale, we overlaid a $1 \text{ km} \times 1 \text{ km}$ grid across the two livestock system expansion areas. Predictor variables were computed for every grid cell, and the fitted model was applied to all grid cells, including those located within municipalities classified as at risk of wolf attack as well as those outside the selected municipalities, to predict the probability of damage across the landscape and orographic gradients.

3. Results

3.1. Regional scale

In La Rioja, the number of damages incidents over the past nine years averaged 202.7 ± 100.6 (mean $\pm$ SD) incidents per year, with sheep being the most frequently attacked species (94.5% of events), whereas cattle and horses accounted for 2.3% and 2.9% of incidents, respectively. In contrast, the CLS experienced fewer damages incidents, averaging 52.0 ± 39.7 (mean $\pm$ SD) incidents per year, with cattle being the most targeted species (54.4% of damage) followed by sheep (31.6%), goats (12.5%), and horses (1.5%). At the regional scale, a positive

temporal trend was detected in La Rioja (Estimate = 17.5; $p = 0.05$), whereas no evidence for a trend was observed in the CLS (Estimate = -0.9 ; $p = 0.73$) (Fig. 2).

Over the last three years of study, the cumulative number of municipalities experiencing damage incidents increased more sharply in La Rioja than in Guadalajara (Fig. S1). However, in municipalities with consistently occurring damage, defined as those with at least five years with damage, the number of damages fluctuated across years but remained relatively stable overall in both livestock systems; no significant temporal trend was detected (Fig. 2).

3.2. Municipality scale

At the municipal scale within La Rioja, the selected model for damage presence (AIC = 291.9) (Figs. S3, S4) substantially outperformed the null model (AIC = 446.2). Distance to breeding centers had a strong negative effect (Estimate = -4.55 ± 0.75 , $p < 0.001$), indicating that municipalities closer to breeding centers experienced a higher likelihood of damage occurrence. Year was positively associated with damage presence (Estimate = 2.11 ± 0.33 , $p < 0.001$), supporting an increasing temporal trend. Landcover variables, including scrubland (Estimate = 1.77 ± 0.50 , $p < 0.001$) and coniferous forest (Estimate = 0.96 ± 0.44 , $p = 0.02$), were also positively related to damage presence, as was sheep density (Estimate = 1.41 ± 0.38 , $p < 0.001$) (Table 1). The model explained a large proportion of the variance (conditional $R^2 = 0.92$; marginal $R^2 = 0.77$) and demonstrated strong predictive performance, with an area under the ROC curve (AUC) of 0.991, indicating a very high discriminatory ability between municipalities with and without wolf damage presence. Regarding the spatiotemporal changes in the predicted probability of damage incidents at municipality scale, modeling

Table 1

Parameter estimates, standard error (SE), Z and p values for the selected model for damage incidents presence at the municipality scale in La Rioja and Guadalajara (Spain). Municipality was included as a random effect.

System	Parameter	Estimate $\pm$ SE	Z value	p value
La Rioja	Intercept	-8.02 ± 1.07	-7.43	<0.001
	Distance to breeding centers	-4.55 ± 0.75	-5.99	<0.001
	Year	2.11 ± 0.33	6.40	<0.001
	Scrubland cover	1.77 ± 0.50	3.55	<0.001
	Sheep density	1.41 ± 0.38	3.71	<0.001
	Coniferous forest cover	0.96 ± 0.44	2.18	0.02
Guadalajara	Intercept	-4.90 ± 0.54	-9.08	<0.001
	Distance to breeding centers	-1.72 ± 0.45	-3.83	<0.001
	Altitude	1.69 ± 0.36	4.69	<0.001
	Water	0.74 ± 0.26	2.81	0.004
	Grassland cover	0.41 ± 0.31	1.32	0.18

shows an increase in the number of municipalities experiencing damage incidents presence increased over the nine-year study period. The highest-risk area was concentrated in the southwest of La Rioja. There is a spatial gradient, with the intensity decreasing toward the east (Fig. 3). Over the years, the number of municipalities at risk has risen and the likelihood of damage has increased (Fig. S4).

At the municipal scale within Guadalajara, the selected model (AIC = 419.4) (Figs. S5, S6) outperformed the null model (AIC = 457.2). Distance to wolf breeding centers had a strong negative effect on damage occurrence (Estimate = -1.72 ± 0.45 , $p < 0.001$), indicating that municipalities located closer to breeding centers experienced a higher likelihood of damage occurrence. The proportion of water bodies within

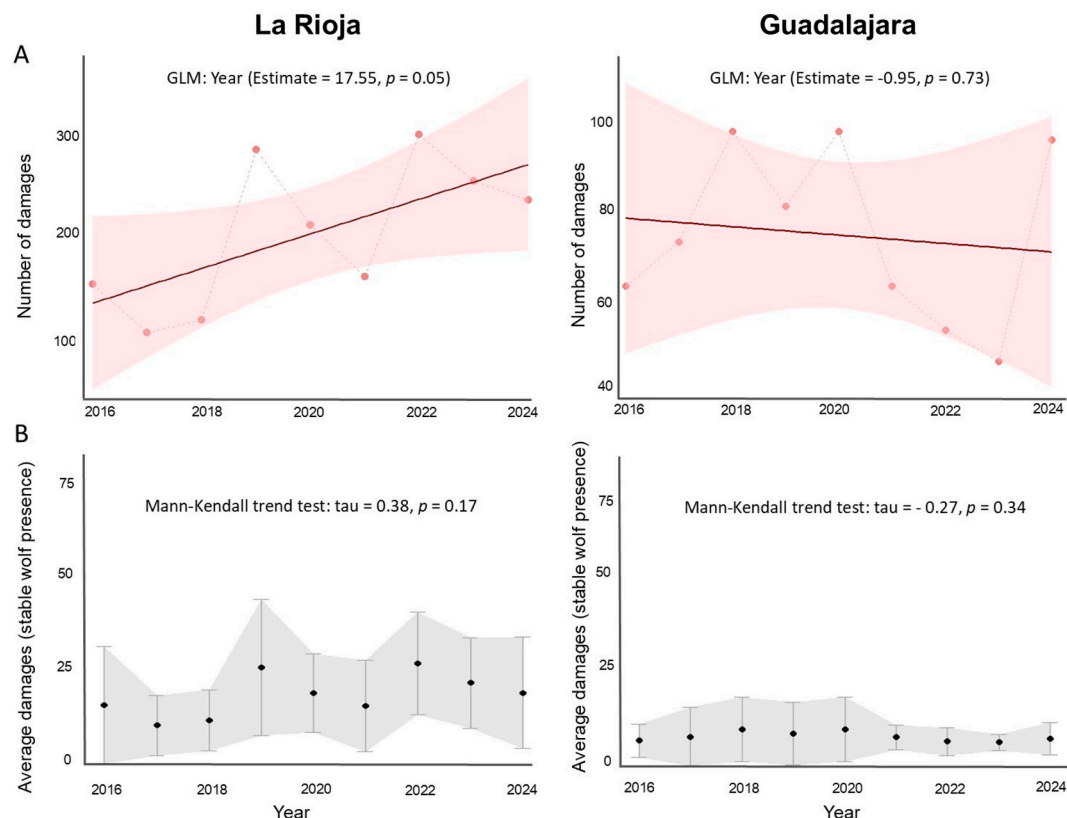


Fig. 2. A. Temporal trend of number of livestock damages per year in La Rioja and Guadalajara (Spain). The red shadowed area shows the 95% confidence interval of the GLM prediction for the number of damages per year. Model estimates and p values are indicated in the inset. B. Annual average on the number of livestock damages (mean $\pm$ SD) in municipalities with stable presence of wolves (at least five of the nine years temporal series) in La Rioja and Guadalajara. Temporal trend was assessed with the Mann-Kendall test, and tau and p values are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

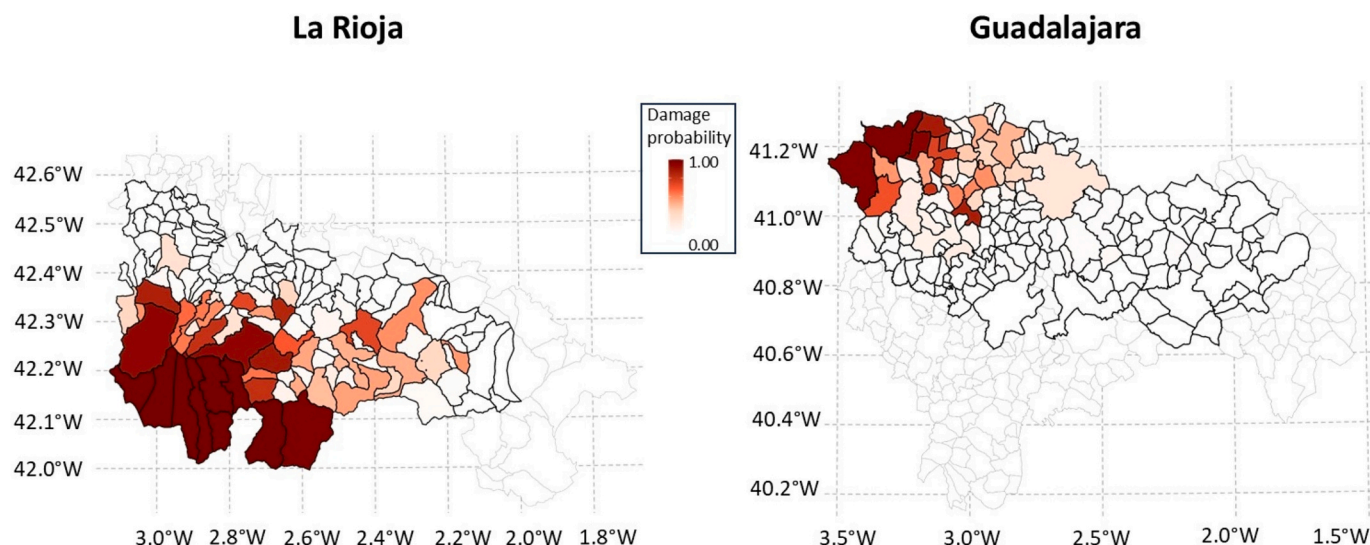


Fig. 3. Predicted probability of wolf damage to livestock per municipality in La Rioja and Guadalajara (Spain) according to the selected model in 2024. The intensity of the red shading represents the damage probability in each municipality as estimated by the selected model. Municipalities outlined in black were included in the model projection. White municipalities within the black outline indicate predicted probabilities close to zero, whereas municipalities outside the black outline were outside the projection domain and therefore were not modeled. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

municipalities (Estimate = 0.74 ± 0.26 , $p = 0.004$) and elevation (Estimate = 1.69 ± 0.36 , $p < 0.001$) were positively associated with damage occurrence (Table 1). The model explained a substantial proportion of the variance (conditional $R^2 = 0.76$; marginal $R^2 = 0.45$) and demonstrated strong predictive performance, with an AUC of 0.96, indicating a very high ability to discriminate between municipalities with and without damage presence. They are mainly concentrated in the north-west of the area. The rest of the territory shows low values or values close to zero (Fig. 3).

Using a univariate model of damage probability for Guadalajara, at the municipal scale for the three years in which livestock density data were available, we found that higher cattle density was significantly associated with an increased probability of damage presence (Estimate = 1.53 ± 0.53 ; $p = 0.003$). In contrast, sheep density showed no significant effect on damage probability (Estimate = -0.77 ± 0.67 ; $p = 0.24$), which matches original expectations

3.3. Local scale

In La Rioja, the selected model (AIC = 557.1) (Figs. S7, S8) at the fine scale outperformed the null model (AIC = 768.9). Shorter distances to breeding centers (Estimate = -2.32 ± 0.37 , $p < 0.001$), grasslands (Estimate = -0.64 ± 0.18 , $p < 0.001$), and roads (Estimate = -0.54 ± 0.12 , $p < 0.001$) were all associated with a higher likelihood of damage incidents, suggesting that damage tends to occur closer to these features. Conversely, increasing distance from forested areas was unexpectedly associated with a higher probability of damage occurrence (Estimate = 0.41 ± 0.18 , $p = 0.026$), indicating that more damage occurs farther from forest edges. Water bodies also had a positive association (Estimate = 0.22 ± 0.12 , $p = 0.006$), whereas anthropogenic land cover was negatively associated to damages (Estimate = -0.83 ± 0.22 , $p < 0.001$). Additionally, the proportion of grassland within the surrounding area was positively associated with damage incidents (Estimate = 0.97 ± 0.20 , $p < 0.001$). Together, these findings indicate that both proximity to key landscape features and land cover composition strongly explain the spatial distribution of damage incidents (Table 2).

The model explained a substantial proportion of variance (Conditional $R^2 = 0.79$; Marginal $R^2 = 0.58$) and exhibited strong predictive performance, with an AUC of 0.93, indicating high discriminatory ability between damage and non-damage locations. At the optimal

Table 2

Parameter estimates, standard errors (ES), Z and p values for the selected model for damage incidents presence at local scale in La Rioja and Guadalajara (Spain). Municipality was included as a random effect.

System	Parameter	Estimate $\pm$ SE	Z value	p value
La Rioja	Intercept	-2.70 ± 0.39	-6.91	<0.001
	Distance to breeding centers	-2.32 ± 0.37	-6.20	<0.001
	Distance to grassland	-0.64 ± 0.18	-3.47	<0.001
	Distance to road	-0.54 ± 0.12	-4.30	<0.001
	Distance to forest	0.41 ± 0.18	-3.47	0.026
	Water cover	0.22 ± 0.12	-4.30	0.006
	Anthropogenic cover	-0.83 ± 0.22	-3.71	<0.001
	Grasslands cover	0.97 ± 0.20	4.68	<0.001
	Intercept	-1.99 ± 0.39	-4.98	<0.001
	Distance to breeding centers	-1.33 ± 0.36	-3.63	<0.001
Guadalajara	Distance to urban	-1.10 ± 0.22	-4.84	<0.001
	Distance to grassland	-0.38 ± 0.21	-1.79	0.07
	Slope	-0.88 ± 0.21	-4.06	<0.001
	Altitude	0.98 ± 0.28	3.51	<0.001
	Anthropogenic cover	-0.36 ± 0.17	-4.98	0.033

threshold defined by the Youden index, the model achieved a sensitivity of 90.5% and a specificity of 88.1%, yielding a maximum sum score (MSSS) of 1.78, which reflects a strong balance between true-positive and true-negative rates.

Fifty percent of the grid cells in the 1 km $\times$ 1 km model had predicted probabilities below 0.01, indicating that most of the area faces very low risk (Fig. 4). The overall mean probability was 0.15, reflecting a subset of cells with higher risk. Only 25% of cells exceeded this threshold, while the maximum predicted probability reached 0.99, highlighting the existence of highly localized areas of extreme risk. The highest-risk area was concentrated in the southwest of La Rioja, although substantial variability in damage probability was also evident in projections based on parameters selected for the local scale model (Fig. S9).

In Guadalajara, the selected local scale model (AIC = 400.4) (Figs. S10, S11) outperformed the null model (AIC = 469.79). Shorter distances to breeding centers (Estimate = -1.33 ± 0.36 , $p < 0.001$), grasslands (Estimate = -0.38 ± 0.21 , $p = 0.07$), and urban areas (Estimate = -1.10 ± 0.22 , $p < 0.001$) were all associated with a higher

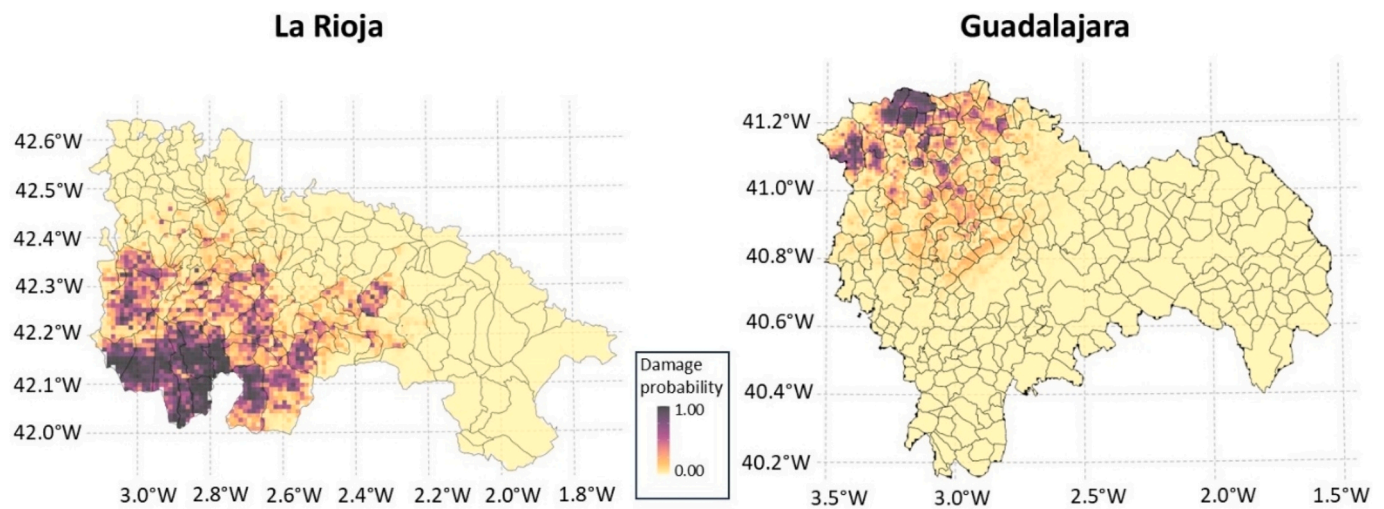


Fig. 4. Probability of damage in La Rioja and Guadalajara (Spain) at a 1×1 km resolution. Grey lines show the municipality administrative boundaries. The intensity of shading represents the damage probability predicted according to the selected model at the local scale. The model was projected across the entire grid. Yellow areas indicate predicted probabilities close to zero rather than unprojected areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

likelihood of damage, indicating that damage incidents tend to occur closer to these features. Slope also was negatively associated (Estimate = -0.88 ± 0.21 , $p < 0.001$). In contrast, elevation showed a positive association with damage probability (Estimate = 0.98 ± 0.28 , $p < 0.001$), while anthropogenic land cover surrounding each location was negatively associated with damage probability (Estimate = -0.36 ± 0.17 , $p = 0.033$) (Table 2).

Overall, these results highlight that both proximity to key landscape features and land-cover composition strongly influence the spatial distribution of damage incidents in Guadalajara. The selected model explained a substantial proportion of variance (Conditional $R^2 = 0.69$; Marginal $R^2 = 0.41$) and demonstrated excellent predictive performance (AUC = 0.94), indicating a high ability to discriminate between damage and non-damage locations. At the optimal threshold defined by the Youden index, the model achieved a sensitivity of 95.2% and a specificity of 74.5%, yielding a maximum sum score (MSSS) of 1.69, reflecting a strong balance between true-positive and true-negative rates.

Predicted probabilities from the $1 \text{ km} \times 1 \text{ km}$ model were generally low, with 50% of grid cells falling below 0.01 (Fig. 4). The mean probability was 0.08, reflecting a subset of cells with higher risk, while only 25% of cells exceeded 0.06. The maximum predicted probability reached 0.98, indicating the presence of highly localized areas of very high risk, with notable variability across region. The highest predicted risk was located in the northwest of the province, according to projections based on parameters from the local scale Guadalajara model (Fig. S12). However, substantial variation in damage probability was observed within individual municipalities.

4. Discussion

Our study provides a multiscale assessment of the factors associated with wolf damage to livestock in two regions with contrasting ecological and livestock management characteristics. At the regional scale, we identified differences in the temporal dynamics of wolf damage between the two study areas, with evidence of an increasing trend in La Rioja but not in Guadalajara. At the municipal scale, broad-scale models identified predictors related to wolf distribution and resource used by them, whereas local-scale models highlighted landscape features associated with livestock location. Together, these findings show that the drivers of wolf damage vary across spatial scales and provide information to support targeted management interventions in expanding wolf

populations.

4.1. Regional scale

We found that the spatial extent of damage incidents expands in parallel with the geographical expansion of the wolf population, as has been reported in other regions (Kiffner et al., 2022). However, at the municipal scale, and considering only municipalities with stable wolf presence, no consistent trends in damage intensity were detected, suggesting that spatial expansion may not necessarily translate into increased local intensity (Fig. 2). This pattern suggests an initial phase of rising damage associated with range expansion, albeit with considerable year-to-year fluctuations, followed by a stabilization phase once wolves have been present in a municipality for five years or more. These patterns match those previously described in the literature (Fowler et al., 2019). We argue that slight interannual variation are possibly reflecting adaptive changes in livestock management practices or wolf population changes (Durá-Alemañ et al., 2024).

Although both study areas are classified as wolf expansion zones, they exhibit markedly different regional-scale trends. In La Rioja, the number of municipalities experiencing damage increased regardless of management regime, both during the period without strict protection (until September 2021), when at least 13 wolves were legally culled in the last fifteen years between 2005 and 2021 (Government of La Rioja, Decreto 12/2023), and during the subsequent fully protected period (September 2021–March 2025), when no wolves were legally killed (Kutal et al., 2024; Quevedo et al., 2019). In contrast, in Guadalajara, located south of the Duero River (Fig. 1), the number of damage events fluctuated considerably but showed no clear temporal trend, despite continuous legal protection throughout the study period. These results highlight that conflict mitigation efforts should be strategically prioritized in newly colonized areas, where the risk of livestock depredation is highest, rather than focusing primarily on long-established wolf territories where damage levels tend to stabilize. This temporal pattern suggests a critical window for early intervention, where proactive measures can reduce the escalation of conflict and facilitate long-term coexistence. This pattern appears to be particularly relevant in systems dominated by free-ranging sheep, whereas its generality may be more limited in systems where cattle predominate, as reported in previous studies (Díaz-Vaquero, 2024).

4.2. Municipality scale

Our analysis of municipal-level damage probability across both scenarios revealed a consistent effect of distance to pack breeding centers, highlighting the central role of wolf pack proximity in shaping depredation risk at the municipality scale (Gula, 2008; Meier et al., 2024). This finding supports the notion that areas closer to established breeding sites experience higher wolf pressure, likely due to increased territorial use and hunting activity (Pimenta et al., 2018). In La Rioja, year emerged as an important predictor of temporal variation, reflecting a gradual population expansion geographically over time, as described in a similar study in Germany's wolf expanding population (Kiffner et al., 2022). The inclusion of sheep density in the final model indicates that the probability of wolf attacks is associated with the local availability of the primary livestock species in the study area. Rather than simply reflecting prey presence, this relationship suggests that variation in sheep density may influence the likelihood of wolf-livestock interactions by altering encounter rates and foraging opportunities. Similar patterns have been reported in other systems, where livestock density shapes predation risk and the spatial distribution of conflicts (Behdarvand et al., 2014; Kuiper et al., 2024). This effect is further supported by the comparison between livestock systems, with sheep systems showing higher levels of conflict than cattle systems (Del Río et al., 2026; Mayer et al., 2025). Additionally, the inclusion of scrubland and coniferous forest in the selected model underscores the importance of landscape features as a mosaic of forest, scrubland and open areas that provide cover, facilitate wolf movement, suitable for breeding, shelter and hunting. Similar landscape configurations have been linked to predator space use in other European systems, such as the forest-dominated landscapes of Poland and Finland, where large carnivores including wolves, bears, and lynx exploit heterogeneous habitats to move, hunt, and reproduce (Bojarska et al., 2021; Kaartinen et al., 2009). In the context of our study area, conservation strategies at the municipal scale should prioritize areas near wolf breeding sites with high livestock densities, where the spatial overlap between wolves and domestic prey is greatest.

In contrast, in Guadalajara, damage probability was primarily associated with orographic and environmental variables, such as elevation and water cover (Kaartinen et al., 2009; Meier et al., 2024). These factors likely influence livestock grazing patterns as well as wolf habitat suitability, thereby increasing spatial overlap between predators and domestic prey (Treves et al., 2004). Although grassland cover exhibited a positive relationship with damage probability, the effect was not statistically significant, suggesting that pasture availability alone does not explain damage patterns at that scale. Notably, wild prey variables were not retained in the final models for either area, despite their documented importance in other studies (Figueiredo et al., 2020; Hanley et al., 2018). This absence is likely methodological rather than ecological, as hunting yield data may not accurately reflect true wild prey densities at the spatial resolution considered and may contribute to the temporal fluctuations observed in damage data. Previous research has shown that the reliability of such data decreases at fine scales, such as the municipal level (Ruiz-Rodríguez et al., 2022). Domestic livestock density remained a significant predictor, with sheep density in the sheep area and cattle density in the cattle area, reflecting the relationship between domestic prey abundance and species-specific predation probability (Mayer et al., 2022). A similar pattern has been reported for snow leopards (*Panthera uncia*), where predation rates were higher in areas with greater predator abundance and livestock density, even when wild prey densities were comparable across sites, suggesting that livestock availability can sometimes drive predation rates (Khanal et al., 2020). However, evidence across the wolf's global distribution indicates that the species generally prefers wild over domestic prey, particularly in Europe (Newsome et al., 2016). Therefore, livestock density alone may not fully explain predation risk, as the influence of domestic prey availability is likely to depend on the abundance of wild prey. Future studies should explicitly evaluate potential interactions between livestock and wild

prey availability to determine whether livestock density increases attack probability primarily in areas where wild prey are scarce. Unfortunately, we could not include cattle density systematically in the final model for the cattle area due to incomplete temporal data in the Castilla-La Mancha dataset. Consequently, its influence may be underestimated, and future studies incorporating more comprehensive livestock data would help clarify its role in determining predation risk. Overall, systematic collection and improved availability of reliable data on both livestock and wild prey by authorities would substantially enhance risk assessment and support the development of effective management strategies.

4.3. Local scale

The results from our analyses suggest that predation risk is higher where livestock grazing areas and non-urban landscapes overlap (Davidson et al., 2012; Zabihi-Seissan et al., 2022). Wolves tend to hunt livestock where it is most accessible, in grassland, as described in other species (Kuiper et al., 2024). Furthermore, the proportion of anthropogenic land cover surrounding attack sites negatively influenced the probability of damage, a pattern also reported in previous studies in Scandinavia (Zimmermann et al., 2014). In addition, wolves may associate communal grasslands with areas where livestock are consistently present and thus preferentially hunt domestic prey in these locations, where prey capture is typically easier for livestock than for wild prey (Huggard, 1993; König et al., 2023). This strategy is also documented for other species such as African wild dog in Zimbabwe hunting cattle and the lion in Zimbabwe (Kuiper et al., 2024). Wolves may associate communal grasslands with areas where livestock are consistently present, potentially increasing the probability of attacks on domestic livestock. However, as we did not quantify predation on wild prey, we cannot infer whether wolves preferentially selected domestic prey over wild prey in these areas (Huggard, 1993; König et al., 2023). In La Rioja, damage risk was further shaped by distance to water availability, and proximity to grasslands, reflecting the spatial distribution of sheep flocks and their reliance on accessible communal grazing land, as described in another study (Chavez and Gese, 2006). Whereas at the municipal scale, forests appear to play a key role in facilitating wolf movement and hunting behaviour (Bojarska et al., 2021; Treves et al., 2011); at the local scale, most attacks occurred in grasslands situated farther from forested areas, suggesting likely reflecting the location of livestock. The risk of damage was also related to proximity to roads, while wolves generally avoid busy roads, they frequently use low-traffic linear infrastructures to move and patrol their territories as described before (Bojarska et al., 2020), which can coincide with areas where livestock graze, as observed in our sheep study area. By contrast, in Guadalajara, the proximity to urban areas emerged as a significant factor, likely reflecting the spatial configuration of cattle holdings in this region, where municipalities consist of very small urban nuclei and livestock are typically kept close to these settlements. Similar patterns have been documented elsewhere, where livestock maintained near human settlements experienced higher probabilities of predation by large carnivores, particularly in human-dominated landscapes where the interface between livestock and predators is intensified (Linnell et al., 2001; Carter et al., 2012). For example, domestic livestock predation increased near villages in a tiger (*Panthera tigris*) livestock system (Mohan et al., 2024). In this context, the lower-risk areas observed in this area, compared with La Rioja, may reflect differences in livestock composition, husbandry practices, and livestock protection measures between the two systems, although these factors were not explicitly evaluated in this study. Future studies incorporating detailed information on these variables would help clarify their contribution to the observed regional differences in wolf depredation risk. Orographic variables, such as slope and altitude, were also influential at this higher resolution in Guadalajara, corresponding to extensive grazing systems and to habitat features shaped by both wolf ecology and cattle management practices. These

patterns likely reflect not only habitat preferences of wolves, but also the spatial distribution of cattle, which is constrained by local husbandry practices and the proximity to human settlements. The rugged landscape in the study area may hinder the implementation of preventive measures by livestock farmers while simultaneously increasing livestock vulnerability to wolf predation (Rostro-García et al., 2016; Torretta et al., 2018). At this local spatial scale, our results emphasize that effective conflict mitigation depends on site-specific interventions that account for livestock grazing patterns and landscape configuration. This reinforces the need for designing management actions based on specific local contexts, such as the strategic placement of deterrents or increased supervision in high-risk grazing areas.

Finally, our findings should be interpreted in light of some limitations. Although our analyses included all confirmed wolf damage events recorded during the study period, the current wolf populations in the two study areas comprise only nine known packs (five in La Rioja and four in Guadalajara). Consequently, multiple damage incidents are likely to be associated with the same packs, meaning that observations are not fully independent. While this reflects the current stage of wolf recolonization in these expansion areas and does not affect the identification of spatial patterns of damage risk, it may limit the extent to which our results can be generalized to other wolf populations or regions with different pack densities. Future studies including a larger number of packs across broader geographic areas would help evaluate the generality of the patterns identified here.

4.4. Applying a multiscale approach for management of wolf predation risk

Although several studies have examined factors influencing predator damage intensity, the risk of wolf predation across multiple spatial scales in expansion areas remains largely unexplored (Bautista et al., 2021; Rostro-García et al., 2016). Furthermore, our findings emphasize the importance of a multiscale perspective, indicating that differences between livestock pastoral systems arise from the factors shaping depredation risk, even though wolf populations are expanding similarly across regions. By explicitly linking ecological processes with management-relevant spatial patterns, this multiscale approach provides a practical framework for evidence-based conservation planning in human-dominated landscapes. Identifying high-risk areas is essential for optimizing the cost-effectiveness of large-scale preventive programs and for developing further strategies to reduce livestock predation (Miller, 2015; Wilkinson et al., 2020).

We recommend that management interventions move beyond generic compensation schemes and adopt adaptive, integrated strategies that combine financial support with proactive prevention and stakeholder engagement, informed by spatial risk assessment like ours. For instance, compensation schemes could be structured to prioritize municipalities with persistent or high-risk damage (Widman and Elofsson, 2018), while simultaneously incentivizing preventive measures, technical assistance, and adaptive management. An example from the expanding wolf population in Northern Italy showed that rewarding farmers with subsidies conditional on adopting preventive husbandry practices can help in promoting preventive and proactive attitudes and ultimately coexistence (Dalmasso et al., 2012). Overall, integrating a multiscale perspective into management enables interventions that are both ecologically effective and socially equitable, thereby supporting long-term coexistence between large carnivore conservation and human livelihoods.

CRediT authorship contribution statement

Lucía Del Río: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carlos Bautista:** Writing – review & editing, Writing – original draft,

Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Rafael Mateo:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization. **Pablo Ferreras:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jorge Tobajas:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization.

Financial interests

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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Declaration of competing interest

The authors declare no conflicts of interest.

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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.2026.112080>.

Data availability

The data set generated and analyzed during the current study is not publicly available as it contains potential sensitive information about den site and rendezvous locations of wolves. Data can be made available from the corresponding author upon reasonable request.

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