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The Landscape of Fear and Wild Boar (*Sus scrofa*) Spatial Use in a Peri-Urban Area from West-Central Spain

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Abstract

The spatial distribution of predation risk creates a landscape of fear that shapes animal behavior. Humans are typically perceived as predators, leading wildlife to adjust their space use accordingly. However, adaptable species like wild boar (*Sus scrofa*) can thrive in human-dominated landscapes such as cities, where they may generate conflicts. In this study, we investigated how the landscape of fear influences wild boar presence in a Mediterranean peri-urban environment in Cáceres (Spain). We quantified wild boar presence (WBp) using 112 footprint traps across three seasons and characterized fear-related variables through vegetation cover and an urbanization gradient derived from distances to the city center and urban edge. Generalized linear mixed models showed that WBp was consistently higher in Cover areas than in Open areas, while the urbanization gradient had no significant effect. Spatial modeling further revealed more localized aggregation in Cover areas. These results indicate that wild boar preferentially use vegetated refuge zones, although seasonal variation suggests that resource distribution may also shape their movements. Understanding how wild boar respond to fine-scale landscape features has key implications for managing their populations and mitigating human–wildlife conflicts in Mediterranean peri-urban contexts.

Keywords: footprint traps; landscapes of fear; predation risk; spatial ecology

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1. Introduction

The activity and success of predators, as well as the accessibility of prey populations, can vary across space [1,2]. This variation creates a landscape of fear in which animals perceive spatial variation in predation risk [3,4]. Predation has a key effect on individual fitness, so the landscape of fear has important consequences for the evolution of populations [4–6]. The presence of areas in the landscape with high or low predation risk can modulate individual behavior, minimizing the probability of being caught by predators. Animals may change their vigilance levels [7,8], reallocate their activity patterns [9,10], and vary their habitat selection [11,12] depending on the distribution of predation risk. Regarding habitat selection, safer habitats might be prioritized at the expense of foraging opportunities [3,4,13].

Humans are typically perceived by animals as predators [14,15], so human presence can induce antipredator strategies such as increased vigilance, early flight initiation, or avoidance [16,17]. Accordingly, human disturbance has negative consequences for the

biology of wild populations [18,19]. These consequences and the strategies triggered by humans might be especially pronounced in large mammals with a history of high levels of exploitation [20]. In such cases, spatial variation in hunting regimes creates pronounced landscapes of fear that influence the distribution of game populations [21,22]. Furthermore, the ongoing process of urbanization is associated with a general decline in biodiversity due to increased exposure to disturbances and stressors, in addition to habitat loss, collisions with buildings and vehicles, and predation by urban dogs and cats [23–25].

Contrary to the general negative effects of urbanization on biodiversity, some species have increased their presence in cities in recent decades [26,27]. These are highly adaptable species that can modify their behavior and exploit human-modified environments by using anthropogenic food resources, favorable climatic conditions, and shelter or nesting sites [28–32]. Despite their relatively high habituation and tolerance to human disturbances, the ecology of wild populations inhabiting urban and peri-urban areas also depends on the landscape of fear, and they can exhibit behavioral variability [33,34]. Thus, animal populations living in human-dominated environments can respond to the extent of human disturbance by varying their spatial behavior and primarily using habitat patches within and around cities that serve as refuges [35,36].

The wild boar (*Sus scrofa*) species is one of the most widely distributed and biomass-dominant wild mammals globally [37]. It occupies a broad range of habitats, including forests, wetlands, agricultural lands, grasslands, and pastures [38–41]. In addition, wild boar have a highly heterogeneous diet, opportunistically feeding on a wide variety of plant and animal matter, which can vary substantially depending on geographic location or season [38,42,43]. Its native range includes Eurasia and North Africa, but it has also been introduced to the Americas and Australia, making it both a key species for ecological balance and a significant source of conflict in areas where it interacts with human activities [44–46].

As an "ecosystem engineer," wild boar exert significant effects on ecosystem structure and function. Among its most notable impacts are the alteration of forest regeneration [47], modification of soil processes [48], and effects on animal populations that form part of its diet [49,50]. However, at high densities in human-modified landscapes, wild boar become a major source of human–wildlife conflict. These conflicts include crop damage [51,52], traffic accidents [53], and the transmission of zoonotic diseases with public health implications [54–56].

In recent decades, wild boar populations have shown significant expansion both within their native ranges and in introduced areas. This process has been attributed to a combination of factors, including high reproductive capacity, the absence of natural predators in many areas, and hunting pressure insufficient to control their numbers [57,58]. A particularly notable phenomenon is the expansion of wild boar into urban and peri-urban areas, where they encounter easily accessible food sources and landscapes with reduced hunting pressure [59,60].

This expansion into urban and peri-urban environments poses unique challenges, as interactions with humans become more frequent and impacts more visible. Additionally, seasonality plays an important role in their behavior: during periods of resource scarcity in natural habitats, cities can become especially attractive, increasing their presence and the associated risks [61–64]. In these areas, both tolerance of human activity and stable food availability increase the likelihood of conflict [33,65].

Here, we investigated the factors shaping the presence of wild boar in the peri-urban landscape surrounding the city of Cáceres (Spain). Specifically, we evaluated how elements of the landscape of fear—namely the urbanization gradient and the availability of refuge areas—affect habitat use by wild boar. Within the landscape of fear framework, we expected wild boar to use areas with vegetation cover more frequently, as it provides refuge from

human disturbance, and to show reduced presence in locations closer to the urban area, where perceived risk might be higher. Studying how the landscape of fear influences the movements of wild boar in urban and peri-urban areas can provide valuable insights into the ecology of this highly adaptable species [33,60], particularly in regions where human–wildlife conflicts are especially intense. Understanding these behavioral responses to perceived risk can help identify the factors driving their use of urban habitats, inform management strategies to mitigate conflict, and improve coexistence between humans and wildlife in an increasingly anthropogenic landscape.

2. Materials and Methods

2.1. Study Area

The study was conducted in Cáceres, in the Extremadura region (southwestern Spain; 39°28′23″ N, 6°22′16″ W), which has approximately 100,000 inhabitants. Beyond the urban area (Figure 1), houses and other anthropogenic structures are scattered throughout the peri-urban zone. The city is located in an area of gentle hills (<700 m above sea level), surrounded by extensive open grasslands and dryland farming areas. The hills are covered by seral stages of Mediterranean forest, with trees such as *Quercus suber*, *Q. ilex*, and *Olea europaea*, and shrubs such as *Pistacia lentiscus*, *Q. coccifera*, and *Cistus* spp. dominating the landscape and forming areas of dense vegetation. The total area of the study site was approximately 44 km^2 (Figure 1).

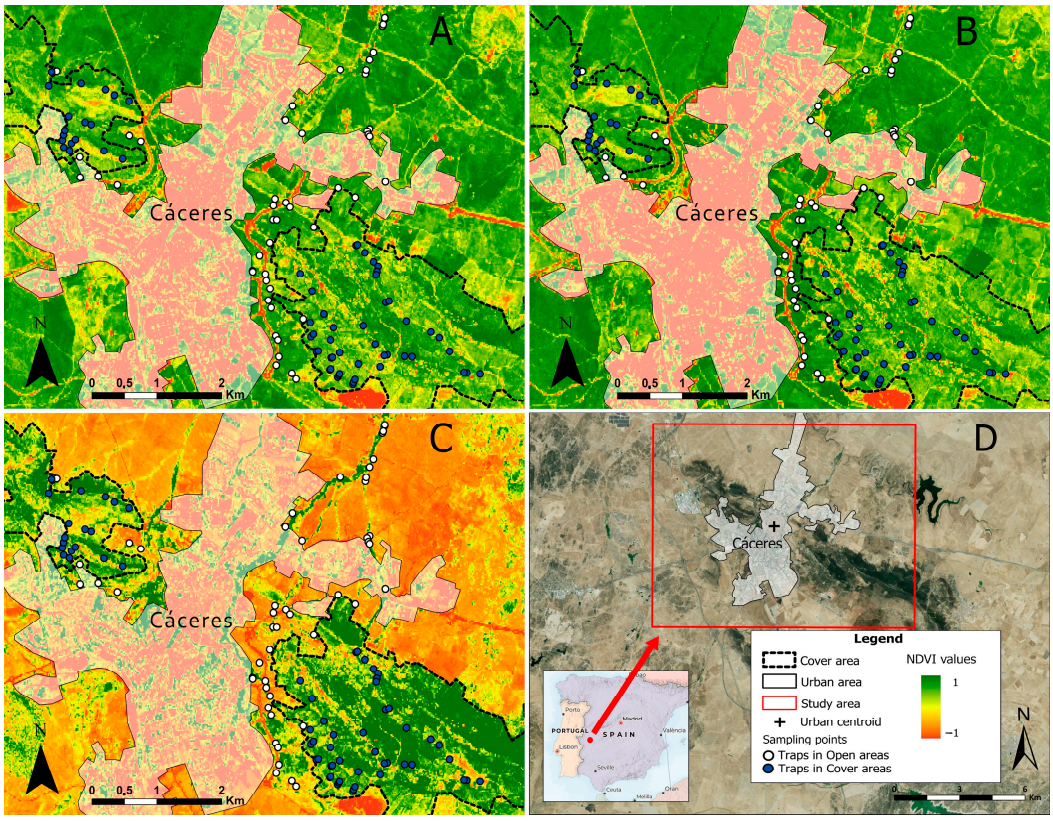


Figure 1. Study area in the Extremadura region (southwestern Spain). The figure shows the urban area of Cáceres, the location of footprint traps (blue: traps in Cover areas; white: traps in Open areas), and the distribution of the Cover areas (seral Mediterranean forests). These features are overlaid on maps with NDVI (Normalized Difference Vegetation Index) values representing vegetation indexes during the acorn abundance period (AAP; (**A**)), the food abundance period (FAP; (**B**)), and the food shortage period (FSP; (**C**)). The centroid of the urban areas is also shown in (Figure 1**D**).

This area experiences a Mediterranean climate characterized by dry, hot summers and mild winters, with precipitation typically occurring from autumn through spring [66]. Resource availability for wild boar varies throughout the year, and three distinct seasons can be used to represent this annual variation [67]. Maximum resource availability occurs in spring, when vegetation productivity peaks and most animals reproduce, allowing wild boar to easily obtain plant food as well as prey on invertebrates or bird species [49,58]. During summer, food availability declines abruptly as most grassland plant species die and the reproductive season ends, although woody species and riparian vegetation remain green throughout the season. In autumn, many tree and shrub species, particularly oaks (*Quercus* spp.), produce acorns, which constitute an important food resource for wild boar. We referred to these three seasons as the Food Abundance Period (FAP), Food Shortage Period (FSP), and Acorn Abundance Period (AAP), respectively. Resource distribution is broadly dispersed during the AAP and FAB (Figure 1A,B) but spatially aggregated during the FSP (Figure 1C). In addition to the information shown in Figure 1A, it is worth highlighting the particularly high resource availability in seral Mediterranean forest during the AAP, driven by acorn production. These changes in the distribution of resource availability may affect wild boar distribution throughout the year.

In southwestern Spain, wild boar is an important game species hunted using various methods, with the Spanish *montería* being one of the most significant in terms of the number of individuals culled. In this method, hunting organizers use packs of dogs to drive animals toward hunters' positions. Although hunting is prohibited in the peri-urban area of Cáceres, *monterías* and other hunting activities take place in the hills surrounding the city. The hunting season typically runs from October to February.

The presence of wild boar in the peri-urban and urban areas of Cáceres has been consistent over the past decade (https://www.hoy.es/caceres/jabalies-destrozan-parques-20170911002349-ntvo.html, in Spanish, accessed 1 July 2025). Here, the animals have been observed searching for food in trash bins and orchards around the city. Their presence has raised public concern, prompting the implementation of municipal programs to remove them from the urban and peri-urban areas.

2.2. Wild Boar Presence

We assessed wild boar presence in the peri-urban area of Cáceres using footprint traps (see, for example, Scottish Wildlife Trust: https://scottishwildlifetrust.org.uk/resource/make-an-animal-footprint-trap/, accessed 15 October 2023). Each footprint trap consisted of a 30 cm × 30 cm surface covered with a 0.5–1 cm layer of fine-grained sand, placed along animal trails. After placement, the sand was smoothed with a ruler and lightly moistened using a water vaporizer. No food or other attractants were used to lure wild boars.

Before installing the traps, we conducted surveys in the peri-urban area to identify and map animal trails likely used by wild boars. Trails used by humans or dogs were excluded, and traps were only installed in areas without pigs, sheep, or goats. Animal trails showing signs such as mud stains or wild boar hair on fences were consistently selected as trap locations. In total, we selected 112 sites for footprint traps (Figure 1).

We conducted three monitoring campaigns to record wild boar presence (WBp) in the peri-urban area as follows: November 2023 (acorn abundance period, AAP), March 2024 (food abundance period, FAP), and July 2024 (food shortage period, FSP). During each campaign, all 112 footprint traps were set on Monday (13 November 2023, 18 March 2024, and 8 July 2024) and checked over the following four days (Tuesday to Friday). Each day, we recorded whether each trap contained at least one hoof print. When a trap showed footprints, the sand was re-smoothed and moistened; if no footprints were present, only moistening was performed. For each trap in each campaign, WBp was recorded as the

number of days with hoof prints, ranging from WBp = 0 (no presence) to WBp = 4 (presence on all survey days).

2.3. Landscape of Fear Variables

The landscape of fear was characterized using the following variables: distance to the urban core, distance to the urban edge, and habitat type. The distance to the urban core was obtained by measuring the distance (in meters) between each footprint trap and the centroid of the polygon representing the urban area of Cáceres. This centroid coincided with the urban center of the city, where human activity and traffic are consistently high throughout the day. The distance to the urban edge was quantified as the minimum distance (in meters) between each footprint trap and the edge of the urban area. Both distances were highly correlated (see Results). To avoid collinearity in subsequent analyses, we summarized both distances into a single urbanization gradient using Principal Component Analysis (PCA).

Habitat type was included in our study as a factor related to the landscape of fear, since previous studies have shown that wild boars use areas of dense vegetation as refuges in both natural and peri-urban environments [33,67–74]. We distinguished two types of habitats: areas with seral Mediterranean forests (Cover areas) and open areas lacking dense vegetation that could provide cover for wild boars (Open areas).

For each footprint trap, we recorded whether it was located in Cover or Open areas. Traps situated on the boundary between Cover and Open areas (N = 5) were classified as Open areas. The number of footprint traps was 63 in Cover areas and 49 in Open areas (Figure 1).

2.4. Spatial and Statistical Analyses

Basic spatial analyses were conducted using ArcGIS Pro 3.2.0, which included mapping the locations of footprint traps, digitizing the polygon representing the urban area, and identifying the centroid of this polygon. ArcGIS was also used to digitalize polygons representing the distribution of seral Mediterranean forests (Figure 1). The distribution of forested area was based on data from the Land Occupation Information System of Spain (SIOSE 2016; https://centrodedescargas.cnig.es/CentroDescargas/siose-ar; accessed 15 January 2025). This information was used to classify traps as being in either Cover or Open areas.

To contextualize resource availability across seasons, we processed Sentinel-2 satellite images in ArcGIS to obtain the Normalized Difference Vegetation Index (NDVI), which indicates the amount and vigor of green vegetation. Images were obtained from the Sentinel-Hub EO Browser (https://apps.sentinel-hub.com/eo-browser/; accessed 15 January 2025). Finally, ArcGIS was also used to generate a kernel density map of WBp across the three seasons, representing the expected WBp per 30 m $\times$ 30 m cell.

Spatial aggregation of footprint traps was analyzed with the spatstat package [75] in R version 4.4.0 [76]. We quantified spatial aggregation using Ripley's K statistic over a range of spatial scales (r) and assessed the significance of distribution patterns via 999 random simulations under the assumption of complete spatial randomness (CSR). Observed K values within the CSR envelope indicate randomness; values above it indicates significant aggregation, and values below indicate significant dispersion.

The R package was used to conduct preliminary analyses such as the correlation test and the PCA for the landscape of fear variables. The factors shaping WBp in the study area were assessed using a Generalized Linear Mixed Model (GLMM) with a Poisson distribution fitted by maximum likelihood. WBp was the dependent variable, while season (AAP, FAP, FSP), habitat type (Cover vs. Open areas), and the urbanization gradient were included as fixed effects. Trap ID was included as a random effect. The interactions between

fixed effects were initially included but removed due to lack of significance. Models were fitted using the lme4 package in R [77]. Graphical comparisons of WBp between habitat types were generated using kernel density estimates obtained in R.

To assess the influence of spatial structure on the relationship between habitat type and WBp, we fitted two additional GLMMs, one for each habitat type (Cover and Open areas). In both models, season was a fixed effect, and spatial structure was incorporated as a random effect using a Matérn correlation function. These models were fitted using the spaMM package in R [78].

3. Results

Distance to the urban core and distance to the urban edge were highly correlated (Pearson's r = 0.833, t = 15.839, df = 110, $p < 0.001$). The first principal component (PC1) obtained from the PCA, including both distances, explained 91.7% of the total variance. Both distance to the urban core and distance to the urban edge loaded positively on PC1 (0.707 each), indicating that higher values of PC1 correspond to locations farther from the urban area. Therefore, the urbanization gradient variable corresponded negatively to the PC1 scores. The urbanization gradient was significantly higher in Open areas than in Cover areas (Urbanization gradient: mean ± standard deviation (SD) = −0.595 ± 1.332 in Cover areas, mean ± SD = 0.764 ± 0.943 in Open areas; F = 36.689, $p < 0.001$).

In both Open and Cover areas, spatial aggregation of footprint traps was significant, as the observed K(r) values exceeded those expected under complete spatial randomness (CSR) (Figure 2).

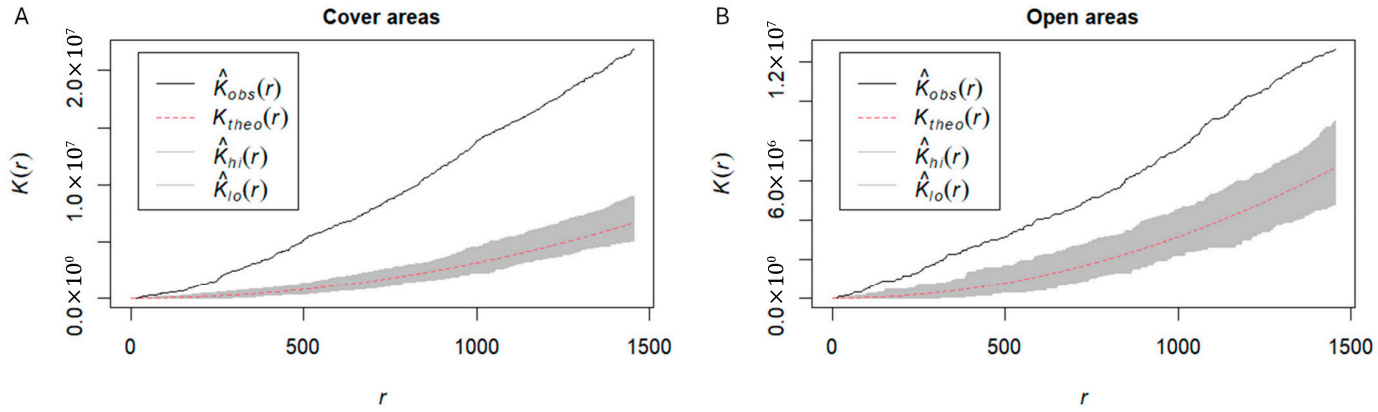


Figure 2. Results of the Ripley's K analysis for the spatial distribution of traps in Cover areas ((**A**), N = 63) and traps in Open areas ((**B**), N = 49). The figure shows the aggregation index K(r) across spatial scales (r) up to 1500 m. K(r) values were calculated for the observed trap locations (obs) and compared to theoretical values under complete spatial randomness (theo). The gray area represents the range of K(r) values obtained from 999 CSR simulations.

Wild boar footprints were recorded in traps located in both Cover and Open areas across all three monitoring campaigns (Cover areas: N = 26 in AAP, N = 30 in FAP, N = 34 in FSP; Open areas: N = 14 in AAP, N = 8 in FAP, N = 17 in FSP). Wild boar presence (WBp) was consistently higher in Cover areas than in Open areas (Table 1, Figure 3) and was also higher across the study area during the FSP (Table 1). However, the urbanization gradient was not related to WBp (Table 1). The interactions between fixed factors did not affect WBp and were therefore removed from the model in Table 1. Importantly, the interaction between habitat type and season did not have a significant effect [Habitat (Open) * Season (AAP): estimate = 0.045, standard error (SE) = 0.385, z = 0.118, $p = 0.906$; Habitat (Open) * Season (FAP): estimate = −0.405, standard error (SE) = 0.424, z = −0.955, $p = 0.340$].

Therefore, the higher WBp in Cover areas was consistent across all three campaigns, with WBp being 35.2% higher in Cover areas compared to Open areas (e^−1.043 = 0.352; see Table 1).

Table 1. Results of the GLMM with wild boar presence (WBp) as the dependent variable, Season (AAP, FAP, and FSP), Habitat (Cover vs. Open areas), and urbanization gradient as fixed effects, and trap ID as a random effect. FSP is the reference category for Season; Cover areas as reference category for Habitat. SE = standard error.

	Estimate	SE	z	*p*
Intercept	−0.073	0.161	−0.454	0.650
Habitat (Open)	−1.043	0.247	−4.223	<0.001
Urbanization gradient	0.080	0.088	0.908	0.364
Season (AAP)	−0.461	0.168	−2.752	0.006
Season (FAP)	−0.514	0.170	−3.018	0.003

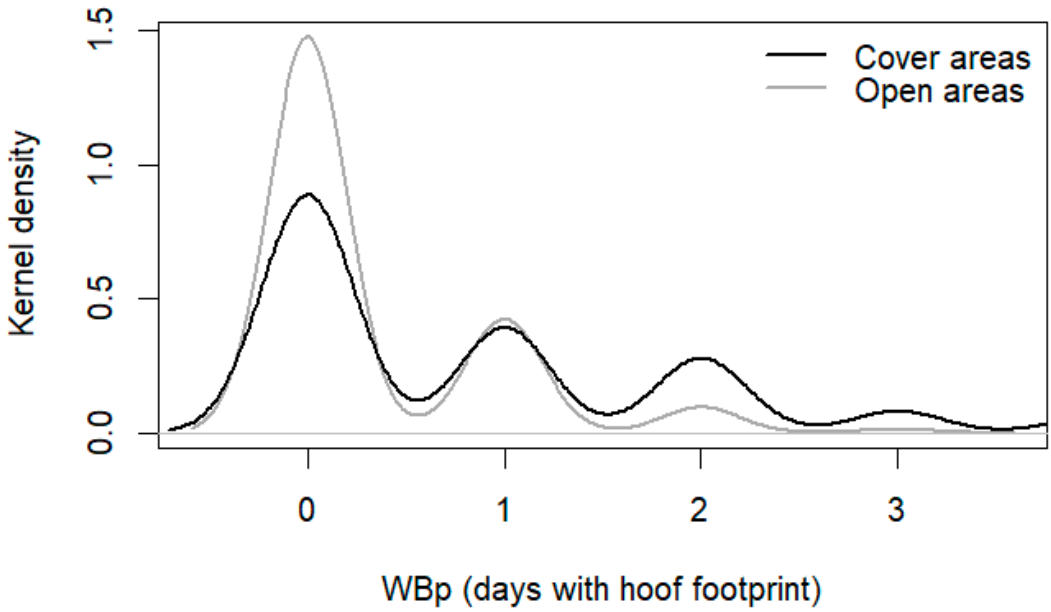


Figure 3. Kernel density of wild boar presence (WBp, number of days with hoof prints) for footprint traps located in both Cover and Open areas.

Spatial modeling using the Matérn covariance function revealed differences in spatial aggregation patterns between habitat types (Table 2). In Cover areas (Table 2(A)), the estimated spatial variance (λ = 0.463) was lower, and the smoothness parameter (ν = 0.599) indicated a more abrupt, localized pattern of spatial aggregation, with smaller and well-defined clusters of high activity.

In contrast, Open areas (Table 2(B)) exhibited higher spatial variance (λ = 0.618), suggesting greater overall spatial heterogeneity. The higher smoothness parameter (ν = 2.031) suggested a more gradual and continuous spatial pattern, with broader zones of elevated activity rather than sharply defined hotspots (Figure 4). These results indicate that, while Open areas showed greater spatial heterogeneity in WBp, the aggregation pattern was more diffuse and less localized than in Cover areas (Figure 4).

Table 2. Results of the models for wild boar presence (WBp), including Season as a fixed effect and incorporating the Matérn covariance function to account for spatial structure (X and Y coordinates). (**A**) Model for Cover areas only. (**B**) Model for Open areas only. SE = standard error. * $p < 0.05$.

	(A). Cover Areas	(B). Open Areas
N	189	147
Number of groups (X + Y)	63	49
Intercept (Estimate ± SE)	−0.069 ± 0.178 (t = −0.388)	−0.984 ± 0.379 (t = −2.599) *
Season AAP (Estimate ± SE and t value)	−0.473 ± 0.197 (t = −2.401) *	−0.427 ± 0.335 (t = −1.275)
Season FAP (Estimate ± SE and t value)	−0.427 ± 0.194 (t = −2.200) *	−0.833 ± 0.383 (t = −2.177) *
Spatial variance (λ)	0.463	0.618
Matérn smoothness (ν)	0.599	2.031

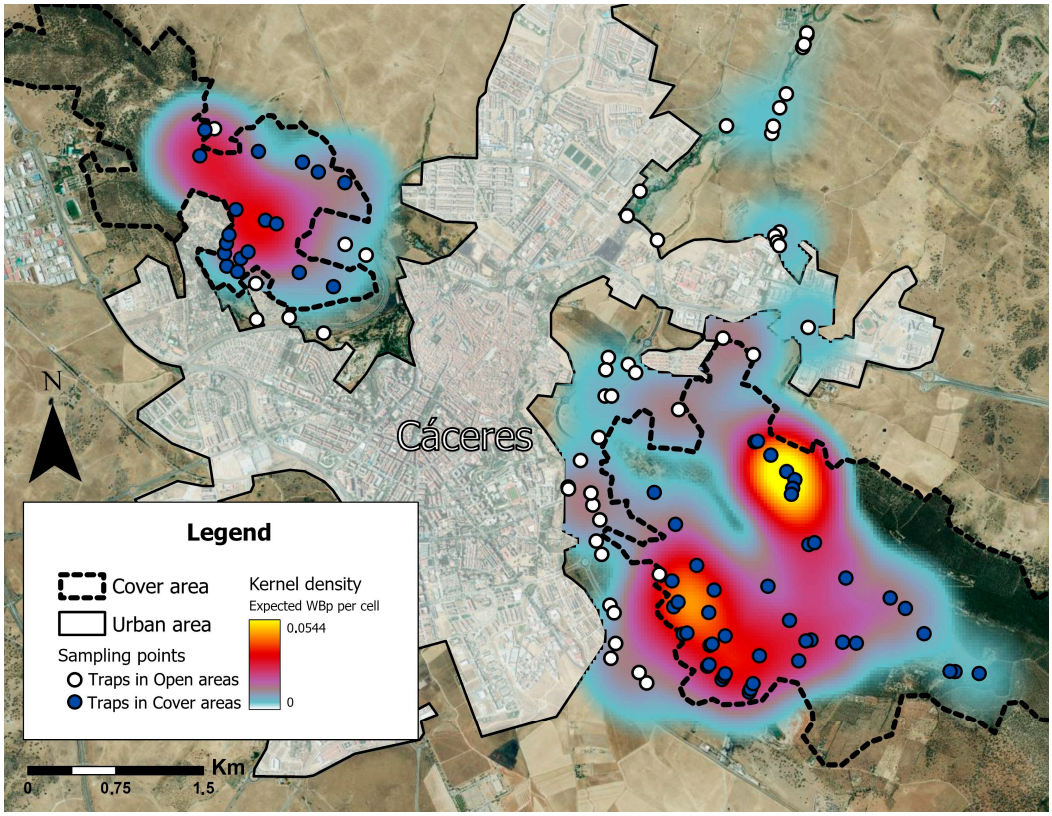


Figure 4. Kernel density map of wild boar presence (WBp) after combining data from all three campaigns. The color scale represents the expected WBp (number of days with footprints) per 30 m × 30 m cell.

4. Discussion

Our results partially supported our initial predictions. As expected, WBp was higher in areas with dense vegetation cover, highlighting the importance of refuge habitats in reducing perceived predation risk and disturbance in peri-urban landscapes. In contrast, we did not detect a significant effect of the urbanization gradient on WBp. This suggests that, in our study system, proximity to urban areas may play a less important role than habitat structure in shaping the spatial distribution of wild boar. Overall, our findings emphasize the dominant role of refuge availability over urbanization gradient in structuring the landscape of fear.

Our spatial modeling results further support the key role of habitat type in shaping wild boar distribution. Cover areas exhibited lower spatial variance and a lower smoothness

parameter, indicating smaller, well-defined clusters of activity, whereas Open areas showed higher spatial variance and a higher smoothness parameter, reflecting broader and more diffuse zones of activity. This suggests that, although wild boar were present in both habitat types, their movements were more localized in Cover areas, consistent with the use of dense vegetation as refuges [33,67–74]. In contrast, Open areas, while used by wild boar, display a more dispersed and less aggregated pattern, which may reflect greater exposure and perceived risk or the need to move more widely in search of resources.

The applicability of our methodology, which relied on the daily monitoring of footprint traps, may be limited in wild boar populations that are not accustomed to human presence. The repeated visits of researchers to sampling points could potentially deter wild boar due to human scent. In addition, our study would greatly benefit from further assessments, including replication across multiple years and in other peri-urban environments. The integration of complementary approaches, such as radio-tracking or camera trapping, could also help validate and refine our interpretations of wild boar behavior. Nevertheless, footprint traps represent a cost-effective, non-invasive tool that can provide valuable insights into spatial and temporal patterns of wild boar presence, particularly in urban and peri-urban contexts where other methods may be more logistically challenging and intrusive.

Although our study focused on spatial variation, we also observed temporal variation in the intensity of WBp, with the FSP (summer) showing the highest activity. Similar patterns have been documented in peri-urban populations of Barcelona and Rome, where wild boar activity peaks during periods of natural resource scarcity [62,63]. The stability and abundance of anthropogenic food sources in urban environments, along with reduced predation and frequent non-traumatic interactions with humans, attract wild boar during these critical periods [79–81]. These considerations suggest that resource distribution may provide an alternative explanation for our results.

During the Mediterranean summer, resource distribution becomes more concentrated in specific areas, and forested habitats may provide resources due to the persistence of green vegetation and the higher abundance of potential prey species in the cooler, shaded conditions created by tree canopies [66]. Furthermore, the high availability of acorns in Mediterranean forests, which occurs from late summer throughout autumn, may also attract wild boar [67]. These processes related to resource availability could explain the higher WBp observed during the FSP and AAP. However, the preferential use of Cover areas was consistent across all seasons, and we also found higher WBp during the FAP, when resource availability was greater and more widely dispersed across both Cover and Open areas. In this case, the use of cover vegetation as a refuge offers the most parsimonious explanation [33,67–74]. While we cannot rule out the potential influence of resource distribution on our results, the effect of predation risk on wild boar movement within the landscape of fear framework provides a compelling explanation for the consistently higher WBp in Cover areas throughout the year.

Wild boar have shown high tolerance to human presence in cities across Europe, where abundant anthropogenic food resources can drive behavioral and even phenotypic changes [33,60,79,82,83]. However, the landscape of fear associated with human activity, including disturbances, hunting, poaching, and control programs, continues to shape their movements and space use [21,33,67,73,84,85]. Our results, showing consistently higher use of Cover areas, suggest that wild boar in peri-urban Cáceres remain highly influenced by predation risk despite the stability of urban food resources. Thus, while urban areas may facilitate population establishment through food availability, the movements of wild boar in Cáceres appear partially driven by refuge availability and risk perception. In this

scenario, increases in wild boar presence within the city may reflect extreme reductions in natural resources outside the urban limits [62,63].

The combined effects of predation risk and resource availability suggest that the studied wild boar population is not fully habituated to the urban environment, a pattern also reported in other cities such as Bordeaux [64]. More broadly, across much of their global range, wild boar are not considered urban adapters. In fact, wild boar and feral pigs are major invasive species in regions like North America and Australia [44,80,86], where they are targeted by eradication programs to mitigate their impacts [87,88]. In such areas, the higher mortality risk and more frequent traumatic encounters with humans may limit the species' potential to adapt to urban life.

Our findings have important implications for managing human–wild boar interactions in peri-urban landscapes. Wild boar presence was more strongly influenced by habitat structure than by proximity to urban areas, underscoring the key role of refuge habitats in shaping their distribution. This suggests that management strategies should not only focus on limiting population growth but also consider how habitat features around cities may facilitate the persistence of wild boar populations. At the same time, our results indicate that wild boar still respond to perceived predation risk, likely due to hunting in nearby areas and other human disturbances in the peri-urban environment. Maintaining this sensitivity to risk is crucial to prevent full habituation, which could exacerbate conflicts within the city. Continued population monitoring, targeted municipal control programs when necessary, and measures that reinforce avoidance of high-risk areas can help sustain coexistence between humans and wild boar in Cáceres and similar Mediterranean cities.

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Data Availability Statement: The data presented in this study is available on request from the corresponding author. The data is not publicly available due to ongoing research.

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