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RESEARCH ARTICLE

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Spatio-temporal patterns and risk factors of wild boar–pig farm contact across Europe

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Abstract

1. Diseases circulating at the wild–domestic animal interface are increasingly difficult to control due to human encroachment into wildlife habitats. Understanding the factors driving wild animals to visit livestock farms is crucial for reducing the risk of disease outbreaks with severe economic and social consequences.
2. In this study, we quantified the contact rate at the wild boar–domestic pig interface across Europe using a large-scale dataset of wild boar GPS tracking and domestic pig farm geolocations. We estimated wild boar contact rate with pig farms at hourly and monthly scales and analysed the influence of environmental, wild boar- and farm-related variables.
3. Across 187 tracked wild boars and 457 pig farms, we detected 3322 contact events, with a highly skewed contact distribution: only 5% of wild boars and 1% of farms accounted for 50% of all events. On average, each wild boar had 1.59 contacts per month with a given farm (95% CI: 1.33–1.85) and 2.58 contacts per month when considering all farms located within its monthly home range (95% CI: 1.62–3.53). Seasonal variation differed between sexes, with a bimodal distribution for males with contact rates peaking in March and August–September, and a slight increase in contact rate throughout winter for females. Monthly contact rate increased with forest cover, human footprint, wild boar population density and individual proximity to pig farms. Farms with more built infrastructure faced fewer contacts, and larger farms had higher contact rates. Contacts occurred mostly after sunset and around sunrise.

Kevin Morelle and Elodie Wielgus contributed equally to this work and should be considered first co-authors.

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4. *Synthesis and applications*. Our results highlight the need to incorporate wild boar spatio-temporal behaviour and farm context into strategies aimed at reducing contact at the wild–domestic pig interface. While physical barriers and avoiding unintentional feeding remain essential, targeted measures during high-risk periods, such as night-time surveillance in summer and autumn, especially around large farms in wooded landscapes or areas with high wild boar density, could help reduce contact occurrence.

KEYWORDS

biosecurity and farm management, disease transmission risk, GPS tracking, human–wildlife conflict, movement models, spatio-temporal contact patterns, wild boar (*Sus scrofa*), wildlife–livestock interactions

1 | INTRODUCTION

The continued expansion of human activities into natural habitats is increasingly bringing humans, livestock and wildlife into closer contact. These expanding interfaces intensify the risk of conflicts, such as competition for shared resources (Darkoh & Mbaiwa, 2009), livestock predation by carnivores (Kissui, 2008), crop damage (Schley & Roper, 2003), hunting and illegal killing (Bachmann et al., 2022; Heurich et al., 2018), and pathogen transmission (Wiethoelter et al., 2015). These conflicts pose significant global threats to wildlife conservation, economy, livestock and human health (Destoumieux-Garzón et al., 2018). Among these interfaces, the wildlife–livestock interface is of particular concern, as domestic animals frequently act as intermediate hosts for pathogen transmission from wildlife reservoirs to humans (Bengis et al., 2004). Gaining a comprehensive understanding of the ecological and anthropogenic drivers behind wildlife–livestock contacts is crucial for developing effective strategies to mitigate disease risks and promote both animal and public health.

At the wildlife–livestock interface, contacts can occur either directly (sharing the same space simultaneously) or indirectly (using the same space at different times), and are driven by species-specific behaviours, such as foraging habits, movement dynamics and activity patterns (Dougherty et al., 2018; Martinez et al., 2024; Salgado et al., 2022). Such behaviours are shaped by a complex interplay of biotic and abiotic factors, including environmental conditions (e.g. habitat type and weather; Mueller et al., 2011), individual traits (e.g. sex and age; Barroso & Gortázar, 2024), anthropogenic pressures (e.g. livestock management practices and wildlife control; Lewis et al., 2021) and physical infrastructure (e.g. roads and fences; Passoni et al., 2021). The nature and frequency of wildlife–livestock contacts can therefore be highly variable across space and time and identifying the factors that influence this dynamic is crucial for disease management (Drewe et al., 2013).

The role and significance of the interface between wild boar (*Sus scrofa*) and domestic pigs (*Sus scrofa domesticus*) have gained attention with the global spread of African swine fever (ASF) in the last decades (Dixon et al., 2020). African swine fever is a contagious disease that threatens both wild and domestic pig populations and has major economic consequences (Chenais et al., 2018; Costard et al., 2009). Beyond ASF, wild boar also carry an array of other pathogens, including zoonoses, which make the species a key node in virus circulation among wildlife, livestock and humans (Tu et al., 2025). Despite its importance in disease transmission and maintenance in the environment (Corner, 2006; Viana et al., 2014), the wild boar–domestic pig interface remains less studied than other wildlife–livestock interfaces (Wiethoelter et al., 2015), such as the European badger–cattle interface, where badger is a central reservoir for bovine tuberculosis (Böhm et al., 2009; Garnett et al., 2002; Woodroffe et al., 2016a).

This gap is particularly striking given the diversity of pig farming systems across Europe, ranging from large-scale conventional indoor units to more differentiated systems, such as smallholder or outdoor farms that maintain varying degrees of outdoor access (Bellini, 2021; Bonneau et al., 2011; Nielsen et al., 2021). Depending on the systems, domestic pig farms present a more or less permeable interface with wildlife, particularly for wild boar which visits are unlikely to occur at random. Farms indeed offer relatively predictable attractants, such as high-calorie food sources (e.g. spilled grains or silage residues) and female pigs in oestrus, both creating a landscape of smell (farm odours, e.g. feed, manure, conspecific scent from domestic pigs) serving as olfactory cues potentially shaping the movement of wild boar towards farms (Anses, 2021; Finnerty et al., 2022). Thanks to their learning and spatial memory abilities (Jansen et al., 2009; Morelle et al., 2015), wild boar can exploit and (re-)visit these resource-rich areas more than expected by chance.

To date, most studies quantifying the interactions between wild boar and domestic pigs have relied on qualitative methods (e.g. Brookes et al., 2021), camera traps (e.g. Cadenas-Fernández et al., 2019) or overlapping home ranges (e.g. Barasona et al., 2014), and were limited in spatial and temporal scope, often focusing on a single study area and/or short period of time. They usually report low-contact rates, potentially reflecting data gaps rather than minimal risk, and originate outside Western Europe (Bora et al., 2020).

As both sides of the wild boar–domestic pig interface are expected to expand, with wild boar populations growing in number and range, and domestic pig husbandry evolving towards more

Journal of Applied Ecology

animal-welfare-oriented outdoor systems (Bartlett et al., 2024), understanding the spatio-temporal dynamics of contact between wild boar and pig farms becomes increasingly important. Using GPS-tracking data from wild boar and geolocations of domestic pig farms across Europe, we aimed to (1) quantify the contact rate between wild boar and domestic pig farms at the monthly and hourly scales, and (2) identify the environmental, wild boar-related and farm-level factors driving these contacts, based on a set of hypothesis-driven predictions (Table 1).

2 | MATERIALS AND METHODS

2.1 | Wild boar data

We used the EUROBOAR database, a collaborative science initiative on wild boar movement that is part of the EUROMAMMALS network (Urbano et al., 2021). Specifically, we focused on study areas that overlapped with regions where pig farm location data were available (see Section 2.2; Figure 1). Trapping and marking of wild boars were performed using approved animal care protocols. Where required, access to field sites was authorized by the relevant national or regional authorities, and is documented together with ethical approvals and permit numbers from the respective regions and countries (Supporting Information 1). The temporal resolution of GPS data varied among the study areas, ranging from one location recorded every 15 to 240 min. All timestamps were recorded in Coordinated Universal Time (UTC). We filtered the data through a sequential process: (1) excluding the first 10 days post-capture to minimize potential bias from capture and handling effects (Brogi et al., 2019; Stiegler et al., 2024); (2) filtering out erroneous locations using the method by Bjørneraas et al. (2010) which identifies outliers based on excessive distance from local medians (using 10 fixes before and 10 after the fix under evaluation, and a threshold distance of 10 km) and detects movement spikes characterized by high incoming and outgoing speeds (>2.5 km/h) and sharp turning angles ($\cos\theta < -0.99$); and (3) including only individuals with at least 1 month of tracking (taking a threshold of minimum of 20 days within a specific month to be accounted for) and whose monthly home range (defined by a 100% minimum polygon convex, MCP, plus a buffer of 50 m to account for farms at the boundary) overlapped with at least one pig farm. As a result, we obtained data at the individual–farm–month level, which served as the basis and unit for all subsequent data extraction and modelling. After this filtering process, our data consisted of the tracking records of 187 individuals, representing 2091 individual–farm–month combinations (average of 3.09 ± 4.36 farms per individual–month; Figure S1).

Among the 187 individuals, 104 were female and 83 were male. Age classes were distributed as follows: 91 adults (>2 years old), 48 yearlings (1–2 years old) and 48 juveniles (6–12 months old). Preliminary investigations revealed significant but limited variation between age classes in monthly and hourly contact patterns. Given the coarse and relatively subjective age class assessment and potential sampling imbalances across the study area, we present analyses pooling age classes together in the main text. Complementary analyses differentiating age classes are provided in Supporting Information (Tables S5 and S6; Figures S6 and S7). The final wild boar dataset covered the period between 2005 and 2022 and was obtained from 32 study areas (Figure 1) across eight European countries (Belgium, Czech Republic, France, Germany, Hungary, Italy, Sweden and Switzerland).

2.2 | Domestic pig farm data

For each of our study areas, domestic pig farm location data were extracted from local databases after requests to national and regional authorities, including veterinary services, agricultural agencies and pig farmers' interest groups. Only data on active pig farms during the periods of interest (i.e. concurrent with individual wild boar tracking project) were requested and provided by relevant authorities. After verifying and correcting where necessary, farm geolocations (Figure S2) were converted into polygons. For this, we used OpenStreetMap (OSM), specifically the 'farmyard' feature from the *land use* key, which includes areas with farm buildings and surrounding open spaces. When OSM data were unavailable, the farm boundaries were manually digitized in QGIS using Google satellite imagery and OSM backgrounds ($N = 387$; see Supporting Information 3). Because detailed, standardized data on husbandry systems (type of outdoor access, pasture vs. concrete runs, seasonal confinement) were not available, we used proxies (farm area, building coverage, pig density and surrounding land cover) to approximate the farming system. For each farm, the surface area was computed from its associated polygon and the proportion of built-up areas within each polygon was calculated using the Global Building Footprint data (Microsoft, 2025).

2.3 | Contact definition and estimation

In our study, we defined a 'contact' as any visit by a wild boar within the boundary of a pig farm that may result in pathogen transmission, either through direct interaction with domestic pigs or indirectly via environmental contamination through contact with farm features, such as feed residues, water, soil or other fomites (Marin et al., 2024).

Traditionally, studies attempting to estimate the contact between animals using GPS data have used a large spatial window to define contact (Miguel et al., 2013; Podgórski et al., 2018), which can reduce the temporal and spatial precision of contacts. To improve the accuracy of contact estimation, we first simulated a movement trajectory for each individual–month by fitting a continuous-time movement model (*ctmm*, Calabrese et al., 2016). *ctmm* assumes that animals move along a continuous path, accounting for the temporal autocorrelations between locations, and generates more accurate trajectories than straight-line trajectories between consecutive

TABLE 1 Hypotheses, predictions and explanatory variables for assessing individual wild boar contact with domestic pig farms across temporal, species, environmental and farm-specific contexts.

Context	Hypothesis	Predictions	Explanatory variable	Data source
Temporal (daily)	Wild boar contact with farms follow the mostly nocturnal activity patterns of the species (Brivio et al., 2017; Johann, Handschuh, Linderoth, Heurich, et al., 2020)	Contacts peak at night	Deviation in hours from sunset (considered as hour 0)	Our study
Temporal (seasonal)	Seasonal drivers of wild boar spatial behaviour, such as mating and food scarcity, increase farm contact rates in specific seasons	Contact rates are expected to peak in autumn and winter due to mating and resource scarcity, but with differing patterns among sexes and age classes (Cavazza et al., 2023)	Month × sex	Our study
Wild Boar	Contacts vary based on individual traits	Males exhibit higher contact rates with pig farms than females, likely due to greater movement ranges and mating-related behaviour (e.g. Johann, Handschuh, Linderoth, Heurich, et al., 2020; Kay et al., 2017).	Sex	Our study
	Contact with pig farms are affected by wild boar population density	Contact rates increase with higher wild boar population density, as the resulting greater competition and resource scarcity drive wild boar to visit farmland (Albery et al., 2024; Augustsson et al., 2024)	Wild boar population density estimates	Enetwild (Illanas et al., 2022)
	The contact rate depends on the proximity to the farm	Proximity to farm increases the contact rate between wild boar and farm, because of higher spatial overlap and easier access to food (e.g. anthropogenic resources) (Aschim & Brook, 2022)	Median distance to farm, calculated as the Euclidean distance between a farm and the median location of an individual's GPS location during a specific month	Our study
Environmental	Forested areas near farms increase contact due to favourable habitat conditions	Higher contact rates are expected with more forest cover and more abundant forest patches	Number of forest patches within a 1-km buffer around the pig farm Proportion of forest cover within a 1-km buffer around the pig farm	Land Cover Map of Europe (Malinowski et al., 2020)
	Human infrastructures affect wild boar–domestic pig farm contact	Increased risk near human-modified landscapes due to potential resource opportunities and disturbance	Mean Human Footprint Index (Relative measures of human impact on ecosystems) within a 1-km buffer around the pig farm. Scale from 0 (no pressure) to 100	Venter et al., 2016
Farm	Larger farms are more attractive but may implement better biosecurity	Wild boar have higher contact rates with larger pig farms	Farm area (m^2)	Anonymized pig farm data, OSM, Microsoft 2025
	High-density building coverage on farms reduces wild boar visitation	Increased building density is associated with lower contact rates, likely due to reduced access and deterrence	Farm building cover (%)	
	Contacts are affected by the density of pigs in farms	Contacts increase with higher domestic pig farm density	Pig number estimates. Classified into three intensity categories: low (0–5 pigs), medium (5–50 pigs) and high (≥50 pigs). To account for potential trade-offs between farm size and pig intensity, an interaction term was tested and included if remaining significantly associated	GLW 4: Gridded Livestock Density (Global—2020—10 km^2) (Gilbert et al., 2018)

Journal of Applied Ecology

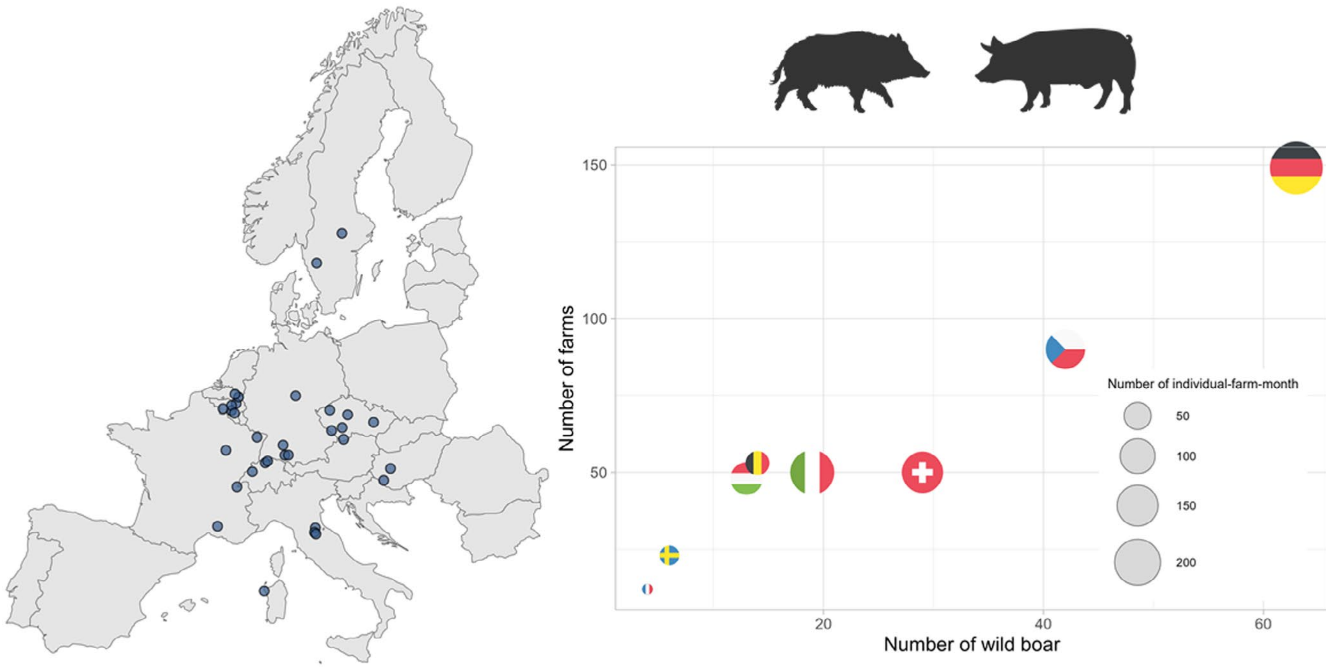

FIGURE 1 Distribution of the 32 study sites across eight European countries where GPS-tracked wild boar data and pig farm geolocations were available. A farm was considered available if it fell within the monthly home range of a wild boar, defined as the minimum convex polygon encompassing all GPS locations.

relocations (Cavazza et al., 2023; Noonan et al., 2019). For each individual–month, we used the fitted *ctmm* to simulate the locations every 5 min and generated 100 simulated trajectories to capture model uncertainty.

We then overlayed these trajectories to the farm polygons, identifying contact events as any of the 5-min relocation recorded within 50 m of the pig farm's polygon boundary to account for GPS errors (D'eon & Delparte, 2005; Ironside et al., 2017). Consecutive contact locations were grouped into a single 'contact event', and events separated by less than 60 min were merged.

2.3.1 | Monthly contact rate

The monthly contact rate was calculated for each individual–farm–month as follows. For each of the 100 simulated *ctmm* trajectories, we counted the number of detected contact events and then averaged these counts across the simulated trajectories. The resulting monthly contact rate for month *m* was then standardized as:

$$\text{Standardized rate} = \text{raw rate} \times \frac{N \text{ tracking days}}{N \text{ days in month } m} \times \frac{\text{Maximum no. days across months}}{N \text{ days in month } m}$$

This procedure adjusted the estimated monthly contact rates per individual–farm–month for differences in tracking duration that may occur between individuals and across months, to (i) avoid unfair comparisons between individuals tracked for fewer days (e.g. 20 days) and those monitored for an entire month (e.g. 30 days), and (ii) prevent longer months (e.g. 31 days) from disproportionately influencing average contact rates.

To explore the distribution of contact rates, we summarized the monthly contact rates at both the wild boar individual and farm levels. High-contact individuals and farms were defined as those cumulatively responsible for 50% of all contact events. For individuals, we calculated the number and proportion of farms contacted within their monthly home range, and the Gini index to quantify the evenness of contact distribution across farms (0 = equal use of all farms; 1 = all contacts concentrated on one or a few farms). Differences between high- and low-contact individuals or farms were tested using the Wilcoxon rank-sum.

2.3.2 | Hourly contact rate

For the hourly contact rate, we processed as follows: for each individual–farm–month, we first extracted the start times of each contact event from the 100 simulated trajectories. Second, to account for seasonal and latitudinal differences in daylight across Europe, we converted each event start time into a deviation (in hours) from the local sunset, computed with the *suncalc* package (Thieurmel & Elmarhraoui, 2025). Next, we counted the number of contact events per hourly bin (i.e. hourly intervals of time deviation from sunset) for each of the 100 simulated *ctmm* trajectories; and for each bin, we then averaged the counts across the 100 simulated trajectories. This resulted in a single distribution of hourly contact rate per individual–farm–month.

For both monthly and hourly contact rates, we rounded the values to the nearest integer to produce a count variable for statistical modelling.

2.4 | Statistical analysis

2.4.1 | Monthly contact model

We used a generalized additive mixed approach (GAMM, Wood, 2017) to model the number of contact events per individual–farm–month, that is the monthly contact rate (n_{ifm}, Equation 1), in relation to explanatory variables describing wild boar characteristics, farm structure and environmental conditions (Table 1). n_{ifm} had a high proportion of zeros (62%), which we interpreted as structural (i.e. true absence of contact), rather than resulting from sampling error (Campbell, 2021). To account for this excess of zeros and overdispersion, we compared Poisson, zero-inflated Poisson, negative binomial (NB) and zero-inflated NB models. The NB provided the best fit (Table S3). Therefore, we assumed that individual monthly contact rates n_{ifm} are generated from a NB distribution of mean μ_{ifm} and dispersion parameter θ, such as:

$$n_{ifm} \sim NB(\mu_{ifm}, \theta)$$

where μ_{ifm} is the mean contact rate between individual i and domestic pig farm f in month m.

All predictor variables were included in a single model, which was specified as:

$$\log(\mu_{ifm}) = \beta_0 + \sum_{k=1}^{3} \beta_k.\text{Wildboar}_{k,i} + \sum_{l=1}^{3} \beta l.\text{Environment}_{l,j} + \sum_{q=1}^{3} \beta q.\text{Farm}_{q,f} + s(\text{Month}_m)_{\text{Sex}_i} + u_{cif} \quad (1)$$

where β_0 is the intercept, and the fixed effects include three sets of predictors: Wildboar_i with k individual- (sex, median distance to farm f) and population-level (density) variables relative to wild boar, Environment_j with l variables (number of forest patches, forest cover and the human footprint index, HFI, in a 1-km buffer around farm f), and Farm_f with q variables, farm area (log-transformed to normalize the distribution), regional pig number (as estimated by the Gridded Livestock Density model; Gilbert et al., 2018) and building coverage relative to each domestic pig farm (Table 1). $s(\text{Month}_m)$ is a cyclic smooth function (e.g. spline) of month m (with separate smooth functions for the sex classes, see Table 1), u_{cif} is a random intercept for individual–farm combination *fi* nested within country c.

We tested the effect of sampling frequency on the monthly contact rate and found no significant influence of resampling interval (Figure S3, Table S1), which was consistent with the expected scale insensitivity of the *ctmm* approach (Noonan et al., 2019). Additionally, we tested for spatial autocorrelation between farms and found no evidence of significance structure in monthly contact rates (see Supporting Information 5, Table S2).

2.4.2 | Hourly contact model

Similarly, we modelled the variation in the hourly contact rate for each individual–farm–month (nh_{ifm}, Equation 2), as a function of deviation time from sunset using a GAMM. We specified separate smooth terms for each sex to capture potential behavioural differences in hourly activity between sexes. nh_{ifm} was modelled using a NB distribution to account for overdispersion. The model was specified as:

$$nh_{ifm} \sim \text{NB}(\eta_{ifm}, \theta')$$

$$\log(\eta_{ifm}) = \beta_0 + s(\text{Hour}_h)_{\text{Sex}_i} + u_{cim} \quad (2)$$

where η_{ifm} is the expected mean contact rate between individual i and a farm f per hour relative to sunset in month m, θ' is the dispersion parameter, β_0 is the intercept, $s(\text{Hour}_h)$ is a cyclic smooth function) of hour relative to sunset h, u_{cim} is a random intercept for individual i nested within country c and month m (to account for possible seasonal variation along wild boar biological and ecological cycle).

Models fit (i.e. hourly and monthly) was visually assessed by plotting the observed versus fitted values and inspecting the distribution of deviance residuals through QQ plots and histograms. The GAMMs were fitted and checked using the *gamm4* and *DHARMa* packages (Hartig & Lohse, 2022; Wood & Scheipl, 2020). All analyses were performed using R Statistical Software version 4.3.1 (R Core Team, 2021).

3 | RESULTS

3.1 | General patterns of contact between wild boars and pig farms

Of the 187 wild boars with at least one pig farm in their monthly home range, 85 individuals (45%) had at least one recorded contact event with a farm. From these 85 individuals, the average number of distinct farms contacted per month was 1.67 (±1.31 SD), ranging from one to up to eight farms. On average, wild boars contacted 54% of farms within their home range, with a large variability between countries (min-max 30%–91%, Figure S5).

In total, 3322 contact events were recorded across 420 (i.e. 20%) of the 2091 individual–farm–month combinations (based on the mean across the 100 simulations), indicating a highly uneven distribution of contact events. Notably, just 10 individuals (five males and five females) accounted for 50% of all contact events (Figure S4A).

On average, GPS-tracked wild boars contacted a given farm with a rate of 1.59 (SD = 6.05, 95% CI: 1.33–1.85) contacts per month. Aggregated contact rate with any farm in an individual's home range was 3.43 per month (SD = 8.91, 95% CI: 3.05–3.81). Considering the 10 high-contact individuals only, this rate reached 19.7 (SD = 16.1,

Journal of Applied Ecology

95% CI: 9.7–29.8) contacts per month with a given farm and 26.2 (SD = 12.7, 95% CI: 18.3–34.1) contacts per month when considering all farms within their home range. In contrast, excluding these 10 high-contact individuals reduced the average monthly contact rate to 1.24. The mean contact duration was 56.2 min (SD = 88.4, 95% CI: 55.9–56.6), which aggregated across all individual–farm–month combinations and all simulations, corresponded to approximately 0.2% of wild boar time.

From a farm perspective, 91 of 457 farms (20%) were visited at least once by wild boar and only six of these farms contributed to 50% of total contact events (see Figure S4B). Aggregating contact events across all wild boar individuals resulted in an average of 0.51 contact events per month (SD = 2.32, 95% CI: 0.30–0.73). Excluding the six farms with the highest number of contact events reduced this average to 0.34 per month.

High-contact individuals did not have access to more farms (4.0 ± 4.0 vs. 5.7 ± 8.3; Wilcoxon $W = 917$, $p = 0.85$), but contacted a greater number of available farms (2.5 ± 2.4 vs. 0.67 ± 1.0; $W = 331.5$, $p < 0.001$). Gini indices (mean = 0.41 ± 0.34) suggest that contact events were unequally distributed, implying farm preference. Comparing 27 individuals with access to both high- and low-contact farms, contact rates were significantly higher at high-contact farms (paired Wilcoxon test, $W = 31.5$, $p = 0.006$). These farms were located closer to forests (median = 0 m vs. 22 m; $p = 0.0016$), had greater forest cover (median = 0.40 vs. 0.22; $p < 0.001$), larger surface area (7359 m^2 vs. 2950 m^2; $p < 0.001$), slightly higher wild boar density ($p = 0.024$) and less built-up area ($p < 0.001$). High-contact farms were spatially aggregated in some study areas, with inter-farm distances of 1.3 and 2.9 km, matching the typical wild boar movement distances.

3.2 | Monthly contact patterns

Contact rates between wild boar and pig farms varied across months but did not differ between sexes ($\beta = -0.07$, 95% CI: −0.49 to 0.36, $p = 0.8$; Table S5a, Figure 2). We detected only weak variation in contact rates across the year for females ($p = 0.049$), with a relatively stable monthly contact rate that only slightly increased during winter (from October to February), whereas males showed a more pronounced seasonal variation ($p < 0.001$), with a bimodal profile peaking in March and August (Figure 2). When attempting to discriminate for age, we found no clear seasonal patterns for yearling males, while patterns differed between age classes for females. In particular, adult females showed no detectable variation across months, whereas juvenile and yearling females exhibited higher monthly contact rates between October and January (Table S5b, Figure S6). ntact rates also increased with wild boar population density ($\beta = 1.1$, 95% CI: 0.36 to 1.9, $p = 0.004$) and decreased with increasing median distance between individual wild boar and a given farm ($\beta = -0.98$, 95% CI: −1.1 to −0.83, $p < 0.001$; Figure 3d,e).

All environmental variables were significantly associated with contact rates: forest cover ($\beta = 3.8$, 95% CI: 2.4 to 5.3, $p < 0.001$), number of forest patches ($\beta = 0.01$, 95% CI: 0.00 to 0.01, $p = 0.011$) and the Human Footprint Index ($\beta = 0.23$, 95% CI: 0.14 to 0.31, $p < 0.001$; Figure 3a–c).

Similarly, farm-level variables significantly affected contact rates (Table S5a). Larger farms had higher contact rates ($\beta = 0.75$, 95% CI: 0.51 to 0.98, $p < 0.001$, Figure 3g), while contact rates decreased with increasing building coverage within the farmyard ($\beta = -3.0$, 95% CI: −5.2 to −0.87, $p = 0.006$; Figure 3f). Domestic pig density modified the relationship between farm area and contact rate: in medium- and high-density regions, contact rates increased with farm area, whereas in low-density areas, contact rates remained relatively

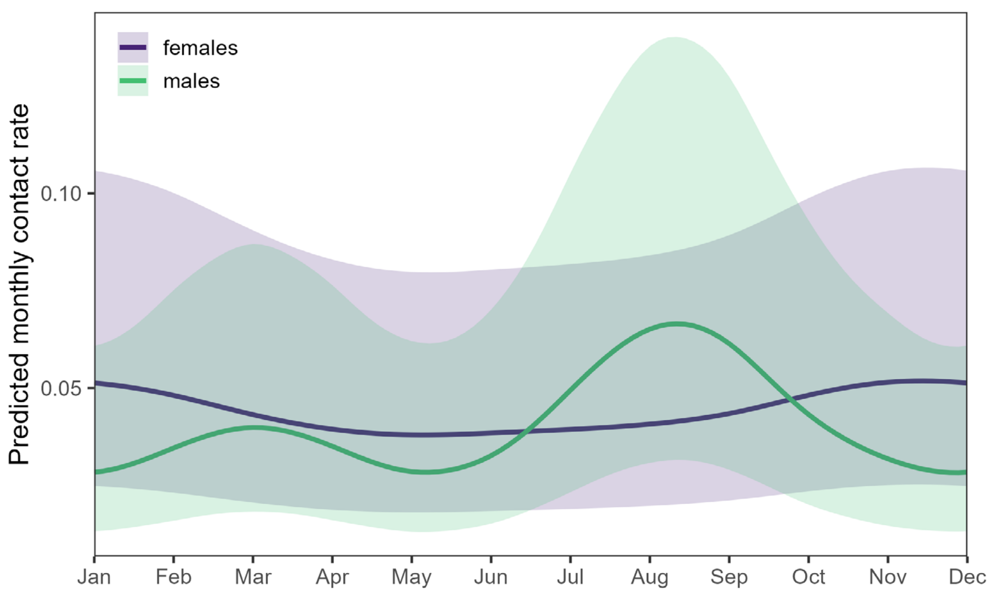

FIGURE 2 Predicted monthly contact rates between wild boar and pig farms by sex, across months. Predictions were derived from a generalized additive mixed model fitted with a negative binomial distribution. Solid lines show the predicted contact rates and shaded ribbons indicate 95% confidence intervals.

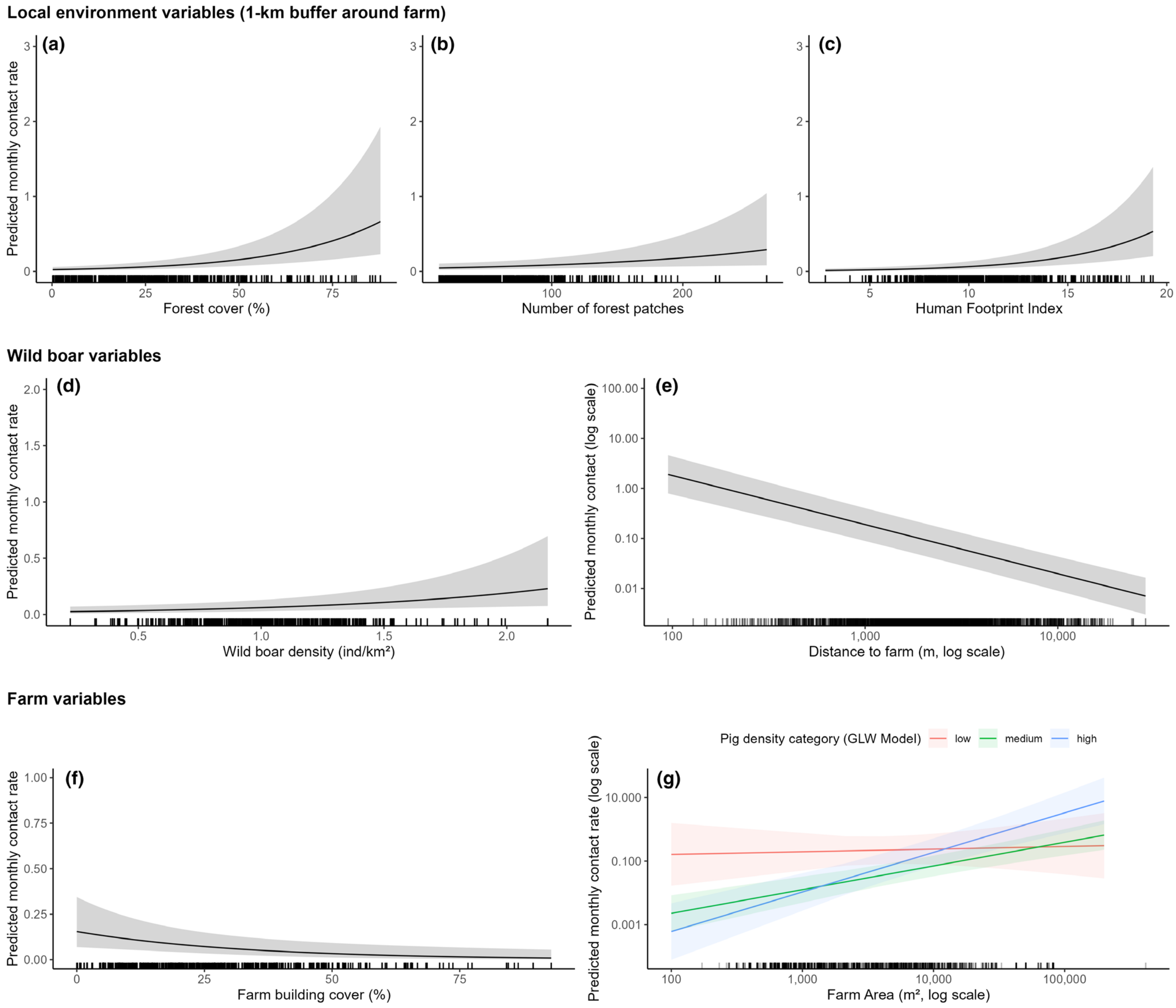

FIGURE 3 Predicted monthly contact rates between wild boar and domestic pig farms in relation to the local environment around the farm: (a) forest cover, (b) number of forest patches and (c) human footprint; wild boar context: (d) wild boar density and (e) median distance between wild boar and a given farm; and farm characteristics: (f) building cover and (g) farm area in interaction with pig density. Shaded areas show 95% confidence intervals. Tick marks indicate the observed values. Note varying scales on *x*- and *y*-axes.

stable regardless of farm size (interaction term for low density: $\beta = -0.66$, 95% CI: −1.2 to −0.08, $p = 0.027$; for high density: $\beta = 0.50$, 95% CI: 0.02 to 0.98, $p = 0.041$; Figure 3g).

Country-level random effects (Figure S5) indicate that most of the variation in monthly contact rates was accounted for by the fixed effects included in the model. However, Hungary had a significantly higher average contact rate than the other countries (Rate Ratio = 4.1, 95% CI: 2.5–6.9), suggesting country-specific factors beyond those explicitly considered in our model.

3.3 | Hourly contact patterns

The hourly contact rate between wild boars and pig farms varied across the diel cycle and showed a bimodal distribution (Figure 4). Contact rates increased shortly after sunset, peaking approximately 4–5 h later (i.e. during the night). A second peak occurred approximately 15 h before sunset, corresponding to the early morning crepuscular hours near sunrise. These temporal dynamics were consistent for both males and females ($p < 0.001$), and no significant difference was found between sexes ($\beta = -0.11$, 95% CI: −0.70 to 0.48, $p = 0.7$, Table S6a). Although most age classes exhibited this bimodal pattern, the amplitude of hourly variation was lower in yearlings and no detectable hourly pattern was observed in juvenile males (Table S6b, Figure S7).

4 | DISCUSSION

This study leveraged high-resolution GPS tracking of wild boar and geolocated pig farms to examine the spatio-temporal patterns

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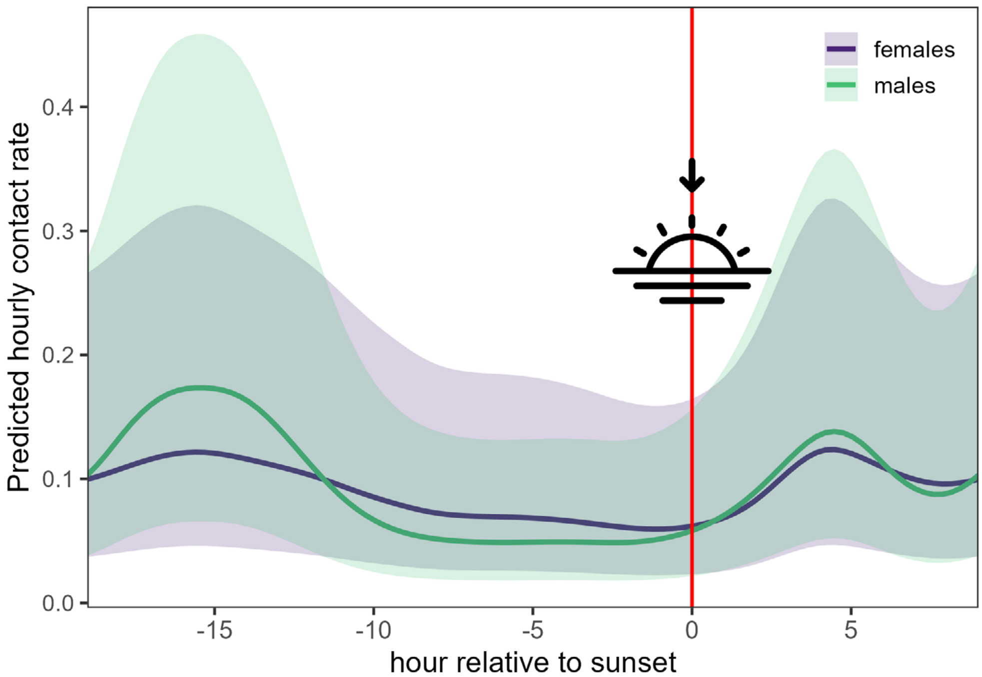

FIGURE 4 Predicted hourly patterns of wild boar contact rates with pig farms by sex. Time is expressed in hours relative to sunset, where 0 indicates sunset, positive values correspond to hours after sunset and negative values correspond to hours before sunset. Predictions were derived using a generalized additive mixed model with a negative binomial distribution. The shaded areas represent 95% confidence intervals (sunset icon created by Mehwish).

of contact across Europe, a critical yet understudied interface for pathogen transmission. Documented contacts between wild boar and domestic pigs remain rare (Brookes et al., 2021), but our findings indicate that such events may be more frequent than previously thought. We estimated that, on average, a wild boar came into contact with pig farms 2.58 times per month, or roughly 31 times per year. Each farm (located within at least one wild boar HR) experienced about 0.57 wild boar contacts per month, or 7 annually, but this is likely a conservative estimate, given that only a portion of the local wild boar population was tracked. Even after excluding the most contact-prone individuals and farms, wild boar still had 1.67 contacts per month, whereas farms had 0.34 contacts per month, underscoring that these events are not negligible. These rates are substantially higher than previous estimates based on farmer surveys, which reported 0.55 contacts per farm per year (95% CI: 0.50–0.61) (Wu et al., 2012). This difference can possibly be attributed to the underreporting of nocturnal visits, which we detected in our data (Figure 4) and is consistent with the species' nocturnal activity patterns (Brivio et al., 2017; Johann, Handschuh, Linderoth, Dormann, et al., 2020).

4.1 | Seasonal variations in contact

We expected contact rates to rise during autumn and winter, the main mating season for wild boar (Briedermann, 1990), but found only weak support for this hypothesis. Indeed, we found that males had higher contact rates during the summer months, with a clear peak in August–September and a secondary, weaker peak around March. This suggests that reproduction may not be the primary driver of contact with pig farms for males. Although wild boar rut typically starts around late autumn (Briedermann, 1990), the oestrus cycle of domestic pigs is often decoupled from this natural rhythm due to farm management practices, such as hormonal treatments or artificial lighting to maximize reproductive output. Thus, potential mating opportunities may not coincide with male wild boar behaviour. Instead, seasonal increases in contact are more plausibly linked to resource-seeking and exploratory movements. Males are known to expand their ranges in summer (Cavazza et al., 2023), often shifting towards agricultural areas (Keuling et al., 2009; Morelle & Lejeune, 2015), and farms may be particularly attractive during this time because of food-related cues, such as silage, grain or manure. For females, the relative increase in contact rate observed during the autumn–winter months somewhat aligns with the peak in oestrus and reproductive synchrony among females (Brogi, Merli, et al., 2022; Servanty et al., 2009), suggesting that mating-related behaviour could drive this behaviour. Contrasting responses to hunting pressure, potentially more pronounced in males or experienced individuals (Olejarz et al., 2024; Saïd et al., 2012), may also contribute to the observed patterns in winter. Indeed, Autumn coincides with the hunting season in many European countries (Putman et al., 2011), which can significantly alter wild boar movement and behaviour (Colomer et al., 2021; Olejarz et al., 2024; Tolon et al., 2009). Hunting pressure may displace individuals or drive them towards refuge areas, including those near pig farms, potentially contributing to increased contact rates during this period. The need for both males and females to accumulate fat reserves before the winter months

(Merta et al., 2014) could also explain the closer proximity to farmland, where feeding resources outside periods of masting are usually higher.

4.2 | Inter-individual differences

Individual differences appear to be central to our findings, as our results show that a small number of wild boars accounted for a disproportionately high number of contact events, suggesting that certain individuals may exhibit behavioural traits or occupy home ranges that increase their likelihood of visiting farms. Such patterns are consistent with growing evidence of individual variation in wild boar movement and personality traits, such as boldness or exploratory behaviour, that influence risk-taking tendencies (Brogi, Apollonio, et al., 2022; Keuling et al., 2009; Masilkova et al., 2025). Importantly, we found that nearly half (45%) of the wild boars with access to farms were detected within the boundary of at least one farm, and among these, some individuals were in contact with up to eight different farms. This suggests that certain wild boars could act as connectors between multiple farms, potentially facilitating farm-to-farm transmission of pathogens. Even with low average contact rates, these 'super-contact' individuals may play an outsized role in disease ecology (assuming they could be superspreaders as well). This highlights the importance of identifying and managing high-contact individuals and farm clusters in future surveillance and control efforts.

4.3 | Role of wild-boar density and proximity to farms

As predicted, the proximity of wild boar to pig farms and local wild boar population density were both positively associated with monthly contact rate, and this is consistent with previous findings across wildlife–livestock interfaces (Aschim & Brook, 2022; Woodroffe et al., 2016b). For instance, at the badger–cattle interface, contact rates increase with badger density and proximity to farms (Woodroffe et al., 2016b). These parallels reinforce that spatial proximity and local wild boar density are key drivers of contact risk and should be prioritized in strategies aimed at mitigating pathogen transmission at the wild–domestic interface.

4.4 | Environmental and spatial influences

Our results suggest that both natural and human-modified landscapes shape the risk of wild boar–pig farm contacts. Forest cover and the number of forest patches around farms increased contact rates, likely because such environments offer both shelter and food resources for wild boar (Morelle & Lejeune, 2015). The Human Footprint Index was also positively associated with contact rates. This suggests a complex dynamic: while natural features promote wild boar presence, human-altered landscapes, typically expected to reduce wildlife movement (Tucker et al., 2018), may still facilitate contact through the provision of anthropogenic food sources, such as crops or waste (Castillo-Contreras et al., 2021; Stillfried et al., 2017). For synanthropic species, such as wild boar, this could lead to locally high densities and increased contact with farm. The apparent overlap between human footprint and local wild boar density requires further investigation, as these factors likely interact in shaping wildlife–livestock interfaces (Jori et al., 2021; Magouras et al., 2020); confirming that, as human activity continues to expand into natural habitats, interactions at wild–domestic interfaces will become more frequent, possibly increasing the risk of disease transmission (Skinner et al., 2023).

4.5 | Implications of farm characteristics on contact

The observed patterns aligned with our predictions, indicating that larger farms (in terms of surface area) experienced more frequent wild boar contacts, possibly because of their greater spatial overlap with natural habitats. In contrast, farms with denser infrastructure, such as extensive concrete surfaces and clustered buildings, attracted fewer wild boars. This may reflect lower accessibility, a deterrent effect and potentially stronger biosecurity practices, although this remains to be validated with higher resolution farm-level information (Wu et al., 2012).

4.6 | Country-level variability in the contact rate

At both monthly and hourly scales, we observed variability in contact rates in most age–sex classes, as indicated by wide confidence in the model predictions (Table S5b). These divergences may reflect differences in individual behaviour or local conditions that were not fully captured by our models. Some of this variation is likely due to the broad geographic and ecological scope of our study. The continental-scale design encompassed a wide gradient of climate, habitat structure and human activity (Macchi et al., 2010), which can obscure fine-scale behavioural patterns. Our analysis revealed notable variations in contact rates between countries, with Hungary showing significantly higher contact levels than the rest of the study area (Figure S5). This suggests that broader landscape and farming system characteristics, which vary across countries, may influence the dynamics of contact. A European-wide assessment from 2014 reported a clear divide in pig production systems between Eastern and Western Europe, highlighting a higher proportion of small-scale, less intensive farms in Eastern countries, including Hungary (Marquer et al., 2014). While current data on these structural differences are limited, our findings suggest that including variables like pig density and farm area did not fully explain the elevated contact rates observed in Hungary. This underscores the need to consider regional agricultural practices and landscape contexts when assessing contact risks and designing mitigation strategies.

4.7 | Limitations

Despite the strengths of this study, namely high-resolution data, large sample size and broad geographic coverage across Europe, it has several key limitations. First, we lacked access to critical farm-level variables, such as biosecurity measures (e.g. fencing and deterrents), attractants (e.g. supplementary feeding) and farming system details (e.g. access/no access to outdoor areas, type of outdoor access, pasture vs. concrete runs, seasonal confinement). Because of this lack of detailed, standardized data, we used proxies (farm area, building coverage, pig density and surrounding land cover) to approximate the farm structure. Future studies should either aim to collect explicit husbandry data to assess disease risk more precisely or European authorities should ensure that these data are accessible for scientific research purposes. These data gaps and possible issues are due to data protection regulations (e.g. General Data Protection Regulation, GDPR), which limit our ability to interpret some results. Nevertheless, our findings demonstrate the value of collaborative frameworks and highlight the need for controlled data-sharing agreements that ensure privacy while enabling research to be conducted. We advocate for harmonized data collection protocols and a European data-sharing framework that reconciles GDPR compliance with scientific and public health priorities.

Second, the approach used to quantify farm area (digitalization using Google Earth images), which was relatively easy for farms located in rural contexts (e.g. farm limits being relatively well visible), became more speculative for farms in more apparent semi-extensive situations (open land, forest area), where the delimitation of the farm area could have led to possible under- or over-estimation bias. Third, the contact events we identified should be interpreted as *potential contacts or visits*, rather than confirmed direct interactions. Due to limitations in farm-level and GPS data accuracy, we could not determine whether these visits involved close physical proximity sufficient for disease transmission. Moreover, the term *contact* may be somewhat misleading in this context, as wild boars could enter or approach farm areas, deposit pathogens in the environment (e.g. contaminating soils, water sources and surfaces), representing a pathway for indirect transmission (Lange et al., 2016). This is a significant but unmeasured risk factor in our study. For instance, shared water sources and contaminated environments are known to facilitate the spread of disease (Yang et al., 2021). Water bodies often act as convergence points between wildlife and livestock (Cadenas-Fernández et al., 2019; Kukielka et al., 2013; Payne et al., 2016), and water scarcity, particularly in Mediterranean regions, is a strong driver of wild boar movement. With climate change increasing drought intensity across Europe, even temperate areas may experience altered dynamics that elevate the risk of indirect transmission. To address these limitations, future studies should integrate local-scale tools, such as camera traps, proximity sensors or environmental sampling, with GPS data to validate contact types and improve risk assessment at the wild–domestic interface.

4.8 | Implications for farm and wild boar management

Our results offer several practical recommendations for reducing the risk of contact at the wild–domestic pig interface. Farms located in high-risk areas, such as wooded landscapes or wild boar hotspots, should prioritize the implementation of enhanced biosecurity measures. These include double fencing (Hart et al., 2021), restricted access points and increased surveillance, particularly at night or during high-risk periods, such as summer and autumn. These recommendations are particularly relevant for small-scale or traditional/differentiated (Bonneau et al., 2011) holdings, which rely partly on outdoor or semi-outdoor production systems (e.g. pasture-based, wooded or fenced yard systems, and outdoor huts), especially in parts of Southern, Eastern and Mediterranean Europe (Nielsen et al., 2021). In these systems, pigs may spend part or all of their time outdoors, sometimes in proximity to forests or woodlands, which increases the permeability of the wildlife–livestock interface. Because outdoor-reared pigs are more exposed to environmental contamination, shared water or soil, or direct/wildlife contact, farms using such systems may be especially vulnerable to wild boar visits and pathogen spillover. For more intensive indoor farms, some measures remain relevant (e.g. deterring wild boar getting too close), but the risk profile may differ substantially.

While farms in low pig-density areas with little surrounding forest may pose lower risk, vigilance remains important across all systems, especially in (semi-)outdoor systems. Controlling wild boar populations around farms can also reduce contact rates. The uneven distribution of contact behaviour between individuals highlights the potential value of targeted management, which would focus on high-contact individuals or zones rather than relying solely on broad-scale culling. Although the selective removal of these 'super-contact' individuals could reduce short-term risks, it is unclear whether such interventions would have any long-term benefits. As contact patterns are primarily driven by structural factors, such as landscape configuration and farm attractiveness, new individuals may quickly fill available ecological niches and adopt similar behaviours. Therefore, durable risk reduction will likely require systemic approaches that address the underlying attractants and reinforce farm biosecurity, particularly in high-risk zones. Integrating environmental, farm-specific and temporal factors into both farm design and wildlife management will be critical to reduce the potential for pathogen spillover.

Although our study focused on Europe, our findings have broader global relevance. Wild boar is among the most widely distributed terrestrial mammals, with expanding invasive populations increasingly intersecting livestock systems in regions, such as North and South

America, Southeast Asia and Australia (Cowled et al., 2009; Miller et al., 2017; Sanchez-Vazquez et al., 2021). We recommend transposing our research approach to these introduced ranges, where the species is likely to reach uncontrollable, high-density populations compared with those of its native Eurasian range (Lewis et al., 2017; Melis et al., 2006). This would allow updating contact rates and the effect sizes of their drivers to better inform management, as our current estimates may be underestimated in such high-density regions.

AUTHOR CONTRIBUTIONS

Kevin Morelle and Elodie Wielgus conceived the ideas, designed the methodology and processed the data stored in the Euromammals database. Kevin Morelle, Elodie Wielgus, Rudy Brogi, Manisha Bhardwaj and Thibaud Porphyre analysed the data and interpreted the results. Kevin Morelle and Elodie Wielgus led the writing of the manuscript. Milos Jezek, Petter Kjellander, Simon Chamaillé-Jammes, Francesca Brivio, Rudy Brogi, András Nahlik, Tamás Tari, Alain Licoppe, Valerie De Waele, Alisa Klamm, Marco Apollonio, Janosch Arnold, Maik Henrich, Marco Heurich, Eric Baubet, Sonia Saïd, Stefan Suter, Claude Fischer, Jim Casaer, Thomas Scheppers and Stefano Focardi contributed data and provided critical feedback on the manuscript. All the authors contributed critically to the drafts, reviewed the manuscript and approved the final version for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The GPS data used in this study are subject to third-party data-sharing agreements and are permanently stored in the EUROBOAR spatial database (https://euromammals.org/euroboar/). EUROBOAR is an open project, and access to the data can be requested by contacting the relevant parties listed on its website. Pig farm data are not publicly available owing to confidentiality restrictions. The code and processed data underlying this study are available on GitHub and Zenodo at https://doi.org/10.5281/zenodo.18431781 (Morelle, 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Monthly distribution of individual-months used in the analyses. Bars represent the number of individual-months across the calendar year.

Figure S2. Examples of corrected pig farm: in red, the original location of the farm, and in green, the corrected location. To ensure privacy, the figures were intentionally blurred so that the location of the farms cannot be identified.

Figure S3. Impact of sampling frequency on the estimated number of monthly contacts between wild boars and pig farms. Each dot represents the number of contact events for an individual wild boar at different sampling intervals (15, 30, 60, 120, and 240 min). Data were collected from 34 individuals initially tracked with a 15-min interval and then subsampled at longer intervals. A linear mixed-effects model was used to assess the effect of sampling frequency on the number of contacts with individual identities included as random effects. No significant differences were observed in the estimated contact rates across different sampling frequencies, suggesting that the contact estimates are robust to variations in GPS sampling frequency.

Table S1. Summary of the linear mixed-effects model testing the impact of sampling frequency on the estimated monthly contact rate. The table shows the estimates, confidence intervals (CI), and p-values for the fixed effects of the model. The intercept represents the baseline contact rate at the 15-min sampling interval. Fixed effects for other sampling intervals (30, 60, 120, and 240 min) were compared with the 15-min interval. Random effects include the variance of individual IDs.

Table S2. Spatial autocorrelation test results for each study area.

Table S3. AIC comparison of candidate count models for farm-individual-month contact rates.

Figure S4. Cumulative distribution of contact events between individual wild boars (Panel A) and farms (Panel B). In both panels, the x-axis represents the ranked entities (individuals in Panel A and farms in Panel B) based on the total number of contact events, whereas the y-axis represents the cumulative number of contact events. The shaded areas represent the proportions of individuals or farms contributing to 50% (dark grey), 75% (medium grey), and 99% (light grey) of the total contact events. The corresponding numbers of individuals or farms required to reach these thresholds are shown in the figure.

Figure S5. Country-level random intercept estimates from the monthly contact model. Points represent the best linear unbiased predictors (BLUPs) of the country-specific random intercepts from the monthly contact GAMM (negative binomial distribution with log link), with horizontal bars showing approximate 95% confidence intervals.

Table S4. Country-level summary of potential contacts at the wild boar–domestic pig interface from two the wild boar and the domestic pig farm perspective. Values are means ± SD with observed ranges (min-max) in parentheses. “N farms in HR” refers to the average number of pig farms within wild boar monthly home ranges; “Contacted farms (%)” indicates the proportion of those farms contacted at least once. From the farm perspective, “N wild boars nearby” refers to the average number of GPS-tracked individuals with the farm in their monthly home range; “Contacting boars (%)” is the proportion of these boars that contacted the farm at least once.

Table S5a. Summary of the generalized additive mixed model (GAMM) describing monthly wild boar contact rates with domestic pig farms. Fixed-effect estimates (β), 95% confidence intervals (CIs), and *p*-values are reported for each predictor. The model includes a cyclic smooth of month stratified by sex and random intercepts for individual wild boar–farm combinations nested within country.

Table S5b. Summary of the generalized additive mixed model (GAMM) describing monthly wild boar contact rates with domestic pig farms including age- and sex-specific effects. Fixed-effect estimates (β), 95% confidence intervals (CIs), and *p*-values are reported for each predictor. The model includes a cyclic smooth of month stratified by sex and an interaction between age class and sex, with random intercepts for individual wild boar–farm combinations nested within country.

Table S5c. Model comparison for monthly wild boar contact rates with domestic pig farms. Models with and without age–sex interactions were compared using Akaike's Information Criterion (AIC), Bayesian Information Criterion (BIC).

Figure S6. Predicted monthly contact rates between wild boar and pig farms by age and sex, estimated using a generalized additive mixed model (GAMM) with a negative binomial distribution. Lines represent marginal model predictions for each age–sex class, while shaded areas indicate 95% confidence intervals. Dashed lines denote age–sex-specific relationships that were not statistically significant.

Table S6a. Summary of the generalized additive mixed model (GAMM) describing hourly wild boar contact rates with pig farms as a function of time of day and sex. Time of day is expressed in hours relative to sunset. Coefficients (β), 95% confidence intervals (CIs), and *p*-values are provided for each predictor. The model includes a cyclic smooth of hour stratified by sex and random intercepts for individual wild boar nested within country, as well as for month.

Table S6b. Summary of the generalized additive mixed model (GAMM) describing hourly wild boar contact rates with pig farms including age- and sex-specific effects. Time of day is expressed in hours relative to sunset. Fixed-effect estimates (β), 95% confidence intervals (CIs), and *p*-values are reported. The model includes a cyclic smooth of hour stratified by sex and an interaction between age class and sex, with random intercepts for individual wild boar nested within country and for month.

Table S6c. Model comparison for hourly wild boar contact patterns with pig farms. Models with and without age–sex interactions were compared using Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC).

Figure S7. Predicted hourly patterns of wild boar contact rates with pig farms by age and sex, estimated using a generalized additive mixed model (GAMM) with a negative binomial distribution. Time is expressed in hours relative to sunset. Lines represent marginal model predictions for each age–sex class, while shaded areas indicate 95% confidence intervals. Dashed lines denote age–sex-specific relationships that were not statistically significant.

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