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RANGE EXPANSION OF THE GOLDEN JACKAL (*CANIS AUREUS*) IN EUROPE

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Abstract

The golden jackal (*Canis aureus*) is undergoing one of the most rapid and extensive range expansions of any terrestrial carnivore in modern Europe, prompting an urgent need to understand its primary drivers. While climate warming has been widely invoked as a facilitating factor, quantitative evidence linking specific climatic thresholds to the expansion has remained limited. Here, we employ a species distribution modelling (SDM) framework using Maxent, calibrated with 840 spatially thinned occurrence records across Europe and evaluated across three independent climate databases (CliMond, WorldClim, and CMCC-BioClimInd). We apply SHAP (SHapley Additive exPlanations) analysis to hierarchically rank and interpret the contribution of individual climatic variables to predicted habitat suitability. Our models demonstrate robust predictive performance (AUC>0.7; continuous Boyce Index>0.7). SHAP analysis identifies five predominant drivers: Temperature Annual Range, Minimum Temperature of the Coldest Month, Temperature Seasonality, Isothermality, and Precipitation of the Warmest Quarter. Critically, the Minimum Temperature of the Coldest Month exhibits a sharp threshold effect, with suitability increasing rapidly above -15°C and peaking near -3°C, consistent with the hypothesis that the northward retreat of severe winter cold is a primary enabler of expansion. Our model predicts high habitat suitability for the golden jackal in polar regions of Norway and Russia, including areas above the Arctic Circle—a prediction that warrants cautious interpretation. This finding suggests that the species may tolerate climatic conditions traditionally considered prohibitive for a mesocarnivore, but confirmation of successful reproduction above the Arctic Circle remains limited. We conclude that the golden jackal's expansion is consistent with a climate-facilitated natural range shift, with direct implications for its legal status and management under frameworks such as the EU Habitats Directive. More broadly, our study illustrates the power of combining SDM with explainable AI to uncover the hierarchical climatic architecture underpinning rapid faunal change in a warming world.

Cite as

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Розширення ареалу шакала золотавого (*Canis aureus*) в Європі

Володимир Титар

Резюме. Шакал золотавий (*Canis aureus*) переживає одне з найшвидших і наймасштабніших розширень ареалу серед усіх наземних хижих ссавців у сучасній Європі, що зумовлює нагальну потребу в розумінні його основних рушійних чинників. Хоча потепління клімату часто називають фактором, що сприяє цьому процесу, кількісних доказів, які б пов'язували конкретні кліматичні порогові значення з розширенням ареалу, досі бракувало. Тут ми застосовуємо підхід, заснований на моделюванні видового ареалу (SDM), калібрований за 840 точками знахідок шакала по всій Європі та оцінений за трьома незалежними кліматичними базами даних (CliMond, WorldClim та CMCC-BioClimInd). Ми використовуємо аналіз SHAP (SHapley Additive exPlanations) для ієрархічного ранжування та інтерпретації внеску окремих кліматичних змінних у прогнозовану придатність середовища існування. Наші моделі демонструють високу прогностичну здатність (AUC>0,7; неперервний індекс Бойса>0,7). Аналіз SHAP визначає п'ять основних рушійних факторів: річну амплітуду температур, мінімальну температуру найхолоднішого місяця, сезонність температури, ізотермальність та кількість опадів найтеплішого кварталу. Критично важливо, що мінімальна температура найхолоднішого місяця демонструє різкий пороговий ефект: придатність середовища різко зростає вище –15 °C і досягає піку близько –3 °C, що узгоджується з гіпотезою про те, що відступ суворих зимових холодів на північ є основним чинником, який уможливлює розширення ареалу. Наша модель прогнозує високу придатність середовища для шакала в полярних регіонах Норвегії та Росії, проте це передбачення потребує обережної інтерпретації. Цей висновок свідчить про те, що вид може витримувати кліматичні умови, які традиційно вважалися неприйнятними для цього мезохижака, проте підтвердження успішного розмноження за Полярним колом залишаються обмеженими. Ми робимо висновок, що розширення ареалу шакала відповідає природному кліматично зумовленому зміщенню ареалу, що має безпосередні наслідки для його правового статусу та управління в межах таких рамкових документів, як Директива ЄС про оселища. Загалом наше дослідження ілюструє корисність поєднання SDM з пояснювальним ШІ для виявлення ієрархічної кліматичної структури, що лежить в основі швидких фауністичних змін у світі, який теплішає.

Ключові слова: *Canis aureus*, розширення ареалу, зміна клімату, Maxent, SHAP-аналіз, моделювання поширення видів.

Introduction

The expansion of carnivore vertebrates in Europe is one of the continent's most significant and surprising ecological stories of the past 50 years, often described as a 'carnivore comeback' [Chapron *et al.* 2014; Cimatti *et al.* 2021]. In this respect, after a population decline and recovery, the Eurasian golden jackal (*Canis aureus* Linnaeus, 1758), one of the southern carnivore species, not only recolonised its previous range, but is also expanding in Europe [Arnold *et al.* 2012; Trouwborst *et al.* 2015]. Recent research documents a substantial range expansion of the species across the European continent, with multiple studies from Central and Northern Europe [Krofel et al. 2017; Hatlauf et al. 2021; Ranc *et al.* 2022; Krofel *et al.* 2023; Kojola *et al.* 2024], as well as from Fennoscandia and the Baltic region [Rykov *et al.* 2022; Bogdanowicz *et al.* 2025]. Parallel evidence from Ukraine has been documented too [Rozhenko 2021; Voitko & Zagorodniuk 2022; Zhyla 2023]. Originally endemic only to fragmented areas along the Mediterranean and Black Sea coasts [Sommer & Benecke 2005], the species initiated a broad-scale dispersal during the twentieth century, a process that appears to have gained momentum in the past two decades [Trouwborst e*t al.* 2015; Spassov & Acosta-Pankov 2019; Bogdanowicz *et al.* 2025].

This rapid and extensive colonisation of novel regions has inevitably prompted an ecological and legal debate: should the golden jackal, a native species expanding its range so dynamically, be classified and managed as an invasive species? Prevailing scientific opinion argues that it should not. The jackal is considered a native component of the European fauna, with fossil records confirming its historical presence [Sommer & Benecke 2005]. Its contemporary expansion is interpreted as a natural recolonisation facilitated by climatic and human-induced landscape changes, rather than a direct anthropogenic introduction into a foreign ecosystem [Trouwborst *et al.* 2015; Krofel *et al.* 2017]. Consequently, under key legal frameworks like the EU Habitats Directive, it is protected as a native species. However, its status as an 'ecosystem newcomer' in many areas necessitates careful monitoring of its ecological and broadly speaking biological impacts, as its novel presence can still trigger significant shifts in local predator-prey dynamics and competition [e.g., Hayward *et al.* 2017; Gaál *et al.* 2025], enhance disease transmission by acting as a new host or vector for parasites like *Echinococcus multilocularis* or *Trichinella britovi* [Gherman & Mihalca 2017; Frey *et al.* 2022], facilitate hybridisation with dogs or wolves, posing a genetic risk [Galov *et al.* 2015], even spark sporadic jackal attacks on humans [Vodopija *et al.* 2016]. To sum up, the golden jackal's trajectory presents a critical test case for defining the boundary between a natural range expansion and a biological invasion.

There is a growing body of scientific literature that supports the role of climate warming as a major factor in the golden jackal's northward expansion in Europe [Arnold *et al.* 2012; Trouwborst *et al.* 2015; Krofel *et al.* 2017; Lanszki *et al.* 2022; Cunze & Klimpel 2022; Flores-Manzanero *et al.* 2026]. The messages in the literature are fairly clear: climate warming is not just a supporting factor but a primary enabler of the golden jackal's expansion into higher latitudes in Europe by reducing the critical limitation of harsh winters. The evidence is ecological, correlative, and increasingly modelled [Bijl *et al.* 2025; Cunze & Klimpel 2022], with ongoing research refining the interplay between climate and habitat. Importantly, a recent landscape-genomic study [Flores-Manzanero *et al.* 2026] has provided independent evidence that climatic predictors, especially variation in precipitation and temperature, are the primary drivers of genetic connectivity and local adaptation across the jackal's expanding range, lending strong support to the hypothesis that climate is central to this expansion process.

To quantitatively assess the primary driver of this expansion—anthropogenic climate change—this study employs a Species Distribution Modelling (SDM) framework [Franklin & Miller 2010]. Our analysis is explicitly designed to test the hypothesis that contemporary climate warming is the dominant factor enabling the species' northward shift. However, we acknowledge that a climate-only model cannot directly compare the relative importance of climate versus non-climatic factors (such as land use, prey availability, or wolf presence). Rather, our study tests whether current occurrence records are strongly associated with climatic gradients, and whether specific climatic thresholds can be identified that correspond to the expansion front. We first model the jackal's climatic niche by correlating available occurrence data with key bioclimatic predictors, particularly those related to temperature and winter severity. The resulting model will serve as a vital tool for management planning and identifying potential habitats for future surveys. It also can contribute to a proactive framework for zoonotic disease risk assessment and establishing a baseline for assessing the future impacts of climate change on this particular species. This research underscores the value of SDMs not merely as cartographic exercises, but as essential instruments for unravelling the ecological narratives that shape the species' niche [Soberón & Nakamura 2009; Soberón & Arroyo-Peña 2017].

To move beyond traditional correlation metrics and identify the drivers within the model, we then apply SHAP (SHapley Additive exPlanations) analysis. This technique allows us to attribute predictive power to specific variables, quantifying and ranking the contribution of climatic factors to the predicted suitability. While SHAP analysis does not convert a correlative SDM into a mechanistic model, it provides a rigorous framework for ranking variable importance and identifying the climatic gradients that most strongly constrain the species' distribution. These contributions can highlight which climatic thresholds, if crossed, would most alter predicted suitability, offering testable hypotheses for physiological studies. This ranking sharpens the focus for subsequent investigations and helps prioritise environmental covariates—natural or anthropogenic—for closer scrutiny in future model iterations. We interpret these patterns as evidence of climatic limitation, but remain cautious about claiming direct causation without experimental validation. If necessary, subsequent analyses can then integrate other (presumably secondary) anthropogenic variables to evaluate their influence within the established climatic envelope.

Materials and Methods

Distributional data

A total of 2395 occurrence records for *C. aureus* encompassing locations across Europe were downloaded from the open-access database of the Global Biodiversity Information Facility (GBIF, www.gbif.org, accessed 11 December 2025, https://doi.org/10.15468/dl.6dh5ax). The GBIF consolidates species occurrence data from various non-systematic sources, such as museum collections and administrative records [Moudrý & Devillers 2020], and facilitates biodiversity data sharing for research, conservation, and policy development [Chapman 2023].

For Ukraine efforts focused on collecting data from UkrBIN (http://ukrbin.com/), but more broadly from social networking sites, microblogs, and media sharing services, which support textual and visual content, and geotagging. These sites include social media platforms such as Facebook, Twitter/X, Instagram, and Flickr, where users share content in private networks or publicly online [Monkman *et al.* 2018; Toivonen *et al.* 2019; Chowdhury *et al.* 2026]. In our case such social media mining is reasonable and useful for biological research as far as the species in most cases is clearly recognisable. Search queries included Latin and vernacular names of the species in Ukrainian and Russian. Data, such as camera trap records, photos of dead animals, pugmarks, occasional sightings, droppings (Fig. 1 *a–b*) etc., indicative of jackal presence were extracted and then georeferenced (if they were not already geo-tagged).

Subsequently we reviewed these datasets by deleting unreliable or ambiguous and excluding those whose geographical location was not precisely defined. To address the inherent heterogeneity in data reliability—which ranges from expert-verified museum specimens to unconfirmed social media reports—we classified records into reliability categories following established protocols. Photographs (especially those from camera traps), specimens, and expert-verified observations were treated as high-confidence records. Indirect signs such as pugmarks and droppings were retained only when accompanied by photographs or when the observer was a recognised expert, and we conducted sensitivity analyses to confirm that excluding uncertain records did not qualitatively alter the main results.

To mitigate overfitting and increase model accuracy due to duplicate coordinates and sampling biases, we applied a spatial protocol performed in SAGA GIS using the ‘Remove Duplicate Points’ module [Conrad *et al.* 2015]. Further on, to reduce sampling bias and spatial autocorrelation spatial filtering/thinning was performed, which can improve model performance [Boria *et al.* 2014].

Fig. 1. Examples of the golden jackal registrations by: (*a*) direct sightings, Khortytsia Island, Zaporizhia, Ukraine. 05.08.2025. By Yuri Bataev (URL); (*b*) droppings (containing asparagus seeds), Tuzli Estuaries National Park, Ukraine. By Ivan Rusev. URL

Рис. 1. Приклади реєстрації шакала шляхом (*a*) прямих спостережень, Острів Хортиця, Запоріжжя. 05.08.2025. Автор: Юрій Батаєв (URL); (*b*) за послідом (в цьому прикладі з насінням спаржі), Національний парк Тузловські лимани. Автор: Іван Русєв. URL

Occurrence points were thinned to a minimum distance of 10′ using the ‘Points Thinning’ module in SAGA GIS. This corresponds with our 10′ (~18.5 km) resolution of environmental variables, ensuring that no grid cell contained more than one occurrence record [Radosavljevic & Anderson 2014]. In the end, the initial dataset was reduced to 840 record points. Years, the longitude and latitude coordinates (WGS84 datum) of the sample records were stored in an Excel database and converted into CSV format for the establishment of SDM models.

Modelling approach

The ‘flexsdm’ R (v. 3.3.3) modelling package [Velazco *et al.* 2022] was applied for projecting the potential geographic distribution of golden jackal across Europe. Spatial block partitioning was used to generate pseudo-absence and background points. For each model, we generated 10 000 background points from the calibration area defined as the intersection of the study extent (Europe) and the known dispersal range of the species, excluding areas outside the climatic envelope for which predictors were available. Pseudo-absence points were selected randomly from the background, with a ratio of 1 : 10 relative to presence points. The calibration area was defined using a 500-km buffer around all occurrence points, following standard practice for species with broad dispersal capacity. The ‘flexsdm’ package offers a wide range of modelling options.

Here, we tested out Maximum Entropy (Maxent) [Phillips *et al.* 2006]. This is one of the most popular SDM modelling methods. Maxent can construct simple to highly complex, nonlinear species–environment relationships using various transformations of variables termed features and represented by a number of feature classes (FC) of which we tested linear (‘l’), quadratic (‘q’), product (‘p’), hinge (‘h’), and threshold (‘t’). To reduce overfitting, Maxent uses a regularisation procedure to balance model fit with complexity, by penalising models based on the magnitude of their coefficients. Tuned models were built using regularisation multiplier values ranging from 0 to 4 with increments of 0.5 and the following FC combinations: ‘l’, ‘lh’, ‘lq’, ‘lqh’, ‘lqhp’, ‘lqhpt’, ‘lqp", ‘qhp", ‘qhpt’ [Mao *et al.* 2024]. Model selection was based on the continuous Boyce Index (CBI) as the primary criterion, with AUC and TSS used as secondary metrics. The final selected settings were: feature classes ‘lqhpt’, regularisation multiplier 1.5, with 10 000 background points and 5-fold spatial block partitioning.

The model’s predictive accuracy was measured using the widely recognised AUC statistic. AUC scores range from 0 to 1, with values closer to 1 reflecting strong discriminatory power in distinguishing habitat suitability [Fielding & Bell 1997] and the true skill statistic (TSS) where the value of > 0.4 is considered good, with the range of 0.4–0.8 indicating ‘good’ performance; a score of > 0.8 is considered excellent [Allouche *et al.* 2006; Zhang *et al.* 2015]. But whereas AUC remains a controversial criterion [Lobo 2008], for greater confidence we employed the continuous Boyce index, CBI [Boyce *et al.* 2002], one of the most reliable presence-only evaluation metrics, and also provided by the ‘flexsdm’ package. It is continuous and varies between −1 and +1. Positive values indicate a model that presents predictions that are consistent with the distribution of presences in the evaluation dataset, values close to zero mean that the model is not different from a random model [Hirzel *et al.* 2006]. Maps of habitat suitability in the GeoTIFF format were processed and visualised in SAGA GIS. Statistical data was analysed using the PAST software package [Hammer *et al.* 2001] and the R environment (https://www.r-project.org).

Environmental variables

Environmental variables focusing on aspects of climate were prepared to summarise important potential drivers of the ecological niche. That is, derivatives of temperature, precipitation, solar radiation, and soil moisture index were obtained from the CliMond archive [Kriticos *et al.* 2012]; http://www.climond.org. CliMond contains gridded historical climate data used at a 10′ resolution and collectively representing a statistical summary of temperature, precipitation, radiation, and soil moisture, primarily using historical data sourced from the WorldClim website [Hijmans *et al.* 2005]; https://www.worldclim.org and the Climate Research Unit datasets (URL).

We used CliMond as our source for climate data alongside the WorldClim set, which is used far more frequently by others, however the latter does not include data on radiation and soil moisture estimates that could be more ecologically relevant. Thirdly, we tested CMCC-BioClimInd, a high-resolution global dataset of bioclimatic indicators developed by the Euro-Mediterranean Centre on Climate Change [Noce *et al.* 2019]. Unlike standard bioclimatic variables (similar to those in WorldClim), it provides a comprehensive set of indices that capture essential characteristics of climate systems relevant to ecosystems and biodiversity. The indicators go beyond simple monthly means to include metrics on: extreme events (e.g., heatwaves, cold spells, drought), seasonal patterns (e.g., growing season length, timing of seasons), thermal and hydrologic thresholds (e.g., number of frost days, dry spells). Compared to the first two datasets, CMCC-BioClimInd is generally more comprehensive and up-to-date, built on a newer historical dataset.

Conditioning factors

Commonly used approaches recommend removing correlated predictor variables before modelling to avoid multicollinearity, which is reported to affect model projections [Zhao *et al.* 2022]. There are several statistical packages offering functions that reduce collinearity in predictors, in our work, however, they were not employed because the benefits of using all available variables may outweigh the drawbacks of collinearity. Latest research indicates that modelling with correlated climate variables increases accuracy of predictions [Hanberry 2023]. Moreover, complex models such as Maxent take advantage of existing collinearity in finding the best set of parameters [De Marco & Nóbrega 2018]. We acknowledge, however, that retaining correlated predictors complicates biological interpretation, as SHAP importance may be redistributed among related variables in ways that are not necessarily biologically meaningful. Therefore, while we present SHAP rankings as a useful heuristic for identifying the most influential climatic gradients, we avoid interpreting each variable as an independent mechanistic driver.

To further explore the impact of the considered above environmental factors, we employed a SHAP framework from XAI (i.e., eXplainable artificial intelligence) to rank and uncover the most influential drivers [Lundberg *et al.* 2018; Farooq *et al.* 2022]. With a SHAP approach there is no need to consider only uncorrelated environmental drivers. SHAP (SHapley Additive exPlanations) is a unified framework in explainable artificial intelligence used to interpret the output of any machine learning model by assigning each feature an importance value for a particular prediction. We post-processed the best model results with SHAP by comparing what a model predicts with and without the predictor for all possible combinations of predictors at every single observation. The predictors are then ranked according to their contribution for each observation and averaged across observations. Another useful item are dependence plots. In our case, the R package 'shap-values' (https://github.com/pablo14/; author Pablo Casas) in a modified version was used to perform the SHAP analysis. The application of SHAP for understanding the influence of environmental factors on species distribution has yet seen limited exploration, but is now being investigated more widely, for instance [Scavuzzo *et al.* 2022; Song & Estes 2023; Li *et al.* 2025; Buebos-Esteve & Dagamac 2025; Chen & Liu 2026].

Results

Model performance and the hierarchical drivers of expansion

Our species distribution modelling (SDM) analysis, conducted using Maxent across three distinct climate databases (CliMond, WorldClim, and CMCC-BioClimInd), yielded models with moderate to strong predictive performance (Table 1). Evaluation metrics confirmed model robustness, with AUC values and the continuous Boyce index ranging from satisfactory to excellent, and the TSS showing 'good' performance.

While these metrics confirm that our models capture the core climatic signal driving jackal distribution, it is worth noting that predictive performance, though robust, did not reach the threshold often considered 'excellent' (e.g., AUC > 0.9).

Table 1. Model performance across three considered climate databases and a combined list of top influential factors

Таблиця 1. Ефективність моделювання за трьома розглянутими кліматичними базами даних та об'єднаний список найважливіших впливових факторів

Model's predictive accuracy* (mean ± SD)	Climate databases			
	CliMond	WorldClim	CMCC-BioClimInd	Combined list of top influential factors
AUC	0.78 ± 0.05	0.82 ± 0.07	0.80 ± 0.06	0.83 ± 0.04
TSS	0.49 ± 0.09	0.55 ± 0.11	0.53 ± 0.10	0.57 ± 0.07
Continuous Boyce index	0.73 ± 0.16	0.79 ± 0.21	0.80 ± 0.07	0.91 ± 0.05

* AUC, area under the curve; TSS, true skill statistic; SD, standard deviation.

This pattern is not unexpected and, in fact, is characteristic of SDMs that deliberately focus on a single class of predictors. Indeed, the use of SDMs has allowed in many cases to identify climatic features that characterise a species' niche ('bioclimate envelope') [Franklin & Miller 2010]. However, predictive performance in such models often falls short of 'excellent' values precisely because ecological parameters beyond climate are necessarily omitted from the modelling framework, leading to an incomplete description of the species' distribution and niche [Hanspach *et al.* 2010]. In our case this could be expected as far as bioclimatic parameters alone were deliberately used in the exercise and it is reasonable to suggest that factors other than climate limit the distribution and shape the niche of the considered species. Including other biologically relevant parameters and non-climate variables can likely contribute important information to generated SDMs, especially when modelers have specific knowledge about how these variables relate to the species [Bucklin *et al.* 2016]. Nonetheless, in terms of climate (or specifically, the 'bioclimate') we consider our results provide a reliable statistical foundation for interrogating the climatic drivers underlying the recent and rapid expansion of the golden jackal across Europe.

To move beyond separate model performance and elucidate the specific drivers facilitating this expansion, we, as mentioned above, applied SHAP (SHapley Additive exPlanations) analysis. This explainable AI (XAI) approach allowed us to quantify and rank the individual contribution of each climatic variable to the habitat suitability predictions. To synthesise the most robust climatic signals, the top influencing variables from each database in our next step were combined into a unified set of ten predictors. A final Maxent model built using this combined variable set demonstrated enhanced predictive performance, particularly evidenced by the continuous Boyce index (see: Table 1, 'Combined list...' column), providing an optimised and statistically reliable foundation for identifying the primary climatic drivers of the golden jackal's recent expansion.

The final SHAP analysis on this aggregated set pinpointed five predominant drivers of the golden jackal's potential distribution (Fig. 3). The response curves for the top factors were largely inverted U-shaped, revealing that the golden jackal responds nonlinearly to climatic gradients, with habitat suitability peaking within specific optimal ranges. Interpreting these optima and the associated tolerance ranges through an ecological lens allows us to frame the species' expansion as a response to progressive climatic release from previously limiting conditions.

The central role of winter severity and seasonal climatic optima

Amongst the most influential variables across all models was the 'Temperature Annual Range', which in the final SHAP analysis unequivocally emerged as an overwhelming factor shaping the potential distribution of the golden jackal. The response curve for this variable indicates a strong positive relationship between moderate-to-high annual temperature ranges and predicted habitat suitability. This is consistent with the hypothesis that the jackal's expansion is favoured in regions where seasonal temperature variation is pronounced but within limits that avoid extreme continental climates.

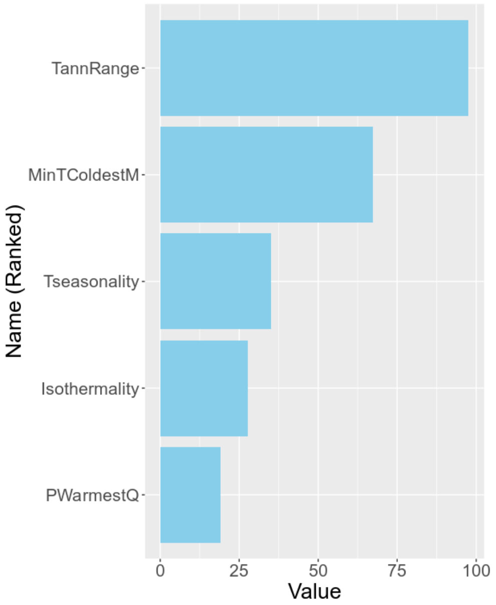

Fig. 3. Summary bar-plots of the average absolute SHAP values (multiplied by 1000) of the five top contributing to the Maxent model variables. The *y*-axis represents variables used in the study: TannRange (Temperature Annual Range), MinTColdestM (Minimum Temperature of Coldest Month), Tseasonality (Temperature Seasonality [standard deviation *100]), Isothermality, PWarmestQ (Precipitation of Warmest Quarter). The *x*-axis represents the corresponding SHAP value.

Рис. 3. Зведені стовпчасті діаграми середніх абсолютних значень SHAP (помножених на 1000) п'яти найбільших змінних моделі Maxent. Вісь у представляє змінні, що використовуються в дослідженні: TannRange (річний діапазон температур), MinTColdestM (мінімальна температура найхолоднішого місяця), Tseasonality (сезонність температури [стандартне відхилення *100]), Isothermality (ізотермічність), PWarmestQ (кількість опадів найтеплішого кварталу). Вісь x представляє відповідне значення SHAP.

The reduction in severity and duration of winter cold spells—a direct consequence of climate warming—likely diminishes a critical physiological constraint, enabling the species to colonise higher latitudes and more variable temperate environments. In other words, the optimum curve indicates the golden jackal is adapted to regions with moderate-to-high, but not extreme, annual thermal amplitude (~15–32°C range, with an optimum of around 24°C). This possibly reflects its evolutionary origins in seasonally variable climates of south-eastern Europe. This expansion pattern is likely driven by two key mechanisms. The first is the climate-mediated relaxation of the winter cold constraint: as minimum winter temperatures rise, the lower bound of the annual thermal range shifts upward, making northern climates increasingly suitable for a species adapted to the seasonal regimes of south-eastern Europe. The second is an upper-bound constraint: the jackal avoids hyper-continental interiors where the annual temperature range becomes excessively wide, supposedly due to associated extremes in both winter cold and summer heat.

The second-ranked factor, 'Minimum Temperature of the Coldest Month', further refines this picture. In almost all considered cases this factor consistently ranked high in SHAP importance, giving only once the way to the modified Kira coldness index (from the CMCC-BioClimInd dataset) which describes the amount of energy inputs in the coldest portion of the year; however, both are tightly correlated (Pearson's $r = 0.89$, $p<0.05$). The response curve for this factor reveals a clear threshold effect: suitability slowly increases where winter temperatures remain above a critical minimum (-15°C), but after the point of -7°C suitability rapidly rises reaching an optimum close to -3°C. This is consistent with the hypothesis that milder winters, rather than just warmer annual averages, are a primary enabler of northward and altitudinal range shifts. Temperatures below this minimum likely impose critical limitations through increased thermoregulatory costs and challenges in foraging through frozen ground or deep snow. The rapid northward shift of this specific isotherm due to anthropogenic climate warming is consistent with the mechanism enabling colonisation, effectively removing the most significant bioclimatic barrier that historically confined the species to southern Europe.

On the other hand, the significant importance of the 'Minimum Temperature of the Coldest Month' extends beyond direct physiological tolerance to encompass a key indirect effect: its role in governing snow depth and persistence. Across the European continent, minimum winter temperature acts as a critical threshold determining whether precipitation falls as rain or accumulates as a persistent snowpack. In continental interiors, where minimum temperatures routinely fall below -8°C to -12°C (e.g., mainland Estonia, interior Finland), sustained cold allows snow to accumulate deeply and persist for months, creating a formidable barrier to jackal movement, foraging, and prey access. By contrast, coastal and maritime regions benefit from thermal buffering, with minimum temperatures typically remaining above -3°C to +2°C. Here, snow accumulation is limited and ephemeral, leaving the landscape largely accessible throughout winter. The observed coastal preference of jackals in Estonia [Männil & Ranc 2022] thus reflects not a direct affinity for the sea, but an indirect avoidance of the deep, persistent snowpack that characterises the continental interior. This interpretation is supported by recent findings that climatic predictors, especially precipitation and temperature variation, strongly shape genetic connectivity patterns across the expanding range [Flores-Manzanero *et al.* 2026].

The combined importance of 'Temperature Seasonality' and 'Isothermality' points to the jackal's affinity for regions with predictable and moderate thermal regimes. High isothermality (a high ratio of diurnal to annual temperature variation) is characteristic of maritime-influenced climates. Values for these variables suggest the species thrives in environments with a strong, reliable seasonal rhythm but avoids areas with highly erratic or extreme continental temperature swings, which may correlate with unpredictable resource availability.

Finally, 'Precipitation of the Warmest Quarter' highlights a vital resource constraint during the period of peak energetic demand (such as pup-rearing or dispersal). The response curve indicates a preference for areas receiving moderate summer rainfall (between 140 and 190 mm). This ensures water availability, supports primary productivity, and maintains populations of key prey species during summer. This factor acts as a conditional filter, ensuring that newly climatically suitable areas also provide adequate resources for successful reproduction and population establishment.

Our Maxent model (Fig. 4) predicts high habitat suitability for the golden jackal in polar regions of Norway and Russia, including areas above the Arctic Circle. However, this prediction requires careful interpretation. Recent field records, camera-trap data, and genetic analyses confirm the species' presence in these high-latitude environments [Rykov *et al.* 2022; Kojola *et al.* 2024; Bogdanowicz *et al.* 2025]. Yet the distinction between presence of dispersing individuals, temporary occurrence, climatic suitability, establishment of resident populations, and confirmed reproduction is critical. While the model indicates that climatic conditions alone may not preclude jackal presence above the Arctic Circle, several records from northern Finland and Norway likely represent rare dispersal events rather than established breeding populations. Bogdanowicz *et al.* [2025] documented genetic evidence of individuals at the expansion front, but confirmed successful reproduction in the Arctic remains limited. Therefore, we interpret the Arctic prediction as indicating potential climatic suitability that warrants monitoring, not as evidence of established populations.

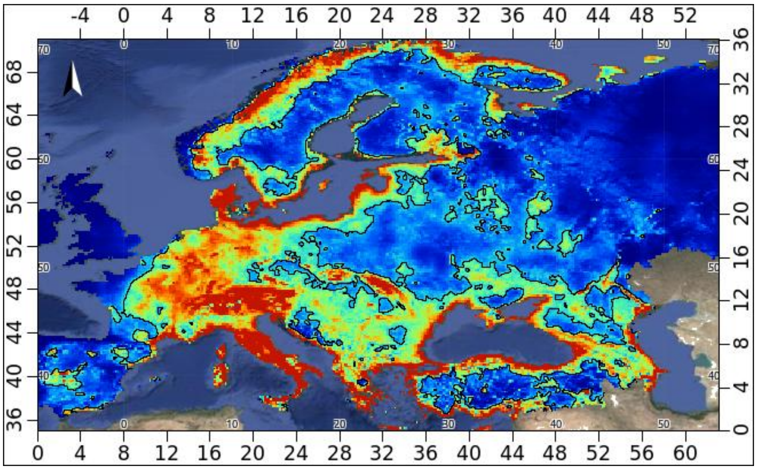

Fig. 4. The model output used to map habitat suitability for the golden jackal throughout Europe; colours show potential habitat suitability ranging from high (red) to low (blue).

Рис. 4. Результати моделі, що використовуються для картування придатності середовища існування для золотого шакала по всій Європі; кольори показують потенційну придатність середовища існування від високої (червоний) до низької (синій).

Discussion

Climatic drivers of expansion: interpretation and context

Our analysis reveals a clear and hierarchically structured climatic signature associated with the range expansion of the golden jackal in Europe. The five factors identified by SHAP analysis—Temperature Annual Range (BIO7), Minimum Temperature of the Coldest Month (BIO6), Temperature Seasonality (BIO4), Isothermality (BIO3), and Precipitation of the Warmest Quarter (BIO18)—do not operate in isolation. Instead, they form an interdependent bioclimatic syndrome that appears to define the species' fundamental niche and illuminates the mechanisms by which climate change may be facilitating its northward and westward dispersal.

The overwhelming importance of Temperature Annual Range (BIO7) underscores that the jackal is not merely a thermophilic species seeking warmer average temperatures, but a seasonal strategist adapted to environments with pronounced, yet predictable, annual thermal cycles. Its high suitability in areas with a broad annual range reflects its evolutionary origins in the seasonally variable climates of the Balkans and the Pontic region. Crucially, our models suggest that climate change is not eliminating this seasonal signal but is asymmetrically modifying its limits. The sharp, threshold-driven response of Minimum Temperature of the Coldest Month (BIO6), our second-ranked factor, provides a key insight: the expansion is fundamentally associated with the retreat of the harsh winter cold pole. As the -10°C isotherm shifts northward, it drags with it the lower boundary of the viable annual temperature range, effectively 'unlocking' vast territories of Central and Northern Europe that were previously thermally hostile. This aligns with the 'winter limitation hypothesis' posited in earlier correlative studies [Arnold *et al.* 2012; Krofel *et al.* 2017] and provides quantitative, model-based confirmation of the specific thermal threshold involved—though we emphasise that this remains a correlative relationship.

The secondary yet significant roles of Temperature Seasonality (BIO4) and Isothermality (BIO3) add a critical layer of nuance. They indicate that the jackal's niche is not defined by temperature extremes alone, but by thermal predictability. High seasonality (BIO4) represents a strong annual rhythm, while high isothermality (BIO3) suggests a climate where daily temperature variation is a dominant feature relative to annual variation—a pattern characteristic of maritime-influenced and some Mediterranean climates. The jackal appears to avoid regions with low isothermality and erratic seasonality, which are typical of hyper-continental interiors. This implies that the species' expansion may follow corridors of climatic stability, potentially using river valleys and coastal zones where maritime influences temper continental extremes, even as winters warm.

Finally, the inclusion of Precipitation of the Warmest Quarter (BIO18) as a top-tier factor highlights that release from winter cold may be a necessary but not sufficient condition for establishment. Successful reproduction and population persistence likely require resource security during the energetically demanding summer period. This hydrologic variable acts as a conditional filter, ensuring that newly climatically suitable areas also provide adequate prey availability and water sources during pup-rearing. This may explain why rapid colonisation is observed in agricultural and riparian landscapes across Central Europe, which often provide mesic microhabitats and abundant prey, even as the broader region warms.

These findings are broadly consistent with previous climatic niche modelling studies. Cunze & Klimpel [2022], using an ensemble forecasting approach, projected expansion of climatically suitable areas towards northern and western Europe, with possible stable populations in Central Europe. Our results extend this work by identifying specific thresholds (e.g., the -15°C to -3°C winter minimum range) and by demonstrating the hierarchical importance of multiple interacting climatic variables. However, we also note that Cunze & Klimpel [2022] found that some northern records occurred in areas not necessarily predicted as suitable by their model, underscoring the importance of distinguishing climatic suitability from actual establishment—a distinction we emphasise in our interpretation.

Recent landscape-genomic evidence [Flores-Manzanero *et al.* 2026] provides independent support for the climatic hypothesis. Using 363 golden jackals and 19 746 SNPs, this study found that, at finer spatial scales, genetic connectivity was best explained by climatic predictors, especially variation in precipitation and temperature. Future climatic conditions were projected to promote continued northward expansion. This genomic evidence suggests that climate is not merely correlated with occurrence but shapes the genetic structure and adaptive potential of the expanding population, lending support to the interpretation that climatic gradients are primary drivers of the expansion process.

Reconciling expansion with invasion: A climate-facilitated natural range shift

These results provide multi-variate evidence consistent with the hypothesis that the golden jackal's expansion represents a climate-facilitated natural range shift, rather than a human-mediated biological invasion. The SHAP analysis demonstrates that the expansion is aligned with changes in the species' fundamental climatic niche, particularly the relaxation of limiting winter minimum temperatures. The process is analogous to the post-glacial recolonisation of Europe by other species, but is now being compressed into decades rather than millennia due to anthropogenic forcing.

This distinction has profound legal and management implications. Classifying the jackal as an 'invasive alien species' under frameworks like the EU Invasive Alien Species Regulation would be ecologically and legally problematic, as it is a native species responding dynamically to environmental change. Our models support its continued protection under the EU Habitats Directive as a species requiring 'strict protection' (where listed in Annex IV), while also necessitating proactive, range-state-specific management plans. Its status as an 'ecosystem newcomer' [Trouwborst *et al.* 2015] remains apt, demanding monitoring not for eradication, but for understanding its integrative ecology.

Ecological consequences and future dynamics

The entry of a new, adaptable mesopredator into European ecosystems will inevitably create novel interactions. Our identification of summer precipitation as a key driver suggests that regions undergoing increased summer drought under climate change (e.g., the Mediterranean basin) may see a contraction or stagnation at the southern range core, while northern areas with stable or increasing summer precipitation will be most susceptible to colonisation. This could lead to a range shift rather than a pure expansion.

In newly colonised areas, the jackal's success will hinge on its ability to exploit anthropogenic food subsidies (e.g., agricultural waste, ungulate carcasses from hunting) and its interactions with extant predators. The potential for competition with red foxes (*Vulpes vulpes*) or for facilitated scavenging following wolf (*Canis lupus*) kills presents complex, location-dependent outcomes. Recent modelling by Serva *et al.* [2023] suggests increased overlap between golden jackal and Eurasian lynx ranges in Europe, indicating that changing carnivore communities may lead to novel interspecific interactions. Regional studies such as Karamanlidis *et al.* [2023] have documented that, at least locally, range expansion depends not only on climate but also on land use, habitat type, source-distance effects, and interactions with large carnivores—factors that our climate-only model does not directly address.

Furthermore, the jackal's role as a new host for parasites like *Echinococcus multilocularis* [Gherman & Mihalca 2017] underscores that the most significant impacts may be in the realm of disease ecology, an aspect partially flagged by its climatic niche's link to seasonal humidity.

Limitations and future directions

We acknowledge several important limitations of this study. First, our analysis is based exclusively on climatic predictors. A climate-only model cannot demonstrate that climate is more important than land use, prey availability, carrion resources, wolf presence, anthropogenic food subsidies, hunting pressure, dispersal corridors, or demographic source effects. Future research should integrate these non-climatic variables to assess their relative importance and to develop more comprehensive predictive models. The work of Karamanlidis *et al.* [2023] provides a valuable template for such integrated approaches, showing that land use and predator interactions significantly influence occupancy probability at regional scales.

Second, while SHAP analysis provides a useful ranking of variable importance, it does not convert a correlative SDM into a mechanistic model. The interrelated nature of temperature descriptors (annual temperature range, minimum temperature, seasonality, isothermality) means that SHAP importance values should be interpreted as indicating climatic gradients of influence, not as independent mechanistic drivers. Experimental studies or physiological measurements would be required to establish direct causation.

Third, the use of heterogeneous occurrence data, including social media records and indirect signs, introduces some uncertainty. While we applied filtering and sensitivity analyses to address this, some misidentifications may remain. Future studies should employ standardised field protocols and genetic verification to improve data quality.

Fourth, our predictions of high suitability above the Arctic Circle require cautious interpretation. While climatic conditions may not preclude jackal presence, evidence of established breeding populations in these regions remains limited. Many northern records likely represent dispersing individuals rather than residents, and the distinction between climatic suitability and actual population establishment requires further investigation.

Conclusions and forward look

In conclusion, our study employs an advanced SDM framework, powered by explainable AI (SHAP), to move beyond correlative mapping and dissect the drivers of one of Europe's most dynamic faunal changes. We provide evidence consistent with the hypothesis that the golden jackal's expansion is associated with anthropogenic climate change, primarily mediated through the abolition of critical winter cold thresholds. This finding supports the jackal's case as a flagship example of climate-facilitated natural range expansion.

Future research should focus on integrating these climatic models with fine-scale landscape variables (e.g., habitat connectivity, human footprint), including non-climatic factors such as land use and interspecific interactions, and, critically, with dynamic population data to forecast not just where the jackal *can* live, but where it will *thrive* and at what density. The recent genomic evidence [Flores-Manzanero *et al.* 2026] provides a promising avenue for integrating climate, connectivity, and adaptation. Such holistic forecasts are essential for developing adaptive management strategies that balance conservation, conflict mitigation, and the monitoring of ecosystem health in a rapidly changing Europe.

Declarations

Funding. This study was conducted on the author's own initiative.

Conflict of interest. The author has no conflicts of interest that could have influenced the content of this article.

Handling of material. The study did not involve the use of live or collected material.

Use of artificial intelligence. No generative artificial intelligence tools were used in the preparation of the manuscript; only basic language editing tools were applied.

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