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# ***Bioclimatic modelling of the spread of *Dirofilaria* spp. in Europe, with a special focus on Ukraine***

## ***Abstract***

**Background:** The zoonotic disease dirofilariosis, caused by *Dirofilaria* spp., is expanding geographically in Europe, a phenomenon increasingly linked to climate change. Understanding the environmental drivers of this spread is crucial for surveillance and public health planning.

**Objective:** This study aims to model the ecological niche of *Dirofilaria* spp. in Europe, identify key climatic drivers, and map areas of high transmission risk, with a specific focus on Ukraine.

**Methods:** We employed a Species Distribution Modeling (SDM) framework, using the Maxent algorithm correlated with high-quality occurrence data and climatic predictors from the CMCC-BioClimInd dataset. Model interpretation was enhanced using SHAP (SHapley Additive exPlanations) to identify and rank influential variables. A complementary Growing Degree Days (GDD) model was used to validate the thermal constraints on parasite development.

**Results:** The model achieved high predictive performance (AUC = 0.75, Boyce index = 0.93). At the European scale, the modified Kira warmth index, a measure of cumulative warmth, was the most important predictor, exhibiting a unimodal response curve that reveals a thermal optimum for transmission. For Ukraine, annual mean temperature and winter cold minima were the dominant drivers, reflecting the country's continental climate. GDD analysis confirmed a significant increase in thermally suitable areas in Ukraine from 2004-2024, indicating a likely northward expansion of transmission risk.

**Conclusion:** Climate, particularly temperature, is the primary determinant of *Dirofilaria* distribution. The identified unimodal response to cumulative warmth refines future risk projections, suggesting that while warming facilitates spread in cooler regions, it may reduce suitability in already-warm areas. The provided high-resolution risk maps for Ukraine offer a critical tool for targeting surveillance and control efforts.

**Key words:** *Dirofilaria*, species distribution modelling (SDM), climate change, vector-borne diseases, SHAP (SHapley Additive exPlanations), ecological niche, Ukraine, risk mapping.

## ***1. Introduction***

Vector-borne diseases continue to increase worldwide (Allen et al, 2017; Rocklöv, Dubrow, 2020). In this respect dirofilariosis is one of the most common vector-borne zoonotic diseases (Ionică et al., 2015; Capelli et al., 2018; Hattendorf, Lühken, 2025), affecting animals and humans across the entire world. The disease is mainly caused by *Dirofilaria* spp. (*D. immitis* and *D. repens*), with the primary reservoir being the domestic dog (McCall et al., 2008) and spread by various species of culicid mosquitoes. The duration of the development of the larvae inside the mosquito vector is strongly temperature dependent. It has been shown that development does not occur if the temperatures are below 14°C (Cancrini et al., 1995; Lok, Knight, 1998) and that the extrinsic incubation period shortens with rising temperatures (Medlock et al., 2007). In Europe the genera *Culex* spp. and *Aedes* spp. are the most important vectors for dirofilariosis occurring throughout the continent (Morchón et al., 2022). However, the number of competent vectors has increased significantly in the last years and new species of mosquitos able to transmit, for instance *D. immitis*, have been identified; moreover, the number of countries that have detected competent mosquitoes has also increased notably (Medlock et

al., 2012; Morchón et al., 2022). In this respect, one invasive species, *Aedes albopictus*, has been a game changer. Its biological and behavioral traits make it an exceptionally effective vector for *Dirofilaria*. This mosquito species has spread from southern to Central Europe and in the near future could move further northwards, changing the epidemiological patterns of dirofilariosis both in humans and animals (Genchi et al., 2009; Wałęka et al., 2023; Varga et al., 2025).

Humans act as accidental hosts (Simón et al., 2022). Yet, there is strong and consistent evidence that human infections with *Dirofilaria* species, particularly *D. repens*, are increasing in Europe and can largely be attributed to climate change considerably extending the habitation area of vector mosquitoes (Genchi et al., 2009; Simón et al., 2012; Capelli et al., 2018; El-Sayed, Kamel, 2020). The increase in temperatures favours the transmission of the disease to animals and humans by allowing the annual periods of activity of the mosquitoes to be lengthened and the stages of development of the larvae to be shortened. Consequently, the disease has expanded from traditional Mediterranean hotspots into Central and Eastern Europe (Fuehrer et al., 2021; Hattendorf, Lühken, 2025), including Ukraine (for instance, Sałamatin et al., 2013; Pękacz et al., 2025).

In such circumstances, surveillance data are key to understanding the epidemiological situation and taking action in at-risk areas, as well as to prioritizing management. Fortunately, recent extensive and high-quality data on the occurrence of dirofilariosis are available in Europe due to its medical importance (Hattendorf, Lühken, 2025). Today this allows to establish the influence of climate and characterize the ecological niche of the parasites, and to make spatially explicit predictions of their current habitat suitability using species distribution modeling (SDM). SDMs have become one of the most widely used tools in ecology, based on correlating species occurrences with environmental data to draw ecological and evolutionary inferences (Elith, Leathwick, 2009; Rathore, Sharma, 2023). This family of methods has a wide range of applications, including identifying areas where a species may occur, which in itself is a prerequisite for research planning and monitoring, and determining their suitability based on the observed relationship of the species to environmental conditions. SDMs in particular have been utilized by researchers as a powerful tool to characterize the ecological distribution of pathogenic species, to identify the habitats of undocumented disease, and thus to anticipate the areas at high risk for disease occurrence (Peterson, 2008; Costa, Peterson, 2012; Bui et al., 2017; Cenni et al., 2023).

Building on this context, the primary aims of this study are to leverage recent, high-quality surveillance data and species distribution modeling to better understand and predict the distribution of dirofilariosis. Our specific objectives are:

- to characterize the ecological niche of *Dirofilaria* spp. in Europe employing species distribution models (SDMs) by correlating occurrence data with key environmental variables based on different sets of predictors, with a focus on climate;
- to identify the environmental drivers affecting the distribution of dirofilariosis;
- to map the current habitat suitability for these parasites and identify high-risk areas for dirofilariosis in animals and humans to inform surveillance and public health strategies in Ukraine, thereby providing a critical tool for proactive monitoring and management.

Also we consider a complementary, physiologically-based approach, especially taking into account the strong temperature dependence for the development of the parasites within the mosquito (Kalluri et al., 2007), by employing a climate-based forecast system grounded in the

concept of Growing Degree Days (GDD)(Ghombavani, Ghahreman, 2011). This model addresses the temperature-dependent development of *Dirofilaria* larvae (Genchi et al., 2009), and through a spatial analysis in GIS, we can map the accumulated GDD and analyze areas of high transmission suitability, particularly during the indicative peak month of July (Genchi et al., 2005; Rinaldi et al., 2007).

## **2. Materials and Methods**

### **2.1. Distributional Data**

The geographic distribution data for *D. immitis* and *D. repens* were compiled primarily from a newly published by C. Hattendorf and R. Lühken (2025) systematic literature review on vectors, host range, and the spatial distribution in the 20<sup>th</sup> and 21<sup>st</sup> century, supplemented by records from the Global Biodiversity Information Facility (GBIF.org, 2025). The initial dataset comprised 2,402 occurrence points, encompassing locations across Europe and Türkiye. To mitigate spatial sampling bias and potential geolocation errors we, after removing duplicate occurrences, implemented a spatial thinning protocol performed in SAGA GIS using the 'PointsThinning' module (Conrad et al., 2015). As a rule of thumb, data points should be at least 2-3 cells apart in order to reduce autocorrelation (<https://damariszurell.github.io/EEC-MGC/index.html>). Following M. A. Nuñez and K. A. Medley (Nuñez, Medley, 2011), we measured the spatial autocorrelation of occurrences by calculating Moran's I for multiple distance classes using the GeoDa software (Anselin et al., 2022); values <0.3 were considered acceptable for building meaningful SDMs (Lichstein et al., 2002). Eventually, 491 record points describing acute infections were left for analysis. 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 the SDM model.

### **2.2. Modelling approach**

The 'flexsdm' R (v. 3.3.3) modelling package (Velazco et al., 2022) was applied for projecting the potential geographic distribution of *Dirofilaria* spp. across Europe. Spatial block partitioning was used to generate pseudo-absence and background points. Filtering the occurrence data was used to reduce sample bias by randomly removing points where they were dense (oversampling) in the environmental and geographical spaces. The 'flexsdm' package offers a wide range of modeling 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, quadratic, product and hinge. To reduce overfitting, Maxent uses a regularization procedure to balance model fit with complexity, by penalizing models based on the magnitude of their coefficients. Tuned models were built using regularization multiplier values ranging from 0 to 4 with increments of 0.5 and all possible FC combinations.

The model's predictive accuracy was measured using the widely recognized AUC statistic. AUC scores range from 0 to 1, with values closer to 1 reflecting strong discriminatory power in distinguishing habitat suitability for the considered species (Wang, 2007). Complementarily, we employed threshold-dependent measures: omission rates (OR) based on the sum of the sensitivity and specificity which is the highest (Zhang et al., 2023). It is a key metric, often presented alongside the AUC of the ROC plot. While AUC gives an overall picture, the OR

tells specifically about the false negative error. Under the applied threshold the resulting omission rate will vary but is usually in the 10-20% range. 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>).

### **2.3. Environmental variables**

Environmental variables focusing on aspects of climate were prepared to summarize 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 collectively, representing a statistical summary of temperature, precipitation, radiation, and soil moisture, primarily using historical data sourced from WorldClim (Hijmans et al., 2005; <https://www.worldclim.org/>) and the Climate Research Unit datasets ([www.cru.uea.ac.uk/cru/data/hrg/](http://www.cru.uea.ac.uk/cru/data/hrg/)). 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 are likely to be more ecologically relevant. Thirdly, we tested CMCC-BioClimInd, a high-resolution global dataset of bioclimatic indicators developed by the Euro-Mediterranean Center on Climate Change (Noce et al., 2019); <https://doi.org/10.1594/PANGAEA.904278>. 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 and higher-resolution historical dataset.

As mentioned above, we additionally employed a climate-based forecast system grounded in the concept of Growing Degree Days (GDD). To operationalize this, we leveraged in SAGA GIS the TerraClimate database (Abatzoglou et al., 2018), utilizing its high-resolution ( $1/24^\circ$ ,  $\sim 4$ -km) monthly climate data to compute GDD. This allows us to map, for key periods like July, the specific areas where thermal accumulation is sufficient to complete the *Dirofilaria* life cycle. The thermal accumulation of approximately 130-150 GDD (base  $14^\circ\text{C}$ ) is considered sufficient for the life cycle to be completed within a mosquito, allowing for the development of infective third-stage larvae (Genchi et al., 2009). Available terracclimate variables (maximum and minimum daily temperatures) can be downloaded using the 'TerraclimateR' package (<https://julianselke.github.io/TerraclimateR/>) and clipped to regions of interest by employing the 'terra' package (<https://cran.r-project.org/web/packages/terra/index.html>).

### 2.3.1. Conditioning factors

Commonly used approaches recommend removing correlated predictor variables before modeling to avoid multicollinearity, which affects model projections (Zhao et al., 2022). There are several statistical packages offering functions that reduce collinearity in predictors, however in our work they were not employed because the benefits of using all available variables may outweigh the drawbacks of collinearity. Latest research indicates that modeling 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).

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 (Nikraftar et al., 2025). 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. Also the package can produce SHAP partial dependence plots, a model agnostic visualization tool that helps understand the relationship between a variable and the model's prediction (Niemann et al., 2020). The application of SHAP for understanding the influence of environmental factors on species distribution has, until today, seen limited exploration, but is now being investigated much more widely (for instance, Scavuzzo et al., 2022; Song, Estes, 2023; Li et al., 2025; Buebos-Esteve, Dagamac, 2025).

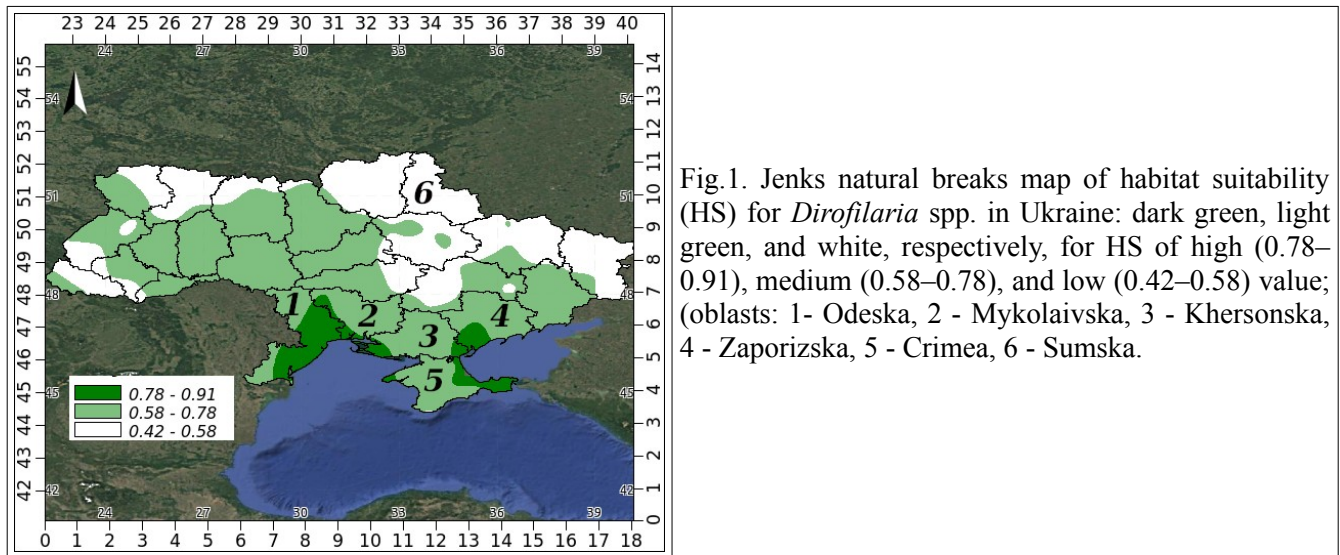
## 3. Results & Discussion

Using the three datasets of bioclimatic indicators described in Section 2.3, we projected the potential geographic distribution of *Dirofilaria* spp. across Europe. Among these, the projection based on the CMCC-BioClimInd dataset was identified as the most reliable (FC linear, regularization multiplier 0.5), with means±standard deviations of AUC reaching  $0.75\pm0.09$ , and a continuous Boyce index of  $0.93\pm0.02$ . The OR of  $15.9\pm0.08\%$  can be seen as a sign of good performance (Liu et al., 2005), indicating that the CMCC-BioClimInd dataset effectively simulates *Dirofilaria* species distribution.

Describing suitability for the species in each country (we focus on Ukraine) can help to quantitatively assess the risk of transmission and hence drive epidemiological surveys (Mwima et al., 2017). In general, the average habitat suitability for *Dirofilaria* is notably high in Ukraine ( $0.628\pm0.002$  SE); also high is the upper limit of HS, 0.906, indicating the presence of areas of high risk regarding dirofilariosis.

Areas in Ukraine affected by dirofilariosis are distributed unevenly, a pattern largely determined by the climate-dependent nature of the parasite's life cycle and requirements of its hosts. To visualize this the top-performing SDM was categorized into areas of low, medium, and high potential habitat suitability. These thresholds were defined using Jenks natural breaks,

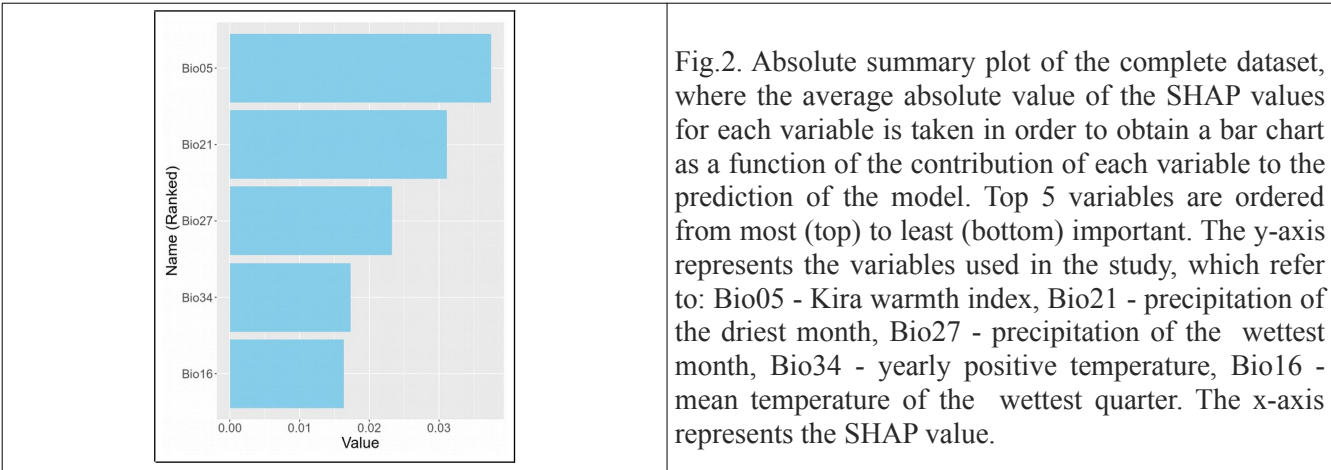
a method that optimizes the grouping of numerical variables by minimizing the deviation within each class while maximizing the deviation from the means of other groups. Jenks natural breaks provide a standardized approach to determining class intervals for continuous numerical variables (Jenks, Caspall, 1971). The corresponding map is presented in Fig.1. In fact, under current climate conditions the whole area of Ukraine is subjected to the risk of infection: from relatively low in portions of the north and north-east, and the Carpathian highlands, to high in the south, particularly regarding Odeska oblast and portions of territory adjacent to the Sea of Azov.



This north-south gradient in habitat suitability can be quantitatively examined by the thermal accumulation required for parasite development. A comparison of GDD between a high-risk southern region, such as Odeska oblast, and a lower-risk northern region, like Sumska oblast, clearly illustrates this climatic driver. For instance, the average in recent years (2015-2024) July GDD in Odeska oblast consistently exceeds  $274 \pm 0.6$  SE, sufficient for multiple parasite generations and leading to intense transmission pressure. This specific area is achieving a maximum of 316 GDD in a single month, which is characteristic of high-risk regions like the southeastern United States or other places of warm climates (Bowman et al., 2016; Walsh et al., 2020). In many northern temperate zones, the entire summer might only accumulate 200-250 GDDs. In contrast to the above, Sumska oblast accumulates within the considered month approximately  $191 \pm 0.5$  GDD (maximum 229), a level that reliably enables the completion of the parasite's life cycle, albeit typically favouring only a single generation per season and/or supporting a slow development cycle.

In terms of GDD dynamics, our analysis reveals a statistically significant increase ( $p < 0.05$ ) in GDD accumulation between the periods 2004-2014 and 2015-2024 for both Odeska and Sumska oblasts. This trend has direct and consequential implications for dirofilariosis risk. The rising thermal accumulation signifies a lengthening of the annual transmission window and an acceleration of the parasite's developmental rate within mosquito vectors. Consequently, the intensity of transmission in already endemic southern regions like Odeska has intensified. More critically, this shift has likely facilitated the geographic expansion of stable transmission into northern regions like Sumska, moving them from a marginal ( $166 \pm 0.8$  SE GDD) to a

consistently suitable habitat for the parasite's life cycle. This data provides quantifiable evidence that the changing climate is actively exacerbating the epidemiology of dirofilariosis in Ukraine.



Looking forward, climate projections from the CHELSA dataset (Karger et al., 2017) suggest a continuation of this warming trend. This implies a further lengthening of the transmission season and an even more rapid parasite development rate in mosquitoes, which will likely intensify the epidemiological burden in existing foci and propel further geographic expansion into previously non-endemic areas.

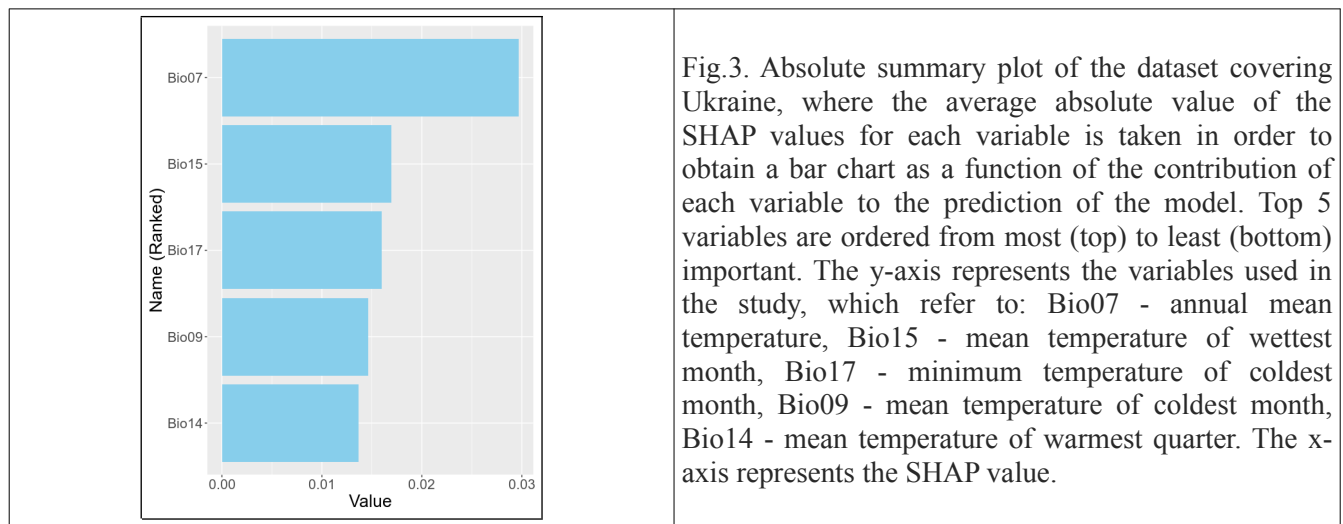
The goal of species distribution modeling is not just to build a predictive model but also to gain insights into the underlying ecological relationships. Here we present an overview of the SHAP values for the final models. We use the mean absolute SHAP value to rank the covariates based on importance. In terms of climatic predictors, the top 5 most important for SDM constructions from the CMCC-BioClimInd dataset at the European scale were (in ranked order): the modified Kira warmth index (Bio05, 0.0374), precipitation of the driest month (Bio21, 0.0311), precipitation of the wettest month (Bio27, 0.0232), yearly positive temperature (Bio34, 0.0173), mean temperature of the warmest quarter (Bio16, 0.0164). [In brackets: code and mean absolute SHAP value]. The corresponding barplot is presented in Fig.2. This analysis reveals that both temperature and moisture availability are critical for the species distribution models at the European scale, with a marked emphasis on temperature-related factors, particularly the modified Kira warmth index, the most important predictor, which broadly captures the cumulative warmth during the growing season. Described by Kira (1991), and partially modified, this indicator describes the amount of energy inputs in the warmest portion of the year.

The model's interpretation via SHAP values, however, shows that the biological response to this energy gradient is not a simple, linear increase. Instead, suitability peaks at an optimal range, of around 80-120 °C, resulting in a unimodal, or hump-shaped, response curve for this critical predictor. The following decline indicates that while warmth is beneficial, excessive cumulative warmth becomes stressful or lethal. The reasons are multifaceted but likely fall into two broad categories: thermal stress (Kartman, 1953; Mordecai et al., 2019) alongside with desiccation and habitat loss as far as high temperatures increase evaporation. The latter can lead to the drying out of the small, ephemeral water bodies (e.g., puddles, ditches, containers) that



many mosquito species rely on for oviposition. Also, extreme heat might reduce the availability of host animals (e.g., birds) for blood meals, as high temperatures can induce heat stress and suppress foraging activity in avian populations (Albright et al., 2017).

This nonlinear response can be crucial for predictive ecology and public health as far it can help to refine risk maps and inform climate change projections. The model with sufficient accuracy predicts that the highest risk is in areas with an optimal amount of cumulative warmth, not the maximum. Next, under climate change, some currently suitable regions may become less suitable if they become too hot and dry, while currently cooler regions may become more suitable as they enter the optimal range. For instance, cooler regions (e.g., Northern Germany, Southern UK) will see a possible rise in risk as they enter the optimal thermal window. Already warm regions (e.g., Southern Spain, Southern Italy) may see a stabilization or even a decline in risk as cumulative heat pushes them over the optimum into the stressful decline phase.



As for Ukraine alone, the top 5 most important predictors for SDM constructions from the CMCC-BioClimInd dataset were (in ranked order): annual mean temperature (Bio07, 0.0297), mean temperature of wettest month (Bio15, 0.0170), minimum temperature of coldest month (Bio17, 0.0160), mean temperature of coldest month (Bio09, 0.0147), mean temperature of the warmest quarter (Bio14, 0.0136). [In brackets: code and mean absolute SHAP value]. The corresponding barplot is presented in Fig.3. For Ukraine specifically, the model reveals a pronounced emphasis on temperature-related factors, with annual mean temperature emerging as the most critical predictor. The response curve for this variable is notably similar to that of the modified Kira warmth index at the European scale, a finding that is unsurprising given the strong correlation between cumulative warmth and mean annual temperature (Pearson's correlation coefficient 0.97,  $p < 0.05$ ). This consistency underscores the fundamental role of thermal energy in driving mosquito activity and parasite development. Furthermore, the high importance of minimum and mean temperatures of the coldest month (Bio17 and Bio09) highlights a key limiting factor: low winter temperatures. This is likely a direct consequence of Ukraine's stronger continentality (Kottek et al., 2006), where harsh winters can cause high mosquito mortality, thereby setting under current climate a critical southern boundary for the species' potential range and transmission risk that in the future could shift northwards.



#### 4. Conclusion

This study successfully leveraged species distribution modeling to delineate the ecological niche of *Dirofilaria* spp. in Europe and map its current habitat suitability, with a focused assessment on Ukraine. Our analysis unequivocally identifies thermal conditions as the paramount driver of distribution, with moisture availability playing a secondary, yet significant, role. The application of the SHAP framework provided nuanced, human-interpretable insights into these complex species-environment relationships, moving beyond mere prediction to ecological understanding.

The key findings of this work are threefold. First, at the continental scale, the modified Kira warmth index emerged as the most critical predictor, with a unimodal response curve that reveals a clear thermal optimum for transmission. This hump-shaped relationship, characterized by a decline in suitability beyond a cumulative warmth threshold, is a critical refinement for risk projections, indicating that the highest transmission risk is associated with an optimal amount of warmth rather than the absolute maximum.

Second, the Ukraine-specific model highlights a pronounced sensitivity to temperature, particularly the annual mean and the temperatures of the coldest month. This underscores the role of continentality, where harsh winter temperatures act as a key limiting factor, currently defining the southern boundary of stable transmission risk in the country's north. The strong correlation between the dominant predictors at European and national scales confirms the robustness of thermal energy as a fundamental determinant of the parasite's distribution.

Finally, the integration of the Growing Degree Days model provided a physiologically-grounded validation of these patterns. The significant increase in GDD accumulation between 2004-2014 and 2015-2024 in both southern (Odeska) and northern (Sumska) oblasts provides quantifiable evidence that climate change is actively intensifying transmission pressure in endemic areas and facilitating the northward expansion of the parasite into previously marginal or non-endemic regions.

In conclusion, the models presented here serve as powerful tools for public health and veterinary preparedness. The generated maps identify high-risk areas within Ukraine, such as Odeska and territories nearby the Azov Sea, which should be prioritized for surveillance, proactive veterinary testing, and public awareness campaigns. Furthermore, the identified thermal thresholds and nonlinear responses are essential for developing accurate, dynamic forecasts of dirofilariosis risk under future climate scenarios, enabling a proactive rather than reactive approach to managing this emerging zoonotic threat.

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