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Patterns of West Nile virus vector co-occurrence and spatial overlap with human cases across Europe

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ABSTRACT

Its geographic range expansion and rising incidence make West Nile Virus (WNV) a major public health challenge in Europe. Although numerous studies have investigated geographic variation in WNV incidence in humans or equines, most have focused on climate and land-use factors; however, the implications of vector co-occurrence and niche overlap remain largely unexplored. Identifying areas where highly competent vectors overlap with favourable environmental conditions is crucial for determining areas at risk for future WNV outbreaks.

We analysed the distribution and habitat suitability of four *Culex* mosquito vectors across Europe using an ensemble of six modelling techniques and relevant environmental variables. We generated probability maps, converted them into binary distribution maps through threshold-based methods, and weighted them by WNV vector competence to identify hotspots of vector co-occurrence and human cases.

Our findings indicate that WNV vectors are unevenly distributed across Europe, with southern regions emerging as hotspots, particularly due to the presence of highly competent vectors such as *Culex univittatus* s.l., *Culex modestus*, and *Culex pipiens*. The overlap of *Cx. modestus*, *Cx. torrentium*, and *Cx. pipiens* in central, western, and eastern Europe indicates that competent WNV vectors are present in nearly all European regions. Among the environmental factors analysed, mean winter temperatures were the most influential, suggesting that mild winters could increase the distribution of WNV competent vectors. Our results also revealed a strong spatial overlap between hotspots of human WNV cases and vector co-occurrence, highlighting regions of elevated transmission risk.

The high-risk hotspots identified in this large-scale study can guide local surveillance efforts and optimize resource allocation, ultimately enhancing the effectiveness of WNV surveillance.

Recent assessments of the impact of global change on vector-borne diseases have highlighted the growing risk of West Nile Virus (WNV) in Europe [1,2]. This concern arises from the increasing number of human cases and the expanding geographic range of affected areas. During the second half of the 20th century, WNV caused geographically isolated and sporadic outbreaks in Europe. However, in recent decades, the virus has experienced a significant increase in human cases across Europe (2083 in 2018, 1340 in 2022 and 1436 in 2024), has become endemic in many southern European countries, (ECDC), and has been spreading towards northern latitudes [3,4]. This increasing WNV incidence over the past decade in Europe's temperate zones has become a significant concern for citizens, public health officials, and epidemiologists promoting numerous research efforts to map the risks associated with WNV. Multiple factors may contribute to this rising trend. Although climate change is regarded as one of the primary factors [5], others factors such as urbanization [6], agricultural practices [7,8], ecological interactions [9], and vector feeding behaviour [10], among others may also play a crucial role in the expansion of the pathogen. These studies have primarily aimed to explain the incidence of reported human and equine cases in relation to environmental factors [11,12], whereas modelling vector distribution and associated risks has typically been conducted at a regional and local scale [12–15].

In Europe *Cx. pipiens* and *Cx. modestus* have been identified as the primary vectors responsible for WNV transmission [16]. *Culex pipiens* is widely distributed across Europe's temperate climate zones, with the majority of WNV transmission studies focusing on this species [17]. Two

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different biotypes and their hybrids coexist in Europe, with different potential impact in the amplification and transmission of WNV [18]. *Culex pipiens pipiens* is proposed to have a more ornithophilic diet while *Culex pipiens molestus* may feed more readily on humans, acting as potential bridge vector between infected birds and humans. However, while these ecological differences in foraging behaviour hold in northern Europe, in southern Europe both biotypes present similar feeding preferences [19]. *Culex. modestus* is known for its high transmission rate and implication in virus amplification during several outbreaks in France [20]. Recent studies have highlighted the importance of other species. In northern Europe, *Cx. torrentium* is an important vector [21], and in southwestern Spain, *Culex perexiguus*, a species included in the *Univittatus* subgroup (together with *Cx. univittatus),* here upon named as *Cx. univittatus* s.l, plays a key role in WNV transmission [16,22].

Despite the recognized importance of these mosquito species, a significant research gap remains regarding their suitability distribution across Europe and the environmental factors (e.g., land-use and climate) that influence their presence. This gap is particularly concerning given the potential for these species to co-occur in certain regions, which could significantly increase the risk of WNV transmission. Understanding where these species are likely to coexist along with their synergistic effects, is crucial for predicting and mitigating the spread of WNV across the continent. In areas where multiple vector species overlap, their interactions can result in complex transmission dynamics [23]. This is due to different species playing distinct roles in the virus amplification and the transmission to humans. For example, highly ornithophilic mosquito species contribute to rapid virus amplification in the sylvatic cycle by primarily feeding on birds [9,24,25]. In contrast, other species that feed on both birds and humans may act as bridge vectors, facilitating the transmission of the virus to humans [22]. Efforts to understand vector distribution and co-occurrence have largely focused on Africa and Asia. Meanwhile, the few existing models for Europe and North America often overlook key vectors of emerging diseases like WNV, emphasizing the pressing need for more comprehensive studies in these regions (e.g., [26]).

To address this gap, we conducted a comprehensive assessment of the distribution and co-occurrence of four key WNV vectors in Europe: *Cx. pipiens* complex, *Cx. modestus*, *Cx. torrentium* and *Cx. univittatus* s.l.. Using relevant environmental factors, along with an ensemble of six modelling techniques, we mapped the current spatial distribution of these vectors and identified the environmental factors influencing their distribution. We then combined the mosquito distributions and weighted them by WNV vector competence to determine high-risk areas based on vector co-occurrence and competence, identifying regions where the incidence of WNV is likely to increase in the coming years.

1. Materials and methods

1.1. Species occurrence data

We obtained mosquito occurrence data from the Global Biodiversity Informatics Facility (GBIF, www.gbif.org) using the third-party "*rgbif*" R package [25]. In addition to the GBIF data, we extracted occurrence records from several published studies, including those for *Cx. pipiens* [13,27,28]. A single model was built for *Cx. pipiens* species complex, because Cx. *p. pipiens* and *Cx. p. molestus* and their hybrid forms can not be identified morphologically and not enough spatial information is available to model their distribution separately. For *Cx. univittatus* s.l. and *Cx. modestus*, we gathered additional data from Ferraguti et al. 2021 [29]. To ensure data quality, we used "*CoordinateCleanir*" R package [30] to scan occurrence datasets for geo-referencing accuracy, temporal precision, and data entry errors. This method allowed us to verify the accuracy and reliability of the geographic coordinates obtained from the GBIF dataset. After integrating the GBIF data with additional data sources, we applied a grid-based thinning process, retaining only one occurrence point per 4 km to ensure spatial independence and to avoid spatial autocorrelation. After data cleaning, the final dataset included the following occurrence points for each mosquito species: *Cx. pipiens* ($n = 2532$), *Cx. modestus* ($n = 220$), *Cx. univittatus* s.l. *(*$n = 189$), and *Cx. torrentium* ($n = 301$).

1.2. Environmental variables selection and preprocessing

To explore the association between climatic factors and the distribution of *Cx. pipiens*, *Cx. modestus*, *Cx. univittatus* s.l.*,* and *Cx. torrentium,* we obtained monthly data from the "*TerraClimate*" dataset [31]. This dataset provides monthly global time-series data for minimum and maximum temperatures and precipitation, actual and potential evapotranspiration, wind speed, climate water deficit, vapor pressure and the Palmer drought severity index (PDSI), with a spatial resolution of approximately 4 km. Our analysis focused on the period from 1990 to 2023, corresponding to the availability of species occurrence data. We used temperature and precipitation data to derive the set of bioclimatic variables for each year within this period, using R package "*dismo*" [32], and then averaged them over the 33-year span. For all other variables, we used the monthly and seasonal average across the entire study period.

To explore the association between mosquito vectors and land-use, we included the CORINE-land-cover 2018 from Copernicus (European Union's Earth observation program). The CORINE dataset is available in shapefile format with 44 land cover classes. To reduce the complexity of the analysis, we reclassified original categories into seven land cover classes: urban area, urban green space, irrigated lands, agricultural lands, inland waters (water bodies), open spaces (e.g., beaches, dunes, sands, bare rocks, burnt areas, glaciers, and perpetual snow), and natural ecosystems (e.g., broad-leaved forest, coniferous forest, mixed-forest, natural grasslands, moors and heartland, sclerophyllous vegetation, transitional woodland-shrub, and sparsely vegetated areas). The proportion of each of the seven land-cover categories was calculated within each 4 × 4 km grid of species ranges. All the analyses were carried out in RStudio version 4.4.0 (R Core Team 2024).

In addition, we incorporated two remotely sensed indices from MODIS products: the Normalized Difference Vegetation Index (NDVI), which measures vegetation health and density; and the Normalized Difference Water Index (NDWI), which assesses water content in water bodies. These indices were included based on the assumption that they provide insights into the environmental conditions that support vector habitats.

To address multicollinearity, we assessed both pairwise correlation and Variance Inflation Factor (VIF). For highly correlated pairs ($r > 0.8$), we retained the variable with greater ecological relevance or stronger association with species presence, and then used VIF to identify and remove more complex multicollinearity patterns. After performing the multicollinearity test, we explored different subsets of models for variable selections, following the principles of parsimony. The subsequent inclusion or exclusion of variables was determined by their statistical significance and contribution to the overall performance. Variables that showed low predictive power or did not meaningfully enhance the model performance were systematically excluded from the final model to ensure both accuracy and simplicity. After applying variable selection and conducting multicollinearity tests, we retained with the final set of variables we used in the final models (See Table S1).

1.3. Statistical analysis

We modelled the distribution of these four *Culex* species as main vectors in Europe as a function of the different environmental variables. To enhance the robustness of our models, we used an ensemble modelling framework [33] that integrated six different algorithms: generalized linear models (GLM; [34]), generalized additive models (GAM; [35]), random forest (RF; [36]), boosted regression tree (BRT; [37]), multivariate adaptive regression splines (MARS; [37]) and

Maximum Entropy (MaxEnt; [38]). Ensemble modelling effectively addresses uncertainties associated with model selection and variability by incorporating multiple models with different algorithms, data, and assumptions. Here, we used an ensemble based on weighted averaging, where individual models were weighted according to their (TSS) performance. This approach improves prediction accuracy and provides more robust and reliable insights by reducing the impact of individual model limitation errors (see also [39]).

Since independent data for testing were unavailable, we employed two data splitting methods: bootstrap sampling and cross-validation to evaluate model accuracy, with 100 replications for each method. Because the species points are presence-only, we generated background points throughout the entire study area with 5000 random backgrounds with 10 times repetition with a certain geographical distance from the presence points [40]). Background points were sampled randomly within a 20 km radius of the presence points.

As a result, a total of 30,000 replications (6 algorithms × 100 evaluation runs × 10 sets of background samples × 5 cross validation) for each species were generated. We then generated a consensus model, using the weighted average probability for vector data, where the weight was obtained from the True Skill Statistics (TSS) in evaluation data. For ensemble modelling, only models with mean TSS ≥ 0.75 among all evaluations were selected.

To assess habitat suitability based on environmental constraints, we converted probabilistic outputs into binary maps (presence/absence) using the Max (Sensitivity + Specificity), which is the recommended threshold technique [41]. Values above or equal to the threshold are classified as predicted species presences, whereas values below the threshold were classified as predicted absences. We then weighted the binary maps for each species based on their vector competence. Vector competence was estimated as the proportion of mosquitoes with a disseminated infection relative to the total number of exposed mosquitoes, and can, therefore, be considered the dissemination rate within a vector population. The vector competence for different species of *Culex* mosquitoes was calculated from results of published experimental infections: *Culex univittatus* sl. = 0.92 [42], *Cx. modestus* = 0.54 [43], *Cx. torrentium* = 0.36 [21] and *Cx. pipiens* = 0.16 [43].

These maps were then combined to create a cumulative risk map, incorporating both vector presence and competence. The greater the values in each grid cell, the higher the associated risk, allowing us to visualize areas with varying levels of WNV vector suitability (Fig. S1). In addition, we quantified the pairwise niche overlap between the four vector species using Schoener's D [44] and Horn's R metrics [45]. Schoener's D measures the absolute overlap in environmental space and Horn's R accounts for relative similarity and species dominance. Both metrics measure niche overlap between species ranging from 0 (no overlap) to 1 (full overlap). We also conducted a Hot Spot Analysis using the Getis-Ord Gi* statistic to assess whether regions with a higher frequency of WNV cases correspond to areas with greater vector co-occurrence. This was done by considering the spatial neighborhood of each NUTS. The Gi* statistic quantifies for each spatial unit (NUTS) whether the concentration of a specific attribute such as the occurrence of WNV or the presence of vectors is statistically significantly different from what would be expected under a random spatial distribution. This statistic generates z-scores that indicate clustering intensity: larger z-scores point to "hot spots" of high values, while smaller z-scores reveal "cold spots" of low values.

2. Results

The ensemble of six modelling techniques showed distinct patterns of individual mosquito vector distribution and co-occurrence, with varying degrees of spatial overlap and risks associated with vector competence. *Culex pipiens,* thrived in the Temperate Oceanic Climate (Cfb), characterized by mild temperatures and low seasonal variation (e.g., western Europe), as well as the Temperate Humid Subtropical Climate (Cfa), with hot summers and mild winters (e.g., Northern Italy, the Balkans). This species is also adapted well to the Mediterranean Climate (Csa) in southern Europe, however, its suitability declined at higher elevations, particularly in mountainous regions such as the Alps (Fig. 1a).

Similarly to *Cx. pipiens*, *Cx. modestus* showed broad suitability across a wide range of the temperate and Mediterranean climate zones in Europe. Its distribution extended from southern Europe to western, central and eastern Europe, including the Balkans and the south of the UK. However, its suitability decreased in higher latitudes and altitudes (Fig. 1a).

In contrast, *Cx. univittatus* s.l. displayed a more restricted range, primarily confined to Southern Europe, favoring Mediterranean climates. Its presence was notable in regions such as Southern Spain, Portugal, Cyprus, Greece, and Turkey. *Culex torrentium*, although partially overlapping with *Cx. pipiens* was predominantly found at northern latitudes. Its highest suitability occurred in Temperate Oceanic (Cfb) and Humid Continental (Dfb) climates, particularly in Scandinavia and the UK (Fig. 1a).

Habitat suitability for the four *Culex* species in Europe increased with rising mean temperatures during the coldest month, particularly when paired with moderate precipitation. Notably, when the average temperature during the coldest month reached 5 °C or higher, the likelihood of species presence significantly increased (Fig. 1b, Fig. S2). Additionally, the mean temperature during the coldest month accounted for more than 50 % of the model's predictive accuracy in determining species distribution (Fig. 2). Other variables, such as the NDWI and the PDSI, contributed less than 7 % to the model's predictive accuracy. However, for *Cx. torrentium*, the contribution of these variables were higher, reaching 15.5 % for NDWI and 29.7 % for PDSI, respectively.

Although bioclimatic variables, particularly temperature, played a significant role in shaping the distribution of *Culex* mosquitoes across Europe, land-use variables and NDVI generally showed very little to no apparent influence at this scale and were removed from the final model. In general, our models demonstrated strong performance, achieving a mean TSS > 0.75 and a mean AUC > 0.9 (Fig. S3).

The spatial overlap of four *Culex* vectors in Southern and Northern Europe revealed different patterns of coexistence. In Southern Spain and Portugal, *Cx. pipiens*, *Cx. modestus*, and *Cx. univittatus* s.l. coexist, potentially increasing the risk of WNV transmission. This elevated risk is particularly concerning due to the high vector competence of *Cx. univittatus* s.l. (0.92), which is further intensified by the presence of *Cx. modestus* (0.54) and *Cx. pipiens* (0.16) (Fig. 4a). In contrast, in Western and Eastern Europe (e.g., Germany, the Netherlands, Belgium, Hungary, Czechia, and Poland), *Cx. pipiens*, *Cx. modestus,* and *Cx. torrentium* (vector competence = 0.36) co-occurred frequently together, indicating different dynamics in vector populations and varying transmission risks in these regions (Fig. 4a).

The pairwise niche overlap analysis in geographic space revealed a high overlap between *Cx. pipiens* and *Cx. modestus*, with geographic similarity ranging from 79 % (Schoener's D) to 92 % (Horn's R), indicating that approximately 90 % of the suitable areas for *Cx. pipiens* were also favourable for *Cx. modestus*. Similarly, *Cx. torrentium* shared a substantial portion of its geographic range with *Cx. pipiens*, with overlap values between 44 % (Schoener's D) and 65 % (Horn's R), suggesting that about half of the areas occupied by *Cx. pipiens* were also suitable for *Cx. torrentium* (Fig. 4b).

The niche similarity between *Cx. modestus* and *Cx. torrentium* was moderate ranging from 36 % (Schoener's D) to 53 % (Horn's R), meaning both vectors shared considerable portions of their geographic ranges but may exhibit distinct environmental preferences in certain areas (See also Fig. S4). Additionally, *Cx. univittatus* s.l. showed low to moderate overlap with *Cx. modestus* (Schoener's D = 0.18 and Horn's $R = 0.36$) and *Cx. pipiens* (Schoener's D = 0.17 and Horn's $R = 0.34$). In contrast, we found a very low spatial overlap between *Cx. torrentium* and *Cx. univittatus* s.l., indicating highly distinct geographic and environmental spaces with little likelihood of co-occurrence for both vectors

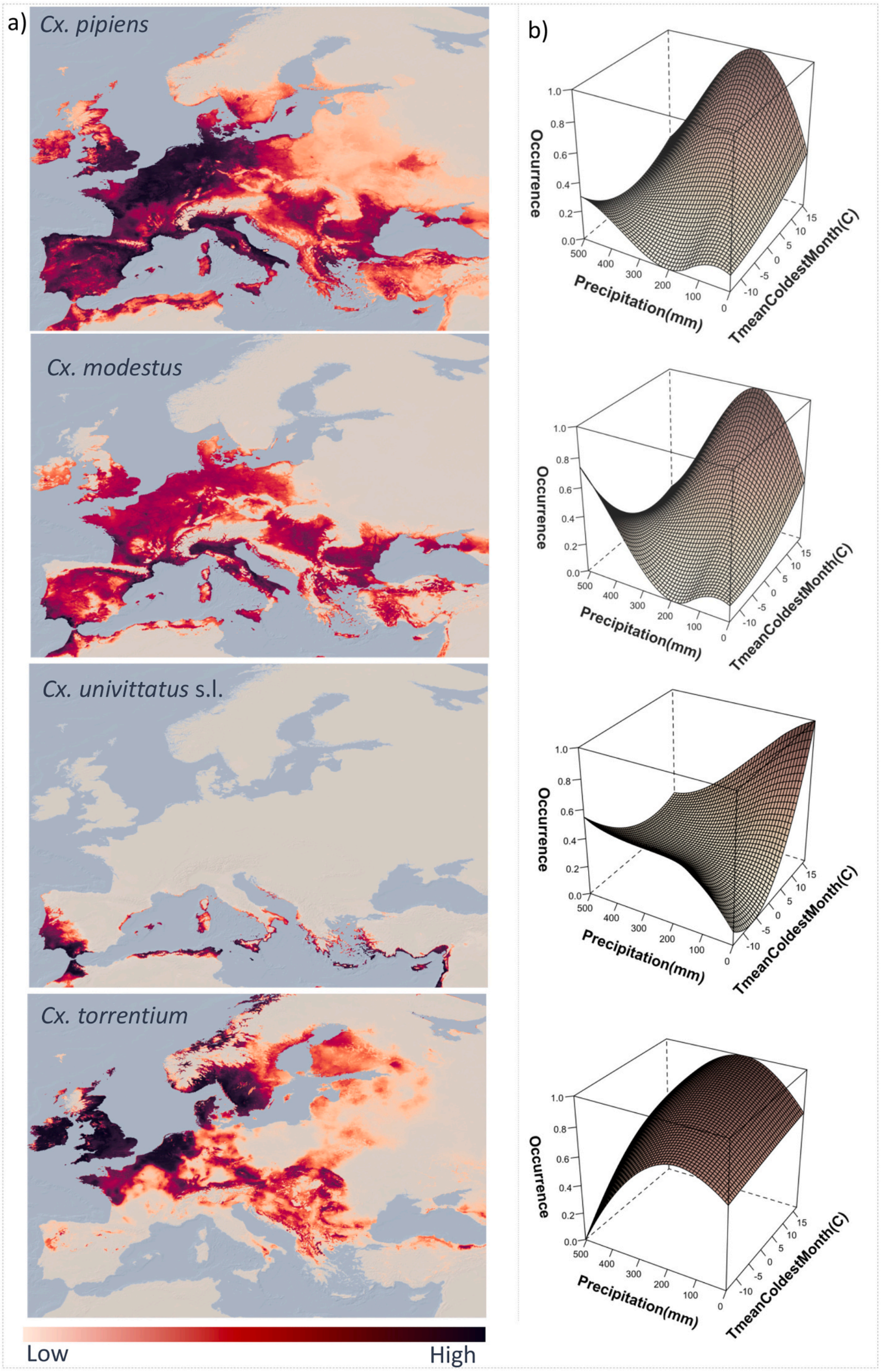


Fig. 1. Habitat suitability maps of four *Culex* species and their responses to mean winter temperature and precipitation in Europe. a) Predicted habitat suitability and geographic distribution of four *Culex* species. b) 3D response curves for the two key variables, mean winter temperature and precipitation, shaping the distribution of the *Culex* species. Darker brown shades indicate lower suitability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(See Fig. S4).

The Hot Spot Analysis demonstrated significant spatial clustering of the weighted variable, which captures the recurrence of WNV cases combined with vector co-occurrence weighted by vector competence across administrative regions (NUTS). Notably, the analysis revealed pronounced hot spots, with z-scores reaching as high as +15. These hotspots were primarily located in Southern Spain, Northern Italy, Eastern European countries, Greece, and Eastern Germany, indicating robust clustering of high values that correlate strongly with elevated vector competence and frequent WNV occurrences (Fig. 4).

3. Discussion

Modelling mosquito vector distribution across diverse environmental conditions and identifying areas of species overlap provide powerful tools for disease surveillance, vector control, and strategic public health planning. Proven vectors of WNV are already present in most parts of Europe, with significant geographic overlap in many

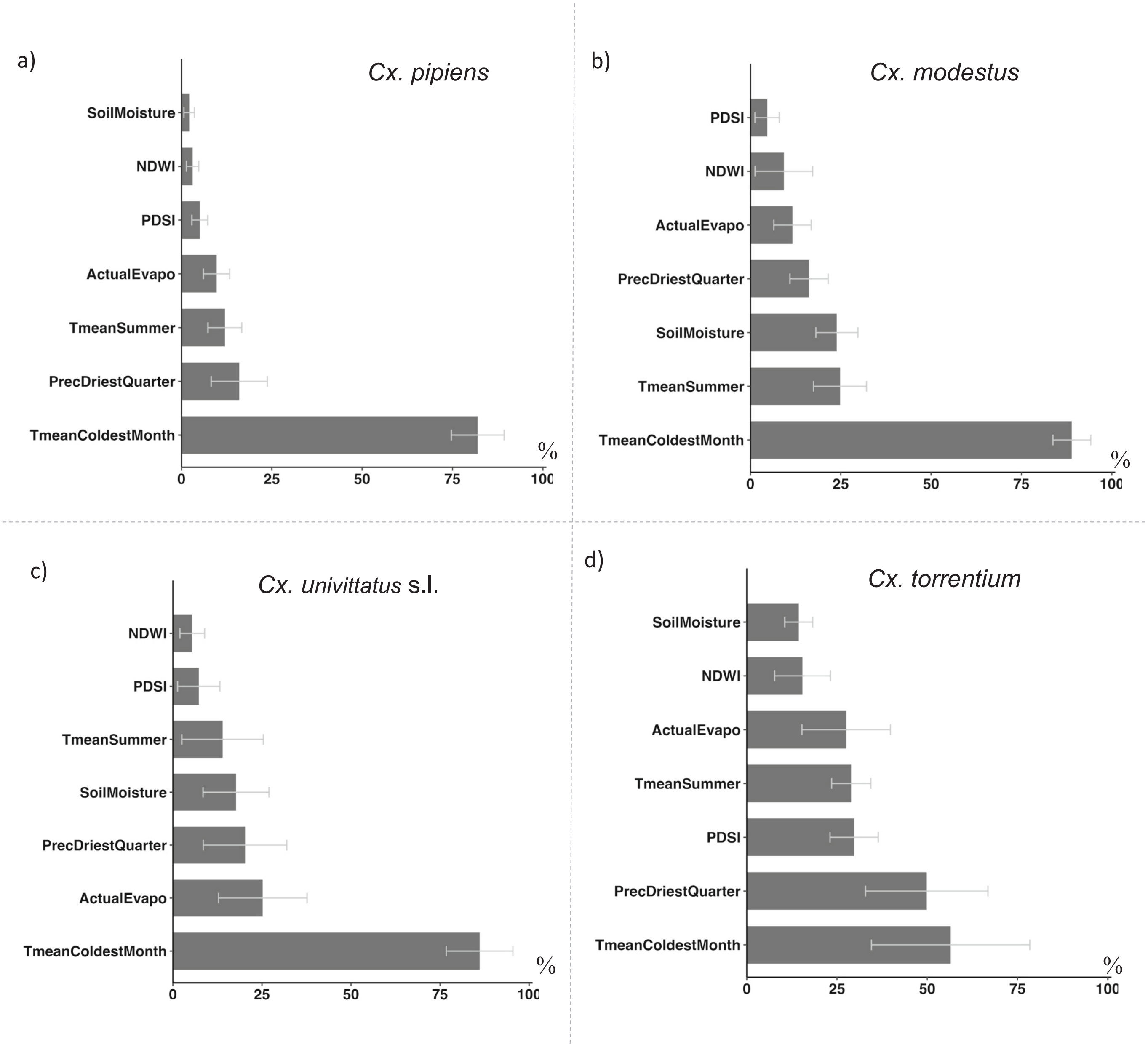
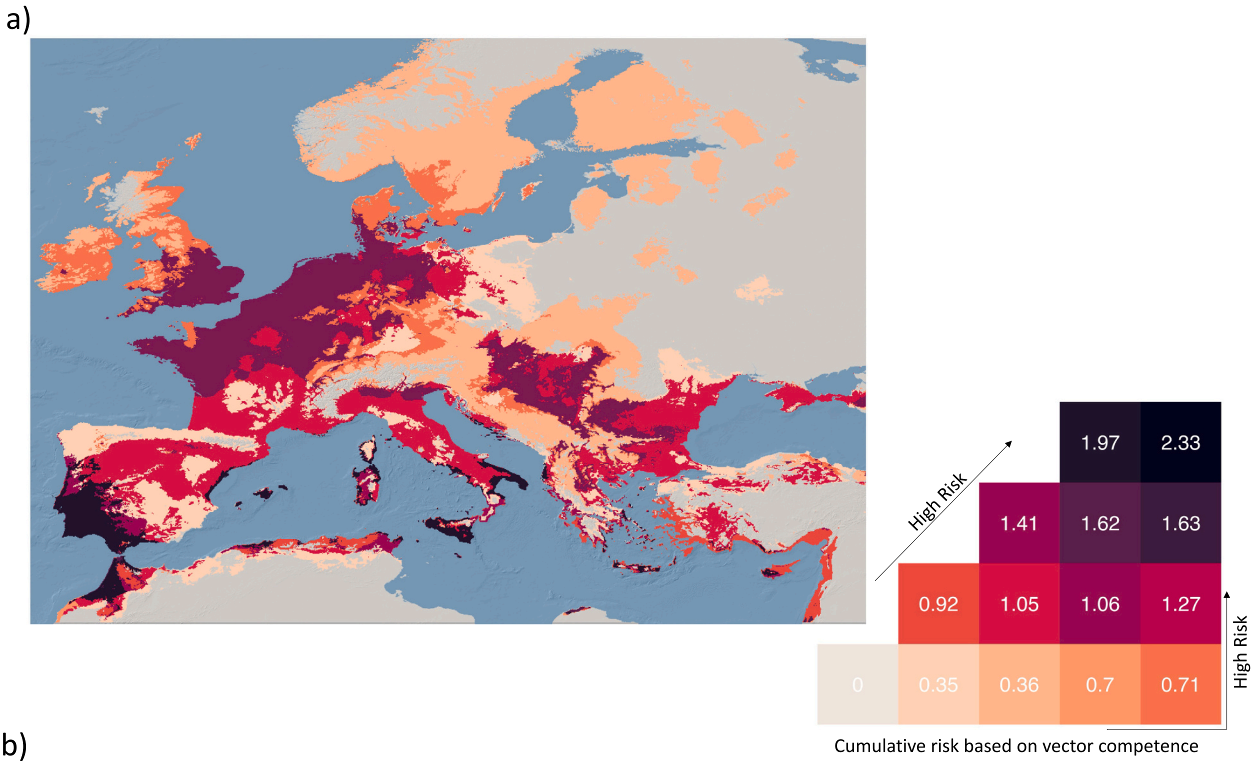


Fig. 2. Variable importance (% IncMSE): quantifies the relative contribution of six environmental variables in modelling the habitat suitability of the four main vectors of WNV in Europe. a) *Culex pipiens,* b) *Culex modestus,* c) *Culex univittatus* s.l.*,* d) *Culex torrentium.* Variable importance was derived from an ensemble of six modelling techniques for the four primary Culex species in Europe, considering the following environmental factors: mean temperature of the coldest month (TmeanColdestMonth), Precipitation, actual evapotranspiration (ActualEvapo), Palmer Drought Severity Index (PDSI), Soil moisture (SoilMoisture), and the Normalized Difference Water Index (NDWI). The error bars in the bar plots represent the variation in variable importance across all runs.

regions. Although some areas show a higher potential for vector co-occurrence, the risk remains in any region where even a single vector species is present (e.g., [46]). This widespread distribution and overlap may support the ongoing geographic expansion of WNV human cases in recent years. This expansion spans multiple directions in latitude and longitude (Fig. S5), suggesting that WNV could continue to spread as the virus finds suitable environmental conditions across an increasingly wide geographic range (See also, [47]).

Average temperature during the coldest month is the most significant ecological factor in determining the distribution of the four *Culex* vectors across Europe. Response curves indicate that optimal environmental conditions for these Culex species include warmer winter temperatures and moderately moist environments, which likely enhance overwintering survival. While reproductive activity is typically paused during winter due to dormancy mechanisms, mild winter conditions may facilitate mosquito persistence, female blood-feeding activity, and allow for and earlier onset of reproduction and virus transmission in transmission season. This aligns with studies showing that warm winters facilitate the overwintering of WNV in various regions of Europe (e.g., [48], and are associated with higher WNV incidence in the following spring-summer [49]. Additional indicators, such as the NDWI and the PDSI, further suggest that these vectors thrive under mild drought stress with stable water sources, where moisture and water availability are balanced for optimal development (see Fig. S3).

While winter temperature is the primary factor for all *Culex* vectors, the significance of the remaining variables varies among species (Fig. 3). This might indicate niche differentiation among the *Culex* vectors, where each species responds to unique environmental conditions beyond winter temperature. For example, although *Cx. pipiens* and *Cx. torrentium* shared substantial geographic overlap, their low niche



b)

Schoener's D				
	Cx. pipiens	*Cx. modestus*	*Cx. univittatus* s.l.	*Cx. torrentium*
Cx. pipiens		***0.79***	***0.17***	***0.44***
Cx. modestus			***0.18***	***0.36***
Cx. univittatus s.l.				***0.02***
Horn's R				
Cx. pipiens		***0.92***	***0.34***	***0.65***
Cx. modestus			***0.36***	***0.60***
Cx. univittatus s.l.				***0.06***

Fig. 3. Niche overlap and co-occurrence of the four major WNV mosquito vectors across Europe and pairwise niche similarity in geographic space. a) Indicates the co-occurrence of four *Culex* species, weighted by vector competence. Darker colors represent areas of high co-occurrence, indicating a greater risk from competent vectors. b) Pairwise niche similarity of four WNV vectors in Europe, using two similarity metrics, with values ranging from 0 to 1, where higher values indicate greater geographic overlap. Following classes are suggested for interpretation of results: 0–0.2 = no or very limited overlap, 0.2–0.4 = low overlap, 0.4–0.6 = moderate overlap, 0.6–0.8 = high overlap, 0.8–1.0 = very high overlap (Rödder & Engler 2011).

similarity (Fig. S4) suggests a limited ecological overlap between the two species. This implies that, despite occupying similar geographic regions, the two species thrive under distinct environmental conditions (Fig. S4). Niche differentiation among vectors may affect disease dynamics through niche complementarity, where less competent vectors fill spatial or temporal gaps left by dominant species (see also, [50]). The interaction between different vectors that occupy various ecological, temporal, and spatial niches contributes to the spread and persistence of WNV across diverse environments. This knowledge is essential for developing more effective and targeted control strategies.

Here, we have highlighted areas that are environmentally favourable for the occurrence of primary WNV vectors. However, these maps may not always align with actual vector distributions in certain regions. Factors such as vector behaviour, dispersal ability, human interventions, geographical barriers, and gaps in data and knowledge can lead to discrepancies between predicted suitability and the actual presence or abundance of vectors, particularly in large-scale studies. For instance, Southern European islands like the Balearic in Spain and Crete in Greece show high suitability for *Cx. univittatus* s.l. Yet, this vector has, apparently, not been reported in these areas despite comprehensive efforts. This suggests that although the climatic conditions are favourable, limitations in the mosquito's dispersal ability may have prevented it from establishing in these isolated regions. In contrast, there have been reports of these *Culex* vectors in areas that our models identify as having lower suitability, likely due to insufficient data that may not provide precise location information. For example, *Cx. torrentium* is known to occupy a larger area in northern Spain than what our maps reflect.

While large-scale suitability models in vector-borne disease offer valuable insight, their limitations should be carefully considered. Vectors are strongly influenced by microhabitat and microclimate conditions [51], which are challenging to incorporate into large-scale models. This may explain why land-use variables did not contribute to our model's performance at a continental scale. Broad land-use categories, such as urban, agricultural, or forested areas, often overlook the small, specific environments where mosquitoes develop, such as puddles or containers. Although land-use can indirectly affect mosquito distribution by altering microclimates or water availability, these influences may not be directly captured by general land-use classifications.

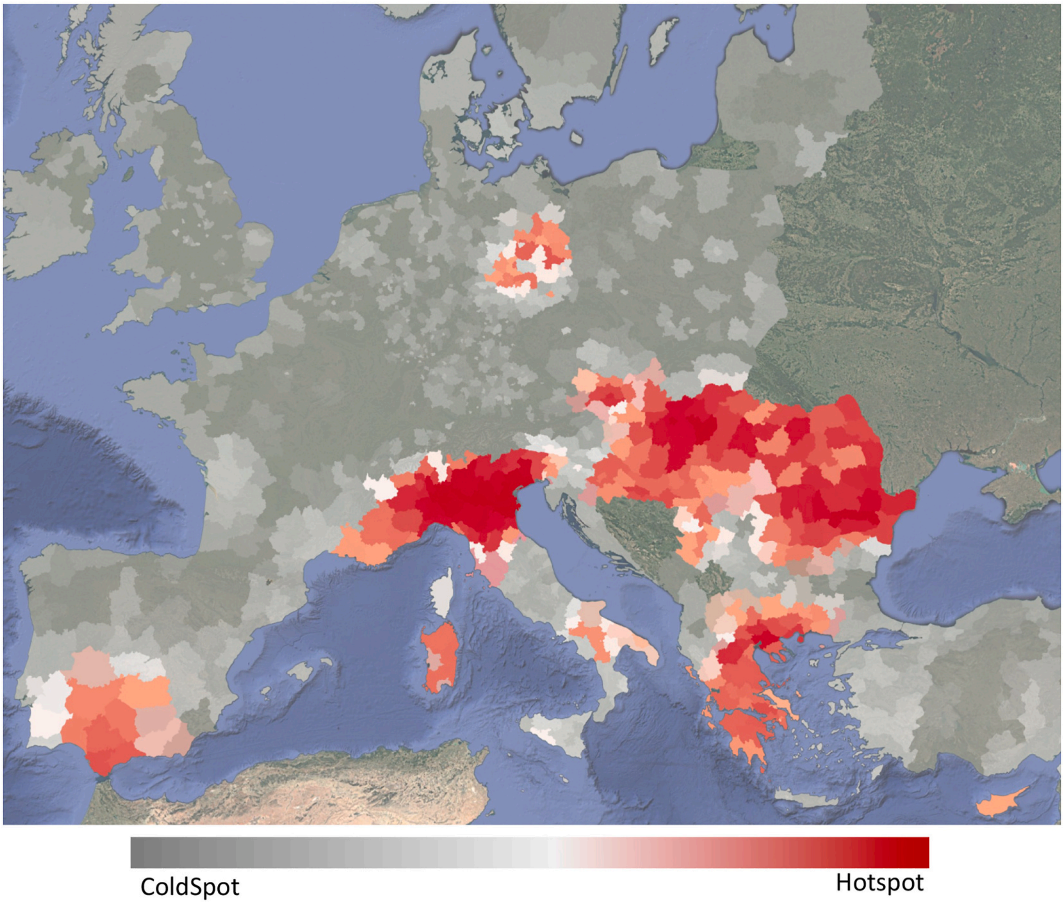


Fig. 4. Spatial overlap between vector co-occurrence and human WNV cases. Local statistics for each NUTS spatial unit reveal statistically significant clustering of vector co-occurrence and human WNV cases. Areas marked by reddish hues represent WNV hot spots, with high levels of both vector overlap and human cases. In contrast, regions shaded in gray are cold spots, characterized by non-significant clustering that indicates a lower risk of disease transmission (coldspots).

Additionally, discrepancies in the timing of land-use and vector data collection could weaken correlations, for example, changes in agriculture may not be immediately reflected in mosquito distributions. This highlights the uncertainties of modelling vectors at large scale, as these models may overlook local environmental factors crucial for vector survival and transmission dynamics [52]. Applying the principle of "think globally, act locally," is essential to complement large-scale insights with targeted local interventions to better combat vector-borne diseases.

To our knowledge, this is the first comprehensive study mapping multiple WNV vectors across Europe and assessing their cumulative WNV risk associated with their co-occurrence. Currently, the European Centre for Disease Prevention and Control (ECDC) provides the primary source of vector data, however, these maps have limitations as they rely on broad administrative regions (NUTS-level), which may not capture the true distribution at finer scales. Many areas remain underrepresented in data collection, and barriers to data sharing further complicate effort to close these gaps; therefore, more efforts should be invested in the monitoring of animal species involved in the transmission of zoonotic pathogens. In particular, the distribution and abundance of natural avian hosts (key amplifiers of WNV in the enzootic cycle) remain poorly documented at the European scale. Incorporating data on host presence and host–vector interactions is essential for understanding the full transmission dynamics of WNV, but such information is currently scarce. Citizen science initiatives could serve as valuable tools for collecting broader data on both natural hosts and vectors; however, the identification of many *Culex* species often requires high-quality images and/or well-preserved specimens; nonetheless, molecular techniques are frequently necessary to ensure reliable species-level identification.

While our approach focuses on species presence and vector competence, we emphasize that incorporating vector abundance and host–vector contact rates would further improve risk assessments. The lack of standardized mosquito surveillance tools across Europe limits the ability to fully quantify entomological risk, highlighting the need for future studies that integrate vector population dynamics and local ecological interactions.

Another key limitation of using reported human WNV cases as a proxy for virus occurrence is the underreporting of asymptomatic and mild infections, as typically only neuroinvasive cases are diagnosed and recorded. Consequently, the true extent of spillover transmission remains uncertain. Geographic disparities in healthcare access and surveillance efforts may also influence the spatial distribution of reported cases, potentially underestimating risk in certain regions.

Ongoing climate change is increasing the risk of both vector expansion and their overlap, which raises the potential for more frequent outbreaks of vector-borne diseases (See Fig. S6). This study highlights these risks by examining the distribution and co-occurrence of vectors in Europe by emphasizing the need for localized research in hotspots of high vector co-occurrence. Such targeted research is essential for understanding disease dynamics and informing interventions aimed at mitigating climate-driven threats. To address these risks effectively, it is crucial to develop standardized and integrated approaches that enhance entomological capacity, improve surveillance, and refine risk assessments across Europe. Collaboration and data sharing between countries are also crucial, especially in regions with a significant overlap of vector species and active research teams. Initiatives such as VectorNet, a joint project by the ECDC and EFSA, aim to improve collecting data on vectors and pathogens relevant to both animal and human health. Such collaboration will be key for gaining a clearer understanding of the current situation and for making more accurate predictions. By cross-boundary collaboration, we can develop effective and environmentally friendly control strategies, particularly in high-risk hotspots (e.g., rice fields, irrigated lands, etc.) where arboviruses are most likely to emerge and spread.

Our findings offer practical value for improving WNV surveillance and control efforts across Europe by identifying areas of elevated risk based on vector co-occurrence and reported human cases. These risk maps can support public health decision-making by guiding targeted vector control (e.g., larviciding, water management), enhance sentinel surveillance in hotspots, and informing urban and environmental planning to reduce areas suitable for mosquito breeding. While developed at a continental scale, the maps serve as a valuable starting point for more localized, data-driven intervention.

CRediT authorship contribution statement

Shirin Taheri: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mikel Alexander González:** Writing – review & editing, Validation. **María José Ruiz-López:** Writing – review & editing, Validation. **Ramón Soriguer:** Writing – review & editing, Validation. **Jordi Figuerola:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.onehlt.2025.101041.

Data availability

Data will be made available on request.

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