Land and Climate Suitability for West Nile Virus in Atlantic Archipelagos Guided by Historical Data from Europe

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Research Article

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Abstract

West Nile (WNV) is a zoonotic mosquito-borne virus with an expanding geographical range and epidemic activity worldwide. Computational studies have contributed to the understanding of factors driving WNV occurrence, particularly in North America and Europe, providing invaluable insights towards surveillance and preparedness. Archipelagos have largely been overlooked, despite the risks WNV poses to unique local avian species and human populations. In this study, we apply a machine learning-based ecological niche approach, trained on WNV occurrence and (a)biotic factors from Portugal, Spain, and Italy, to estimate ecological suitability for WNV occurrence across several Atlantic archipelagos. The approach gives weight to the temporal dimension, moving beyond conventional spatial suitability estimations, and generating novel insights on seasonality both for Europe and the archipelagos. For Portugal, Spain and Italy, modelling results align with previous findings on spatial hotspots and (a)biotic drivers of WNV occurrence, while further unraveling properties of at-risk human populations within dynamically suitable land areas. For Atlantic archipelagos, results constitute a novel and detailed perspective on local ecological suitability for WNV occurrence, providing a data-driven framework that identifies spatial hotspots, defines seasonal patterns and quantifies the local population at risk. The synthetic data generated in this study supports the development of targeted preparedness, surveillance and mitigation plans tailored to the unique ecological and seasonal dynamics of each region under study.

Keywords

West Nile Virus; modelling; ecology; climate; machine learning; seasonality; risk; archipelago.

Introduction

West Nile (WNV) is a mosquito-borne virus of the *Orthoflavivirus* genus, *Flaviviridae* family, and part of the Japanese Encephalitis serocomplex. It is maintained in an enzootic cycle between avian and mosquito species [1]. Mosquitoes of the *Culex* genus, particularly *Culex pipiens*, are recognized as the main vectors in Europe and North America, although five other mosquito genera have also been implicated in transmission [2]. Occasionally, epizootic spillover events affect mammals, including humans and equines. First identified in Uganda in 1937, WNV has expanded its geographical transmission range over the past decades, with human infections now recorded on every continent except Antarctica [3]. Although the majority of human infections are asymptomatic (70%-80%), some progress to neuroinvasive disease, manifesting as encephalitis, meningitis or acute flaccid paralysis, with severe cases potentially leading to death [4].

WNV reporting in the European Union is mandatory, with surveillance efforts focusing on humans, equines, birds and mosquitoes across member states. Epidemic activity in Europe has increased in recent years, spanning a ever wider geographic area, with notable expansion and activity in France, Italy, Greece, Spain, Hungary, Romania, Bulgaria, Serbia and Ukraine [5,6]. The continent's largest recorded epidemic occurred in 2018, with 2,083 cases surpassing cumulative infections since 2010 [7]. In 2020, Spain experienced an unprecedented WNV epidemic marked by high numbers of human infections and deaths, including previously unaffected areas [8,9]. The second-highest annual count of locally acquired cases was recorded in 2022, with Italy reporting its highest number to date [10]. In 2023 alone, seven European Union countries reported over 150 outbreaks among equids and eight reported over 250 outbreaks among birds [10]. In 2024, WNV was included in the WHO pathogen prioritization list, recognizing its potential to cause public health emergencies of concern across five continents [11].

Historically, WNV-focused epidemiological studies have mostly explored the African and Middle Eastern settings [1,12]. The key epidemiological event of WNV introduction into North America in 1999, after which it became endemic across the Americas, marked a turning point in global awareness of the virus. Since then, the range of countries contributing to WNV body of knowledge has widened, with most outputs remaining focused on the North American and European (a)biotic settings [13], albeit with growing interest in Africa [14–16]. Within this output, computational approaches have largely focused on large spatial scales, typically covering inland subcontinental regions (e.g. Iberian Peninsula [17]), entire countries (e.g. USA [18], Greece [19]) or continents (e.g. Europe [20], Africa [16]). At such scales, a combination of mechanistic, machine learning and statistical approaches (e.g. [14–24]) now support the identification of spatio-temporal hotspots for WNV epidemic activity and drivers of such activity, which ultimately have the potential to inform the development of local preparedness, surveillance and mitigation plans. For example, by identifying climate change as a key driver of WNV circulation and expansion in Europe [20], and determining ecologically favorable regions for WNV circulation in Africa [14]. In contrast to the aforementioned large-scale regions, archipelagos and islands have generally been overlooked in computational studies, despite accumulating evidence of WNV circulation in these bio-climatic settings (e.g. Caribbean islands [25–29], African islands [30], Mediterranean islands [31–34]). Beyond the public health risk WNV may pose to local human populations, two other critical reasons support a deeper understanding of WNV eco-epidemiology on islands. First, islands are avian biodiversity hotspots, with unique indigenous assemblages, and they serve as key stepping stones along avian inter-continental migration routes [35], potentially acting as hotspots for viral acquisition, global dispersal and genetic mixing [15]. Second, many insular avian species already face significant human-driven threats, such that particular concerns on the impact of WNV circulation to their conversation have been raised, following the well reported population decreases in several North American avian species after WNV introduction in 1999 [36].

Some archipelagos that have been neglected in field monitoring and computational studies include those in the Atlantic Ocean, such as the Azores (Portugal), Madeira (Portugal), the Canaries (Spain), Cape Verde, and São Tomé and Príncipe. These archipelagos are crucial to the long-distance, inter-continental migration routes of avian species between the Arctic and Antarctic regions [37]. The history and current state of mosquito-borne viruses on these islands, specifically WNV and its mosquito-vectors, are generally incomplete. In the Portuguese archipelagos, no historical reports of WNV occurrence exist, although relevant mosquito-species are established, including *Culex theileri* in Madeira [38], and *Culex pipiens* in both Madeira [38] and the Azores [39]. The bio-climatic setting of Madeira has previously demonstrated potential for mosquito-borne transmission, when in 2012 the

island witnessed the first European sustained outbreak of the dengue virus [40], supported by a resident population of *Aedes aegypti*. In the Canaries, *Culex pipiens* is also established [39], and antibodies against WNV have been detected in Eleonora's falcons (*Falco eleonorae*) [41] and dromedary camels (*Camelus dromedarius*) [42]. In the African archipelagos, São Tomé and Príncipe host persistent populations of vectors for dengue, chikungunya, Zika, and Yellow Fever viruses (*Aedes aegypti, Aedes albopictus*) [43], as well as *Culex quinquefasciatus*, a vector of WNV. Between 2022 and 2023, the first dengue outbreak was reported in São Tomé and Príncipe [44]. The sole local evidence of WNV circulation comes from a serological study that reported cross-reactivity in humans by indirect ELISA [45]. In Cape Verde, mosquito-borne outbreaks of dengue and Zika viruses have been reported in the past [46], but no evidence exists for WNV circulation albeit the presence of *Culex pipiens* and *Culex quinquefasciatus* [47].

In this study, we developed an ecological niche modelling approach with the primary goal of projecting and understanding the ecological suitability for WNV occurrence in Atlantic archipelagos, where mosquito species capable of transmitting the virus are established, but local transmission risk as determined by (a)biotic factors is largely unknown. The approach is based on training a series of machine learning models using WNV occurrence and (a)biotic data from European countries, and subsequently projecting ecological suitability for the archipelagos. The approach critically gives weight to the temporal dimension, allowing to go beyond typical estimations of the spatial landscape of ecological suitability, but also being able to estimate seasonal dynamics in both the European and archipelago areas of study. For mainland Europe, results corroborated previous findings on spatio-temporal hotspots and (a)biotic drivers of WNV occurrence, while also revealing local patterns of seasonality, including spatio-temporal variations in the size of at-risk human populations. For the Atlantic archipelagos, novel findings provide a perspective on the spatio-temporal dynamics of WNV ecological suitability, offering a data-driven framework that identifies spatial hotspots, temporal signatures, and the at-risk human population. Ultimately, these results support the development of tailored preparedness, surveillance and mitigation strategies, addressing the unique ecological and seasonal dynamics of each region under study.

Materials and Methods

Study areas

The study includes data and modelling output for three European countries (Portugal, Spain, Italy), as well as five Atlantic archipelagos - Madeira (1 island), Azores (9 islands), Canaries (7 islands), Cape Verde (9 islands) and São Tomé e Princípe (2 islands). The European countries were selected based on the availability of reported WNV occurrence for several consecutive years, and the archipelagos based on the availability of (a)biotic variables at sufficient spatial resolution.

Summary of modeling approach

We developed a supervised machine learning (ML) classification approach (summarized in **Figure 1**) informed by ten (a)biotic variables (predictor variables, **Supplementary Table S1**) and WNV reported occurrences (target variable, **Supplementary Table S2**). The ML approach used five model types, including random forests - RFA, extreme gradient boosting trees - XGBTREE, support vector machine - SVM, neural networks - NNET, and flexible discriminant analysis - FDA. Further information in **Supplementary Text.**

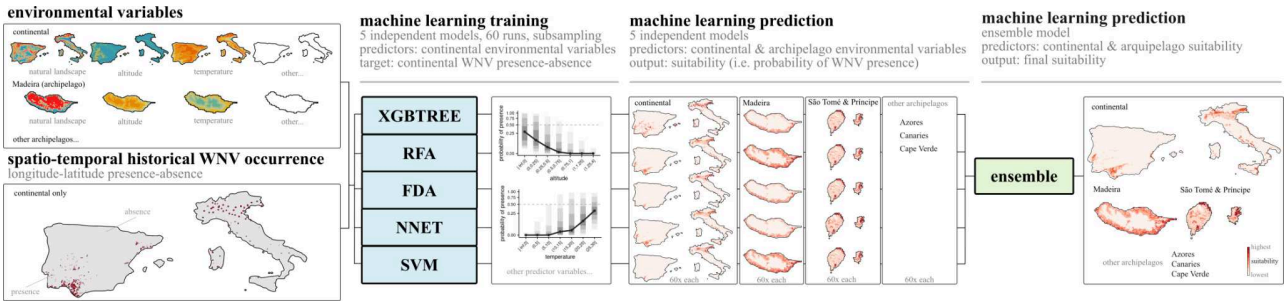

Figure 1. Summary diagram of the modelling approach. The figure summarizes the modelling approach, informed by (a)biotic predictor variables and target WNV reported occurrences, towards estimating the probability of WNV "presence" per geographical location (termed WNV suitability). Model types include: random forests - RFA, extreme gradient boosting trees - XGBTREE, support vector machine - SVM, neural network - NNET, flexible discriminant analysis - FDA.

Training was performed on all geographical locations (longitude-latitude points) at a spatial resolution of ~5 Km^2 for Portugal, Spain and Italy. Locations with reported WNV occurrences were defined as "presence" and all others as "pseudo-absence". The training dataset comprised records associated with each location, including: one target variable with a value of "presence" or "pseudo-absence" based on WNV occurrence reports; four predictor variables related to landscape properties specific to the location (constant over time); and six predictor variables related to climate properties specific to both location and month of the year. Five different ML model types were used to independently estimate the probability of WNV "presence" (here termed WNV suitability for occurrence), between 0 and 1, for which the threshold 0.5 was used for classification (e.g. [48]). We considered M=60 independent runs of each model under a cross-validation strategy parameterized with K=25 folds, P=0.8 subsampling of input data and downscaling for WNV "presence" data points. In effect, each fold of each model type was trained on N locations representing an equal number of WNV "presence" and "pseudo-absence" data points (N equal to 80% of existing WNV "presence" data points). In light of the WNV occurrence dataset being unbalanced towards "pseudo-absence", the large number of model runs and folds guaranteed that the ecological background of each WNV "presence" data point was considered against a wide range of ecological backgrounds of the WNV "pseudo-absence" data points. A similar subsampling strategy was used on a recent ML approach successfully applied to WNV modelling in Portugal [21].

For each model type, M suitability estimations were generated for each country and archipelago, per month. The weighted mean of the M suitability estimations per month was calculated using observed model accuracy, resulting in a single suitability estimation per model type per month. The latter were then used as predictor variables to train an RFA model, resulting in a final ensemble estimation of suitability for every territory under study per month. Suitability estimations were generated at a spatial resolution of 5 Km^2 for countries and 0.5 Km^2 for archipelagos. Several summary measures across model types (including the ensemble model) are reported, such as (a)biotic variable importance, accuracy, true positive and negative rates. Partial plots were generated by crossing final ensemble suitability estimates with (a)biotic variables per geographical location. Further details on methodology and variables are provided in **Supplementary Text.**

Ethical approval

No ethical approval was needed for this study, since all data sources are of public access, none of the generated data is at the individual level nor can it identify individuals, and WNV occurrence data used were already anonymised (as made available in the public repositories or literature).

Results

In preparation for the modelling, we performed a broad literature review focused on mosquito-species of interest, WNV and other mosquito-borne viral occurrences in the archipelagos under study. This review was translated into a report providing an aggregated historical and contextual perspective, made available in **Supplementary Text**.

Ecological niche modelling captures the spatio-temporal signatures of reported WNV occurrence

Across ML model types, measured predictor variable importance was organized around three groups (**Figure 2A**): the first group with the highest importance included *alt* (altitude) and *tempmin* (minimum temperature); the second group, with intermediate importance, included *temp* (mean temperature), *wind*, *prec* (precipitation), *cmi* (moisture index) and *nat* (natural land cover); the third group with the lowest importance included *hum* (humidity), *mixed* (natural and crop land cover) and *crop* (crop land cover). Partial plots of predictor variables versus estimated WNV suitability revealed that some variables were positively associated (e.g. temperatures) while others were negatively associated (e.g. altitude) (**Figure 2B, Figures S1-10**). Given that there were large differences in the number of data points representative of predictor variable value ranges in the partial plots (**Figure 2B, Figures S1-10**), we also performed Multiple Factor Analysis, to extract the nature (negative or positive) and strength of relationships within the factor space (**Supplementary Text**). We found that the relationships were consistent among Portugal, Spain and Italy, with WNV suitability positively associated with increasing temperatures (*temp*, *tempmin*) and the proportion of land types attributed to crop (*crop*) and mixed (*mixed*). In contrast, WNV suitability was negatively associated with increasing levels of *wind*, *prec*, *cmi*, *hum*, *alt* and natural land cover (*nat*) (**Table S3, Figure S11**).

Accuracy across model types was generally above 0.8, with the tree-based models (RFA, XGBTREE) being marginally better (**Figure 2C**). The ensemble model outperformed the independent results of all other models with accuracy at ~0.92. The tree-based models had higher true negative rates (TNR) and lower true positive rates (TPR) than other models (**Figure 2C**). The ensemble model once again outperformed all other models in both rates, and its TNR of ~0.91 meant that in approximately 9% of all locations (longitude-latitude data points) for which there was no evidence of WNV circulation, the model concluded otherwise, potentially identifying locations where surveillance is missing or insufficient. The generally high accuracy meant that the spatio-temporal distribution of estimated WNV suitability mirrored existing WNV evidence, both in space (**Figure 2D**) and time (**Figure 2E**). For all continental regions used to train the models (Portugal, Italy, Spain), the temporal signal in estimated suitability could explain the timing of peaks in local reporting, as well as the timing during which there is no evidence of WNV occurrence (**Figure 2E**).

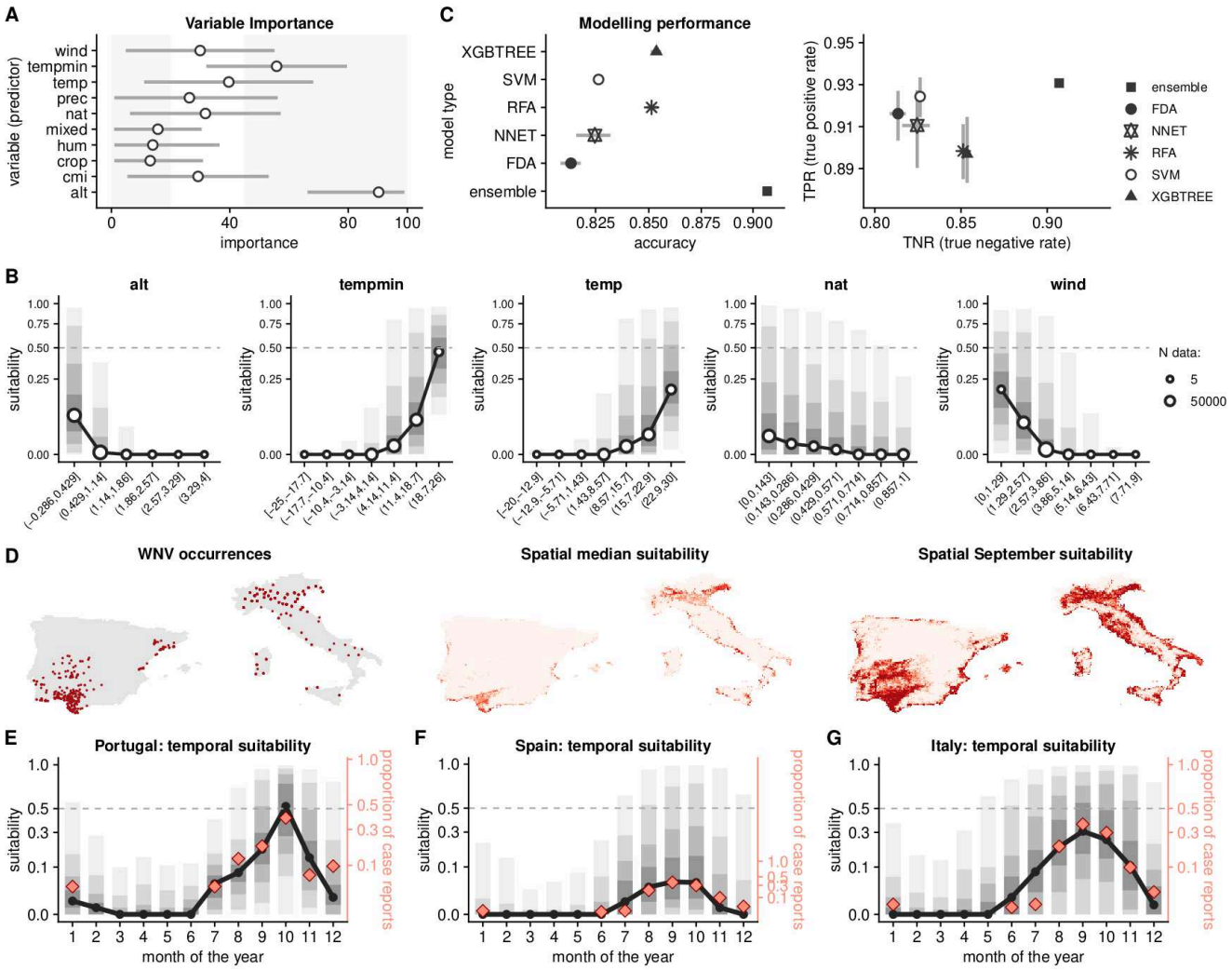

Figure 2. Summary of modelling variable importance, performance and estimated suitability. (A) Variable importance across model runs. Points are the median and bars the 95 percentile. (B) Partial plots of estimated suitability versus the top five most important variables, presented as aggregates across continental Portugal, Spain and Italy. Horizontal dashed lines at suitability 0.5 show the threshold for model decision on suitable versus unsuitable. (C) On the left, model performance as measured by accuracy for each model across model runs. On the right, model performance as measured by true positive rate (TPR) and true negative rate (TNR) for each model across model runs. Models are represented by symbols as indicated in the legend to the right. Points are the median and bars the 95 percentile. (D) Maps presenting the distribution of WNV occurrences used to train the models, and estimated suitability in September and median across time. (E,F,G) Temporal dynamics of estimated suitability for each of the three countries used for training, together with the proportion of case reports per month within each country (orange). For panels (C, E-G), the shaded bars per month present the 25, 50, 75 and 95 percentiles (from darker to lighter), and points and lines present medians.

Ecological suitability is rich in spatio-temporal dynamics

The seasonality of estimated WNV suitability exhibited similar patterns across the continental regions used to train the models (Portugal, Italy, Spain; **Figure 3A-C**). In particular, suitability troughs were generally estimated between January and May, with peaks occurring from August to November, largely driven by shifts in the proportion of land deemed suitable (suitability ≥ 0.5). Seasonally, the proportion of land deemed suitable could go from ~0% (during troughs) to ~50% (during peaks) in Portugal (**Figure 3A**), ~0% to ~20% in Spain (**Figure 3B**), and ~0% to ~40% in Italy (**Figure 3C**). There were also marked time-varying changes in absolute suitability both within land deemed suitable (**Figure 3a1,b1,c1**) and land deemed unsuitable (**Figure 3a2,b2,c2**), highlighting that seasonality for WNV occurrence is driven by an interplay of changes within both suitable and unsuitable land.

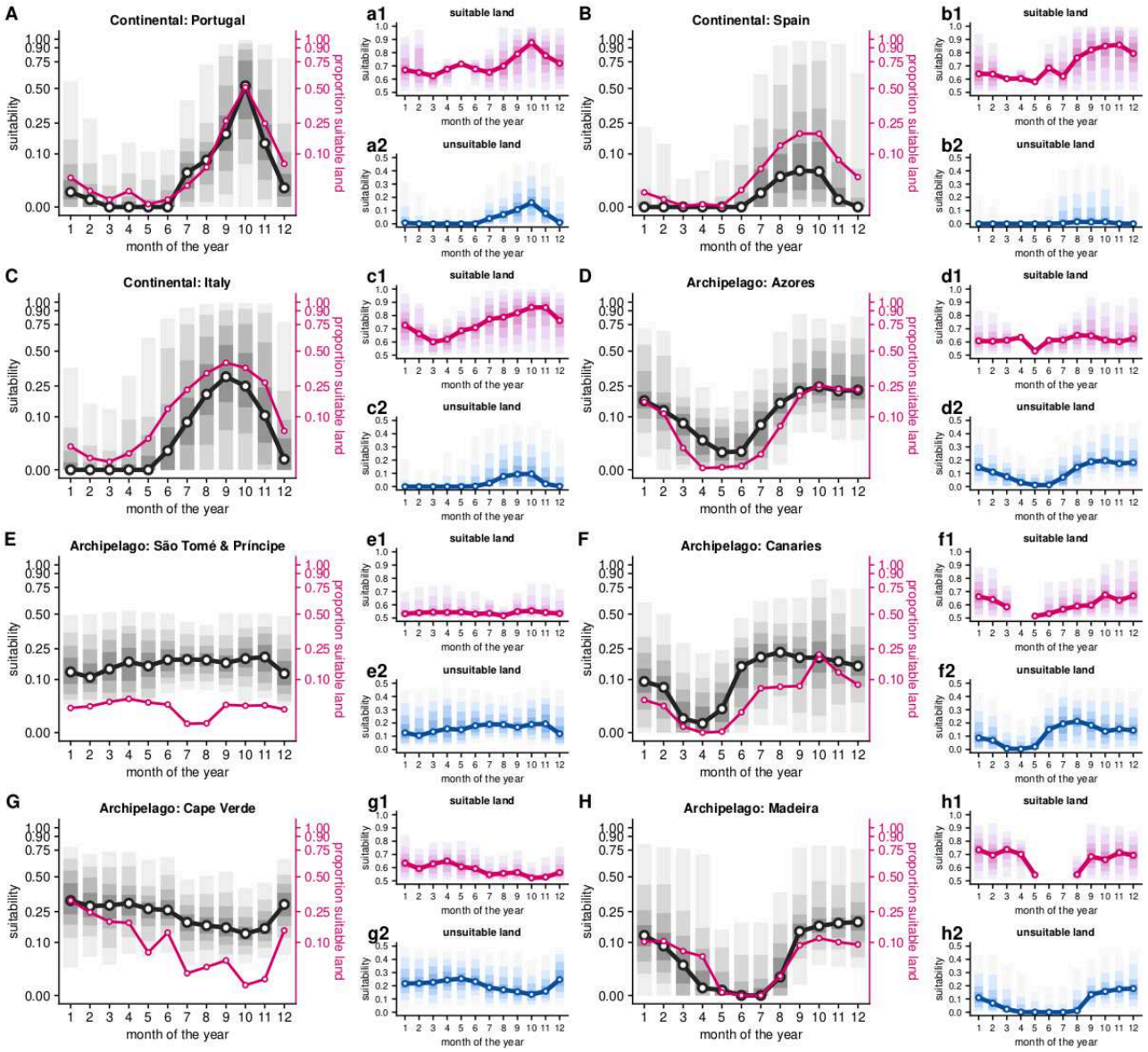

Figure 3. Temporal dynamics of estimated suitability across regions of study. For (A) Portugal, (B) Spain, (C) Italy, (D) Azores, (E) São Tomé & Príncipe, (F) Canaries, (G) Cape Verde and (H) Madeira. Each panel (A-H) is composed of: (left) a large subpanel presenting the distribution of monthly suitability and the monthly proportion of suitable land; (right-top) a smaller subpanel presenting the distribution of monthly suitability in suitable land (spatial pixels with suitability >= 0.5); (right-bottom) a smaller subpanel presenting the distribution of monthly suitability in unsuitable land (spatial pixels with suitability < 0.5). For all sub panels the shaded bars per month present the 25, 50, 75 and 95 percentiles (from darker to lighter), and points and lines present medians.

Among the archipelagos, estimated WNV suitability exhibited varying seasonal characteristics (**Figure 3D-H)**. Only archipelagos with subtropical climates (Azores, Madeira, Canaries) displayed distinct seasons, marked by consecutive months with either troughs or peaks in suitability, along with concurrent oscillations in the proportion of land deemed suitable (**Figure 3D, F, H**). These archipelagos were also characterized by longer peak seasons in suitability compared to continental regions, with short troughs occurring between April and June in the Azores (**Figure 3D**), March and May in the Canaries (**Figure 3F**), and April and August in Madeira (**Figure 3H**). Seasonally, the Azores showed the largest variation in the proportion of suitable land, ranging from ~0 to 26%, followed by the Canaries and Madeira, where the proportion varied from 0 to ~21% and ~12%, respectively. The Azores was unique in maintaining a semi-constant suitability level within land classified as suitable, concurrent with a seasonal variation in suitability within unsuitable land (**Figure 3d1-2)**. In contrast, Madeira and the Canaries showed seasonal variation within both suitable and unsuitable land, similar to continental regions (**Figure 3f1-2, 3h1-2)**. Seasonality in estimated WNV

suitability was generally weak for the two tropical archipelagos (Cape Verde, São Tomé & Príncipe; **Figure 3E, 3e1-2, 3G, 3g1-2**). The seasonal variation in the proportion of land deemed suitable in these archipelagos was also significantly different, varying little from ~0% to 4% in São Tomé & Príncipe (**Figure 3E**) and widely from ~0% to 32% in Cape Verde (**Figure 3G**). In both archipelagos, there was no month of the year presenting zero proportion of land deemed suitable. Notably, Cape Verde's large variation in the proportion of suitable land was estimated to have a trough between July and November, contrasting to all continental regions.

The association between ecological suitability and human populations reveals subregions of public health importance

Overall, the seasonal characteristics of estimated WNV suitability across the study regions highlighted that seasonality is as much about time (periods with troughs and peaks) as it is about the proportion of land deemed suitable. We thus aimed at identifying and mapping geographical hotspots deemed suitable (**Figure 4A**), quantifying their respective proportion of land within the territory over a year (**Table S4**). The vast majority of land had at most one month of the year deemed as suitable (grey areas in **Figure 4A)**. In total, 27% of land across all continental regions, and 23% across all archipelagos was deemed suitable for more than one month (non-grey areas in **Figure 4A**), with proportions of 40% for Italy, 32% for Cape Verde, 27% for the Azores, 22% for Portugal, 19% for the Canaries, 18% for Spain, 12% for Madeira and 6% for São Tomé & Príncipe. In continental regions, this proportion of suitable land presented a clear north-south pattern, mirroring the known distribution of WNV occurrence (**Figure 2D**), with suitable land predominantly in southern Portugal, the southwestern interior and eastern coast of Spain, and northern and coastal areas of Italy (**Figure 4A)**. Within archipelagos, the proportion of suitable land varied significantly from 8% (Fogo) to 88% (Sal) in Cape Verde, 13% (La Palma) to 24% (Lanzarote, Fuerteventura) in the Canaries, 13% (São Jorge) to 71% (Graciosa) in the Azores, 12% for the island of Madeira, and 7% for both islands in São Tomé & Príncipe. Of the 29 islands modelled, the five with the largest proportion of suitable land belonged to Cape Verde and the Azores.

Focusing on land suitable for more than 6 months in a year as a proxy for high transmission risk (magenta areas in **Figure 4A)**, we estimated a total of 6% in Madeira, 4% in the Azores, Cape Verde and Italy, 3% in São Tomé & Príncipe, and 1% in Portugal, Spain and the Canaries. In total, this equated to ~2% of land for both the continental and archipelago territories. Again, the five islands with the largest proportion of such land belonged only to Cape Verde and the Azores. This proportion of land varied between 0% (Brava) to 11% (Maio) in Cape Verde, 0% (four islands) to 2% (Tenerife) in the Canaries, 1% (São Jorge, Faial) to 19% (Graciosa) in the Azores, 6% on the island of Madeira, and 1% (Príncipe) to 3% (São Tomé) in São Tomé & Príncipe.

As such, across the regions of study, the proportion of land (**Table S4**) and total land area (**Table S5**) deemed suitable within each region decreased with the length of time considered (**Figure 4A**). In contrast, analyzing the distribution of human population sizes within land deemed suitable over increasing periods of time revealed a positive association (**Figure 4B**). This implies that while locations deemed suitable for longer periods of time represent the smallest proportion of land, they disproportionately contribute to higher exposure risk to humans by harbouring larger communities (with the exception of Cape Verde) (**Table S6**).

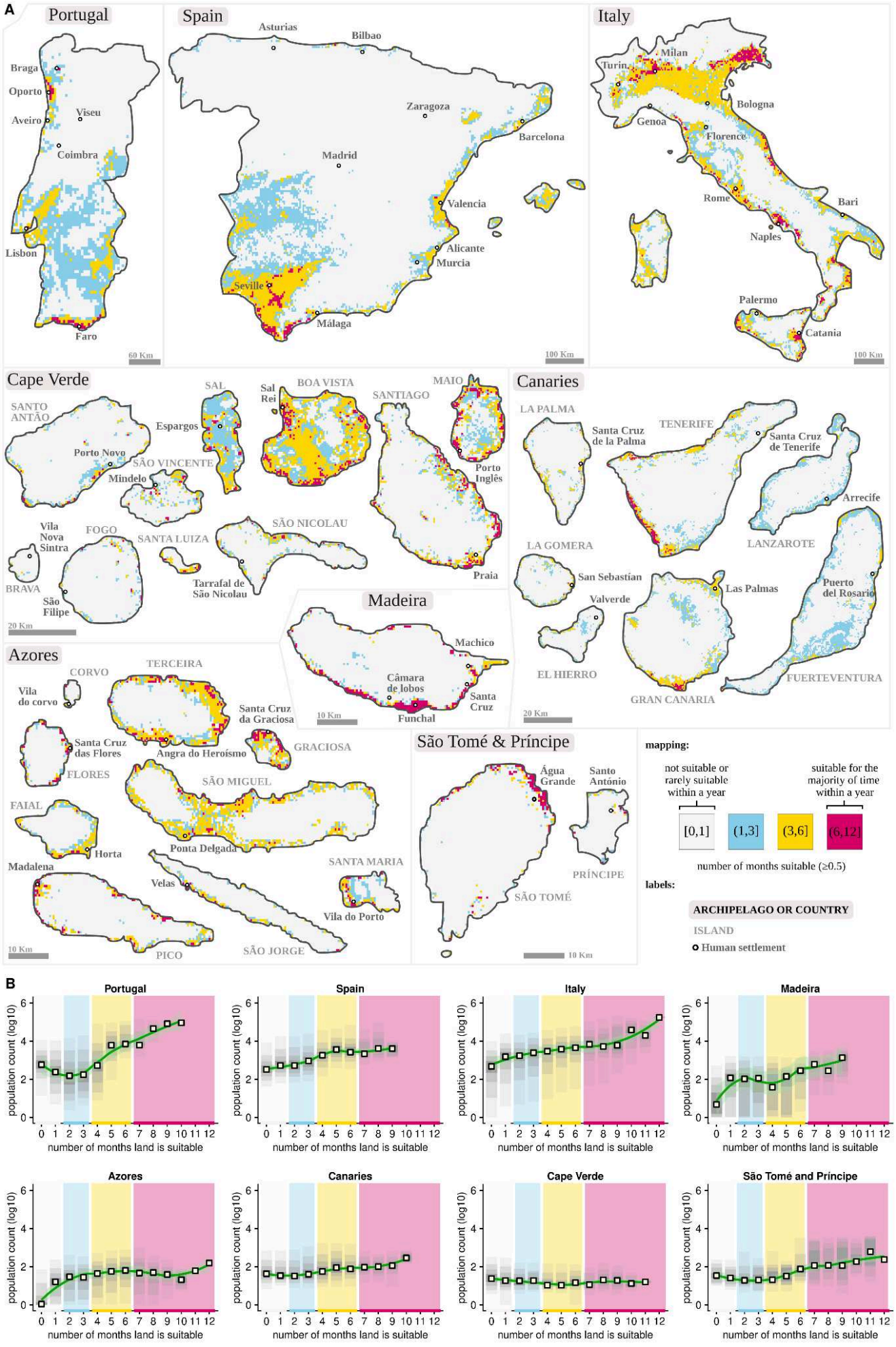
A
Portugal
Braga
Oporto
Aveiro
Viseu
Coimbra
Lisbon
Faro
60 Km
Spain
Asturias
Bilbao
Zaragoza
Barcelona
Madrid
Valencia
Alicante
Murcia
Seville
Málaga
100 Km
Italy
Milan
Turin
Bologna
Genoa
Florence
Rome
Bari
Naples
Palermo
Catania
100 Km
Cape Verde
SANTO ANTÃO
Porto Novo
Espargos
SAL
Sal Rei
BOA VISTA
SANTIAGO
MAIO
Porto Inglés
SÃO VINCENTE
Mindelo
Vila Nova Sintra
FOGO
SANTA LUIZA
SÃO NICOLAU
Tarrafal de São Nicolau
Praia
BRAVA
São Filipe
20 Km
Canaries
LA PALMA
Santa Cruz de la Palma
TENERIFE
Santa Cruz de Tenerife
Arrecife
LANZAROTE
LA GOMERA
San Sebastián
Valverde
Las Palmas
Puerto del Rosario
EL HIERRO
GRAN CANARIA
FUERTEVENTURA
20 Km
Madeira
Machico
Câmara de lobos
Santa Cruz
Funchal
10 Km
Azores
CORVO
TERCEIRA
Vila do corvo
Santa Cruz da Graciosa
Santa Cruz das Flores
Angra do Heroísmo
GRACIOSA
FLORES
SÃO MIGUEL
FAIAL
Ponta Delgada
Horta
Madalena
SANTA MARIA
Velas
Vila do Porto
PICO
SÃO JORGE
10 Km
São Tomé & Príncipe
Água Grande
Santo António
PRÍNCIPE
SÃO TOMÉ
10 Km
mapping:
not suitable or rarely suitable within a year
suitable for the majority of time within a year
[0,1]
(1,3]
(3,6]
(6,12]
number of months suitable (≥0.5)
labels:
ARCHIPELAGO OR COUNTRY
ISLAND
Human settlement
B
Portugal
Spain
Italy
Madeira
Azores
Canaries
Cape Verde
São Tomé and Príncipe
population count (log10)
number of months land is suitable

Figure 4. Spatial hotspots and human population under land deemed suitable for varying periods of the year. (A) Maps of all studied regions are presented, coloured according to the legend on the bottom right: univariate categorized 1x4 color scale representing the total number of months within a year for which a location is suitable (the machine learning classification threshold of suitability ≥ 0.5). For countries, the main human settlements (cities, towns, etc) of the top 10 metropolitan regions are identified (except for Portugal, for which only seven exist according to Eurostat). For archipelagos, the name of each island (capital, light grey) and largest human settlement (dark grey, open circles) are identified. For visualization, the position of some islands do not reflect their real location, and some areas of sea were removed such that the spatial scales presented in kilometers refer solely to land area. (B) Distribution of human population size under suitable land (suitability >= 0.5) according to the number of months the land is suitable. For all sub panels, the shaded bars per month present the 25, 50, 75 and 95 percentiles (from darker to lighter) and Loess curves (green lines) represent the trend of the median values (squares). The colors in the x-axis follow the color scale of panel A.

To formalize the aforementioned relationship between ecological suitability and human population sizes, we defined the *risk to the human population* per subregion as the weighted median of suitability by population size (**Figure S20**; full distributions in **Table S7**). In practice, we considered the estimated spatio-temporal suitability and known population size of all geopixels within well defined subregions, using NUTS III boundaries (Nomenclature of Territorial Units for Statistics, level 3) for European countries and island boundaries for archipelagos (**Figure 5**). The spatial distribution of risk to the human population presented patterns of public health relevance. In Portugal, the Algarve presented the highest risk, followed by the subregions within and neighbouring the largest urban centers of Oporto and Lisbon. In Spain, a clear hotspot with highest risk was centered in Seville and neighbouring subregions, followed by Eastern coast subregions including Alicante, Valência, Castellon, Tarragona and Barcelona presented non-negligible risk. A few hotspots with highest risk were identified for Italy, including the subregions of Milan and Naples, and a large cluster of Northeastern subregions including Pordenone, Udine, Gorizia, Treviso and Venezia. At the same time, a large number of subregions presented non-negligible to intermediate risk across the entirety of the north, and the islands of Sicily and Sardinia.

Across all islands of the archipelagos under study, none had negligible risk. Azores and Cape Verde had the islands with the highest risk across all archipelagos. In the Azores, the islands of Graciosa and Flores were similar, presenting the highest risk, at approximately double of the lowest risk found for the island São Jorge. In Cape Verde, the islands Sal, Maio and Boavista had the highest risk, also at approximately double of the lowest risk found for Fogo. In the Canaries, La Gomera was found to have the lowest risk across all archipelagos, Lanzarote to have the highest within the archipelago. When compared across the islands of all archipelagos, the island of Madeira had intermediate risk. Finally, in the archipelago of São Tomé and Príncipe, the island of São Tomé had the highest risk, but overall intermediate in the context of all archipelagos.

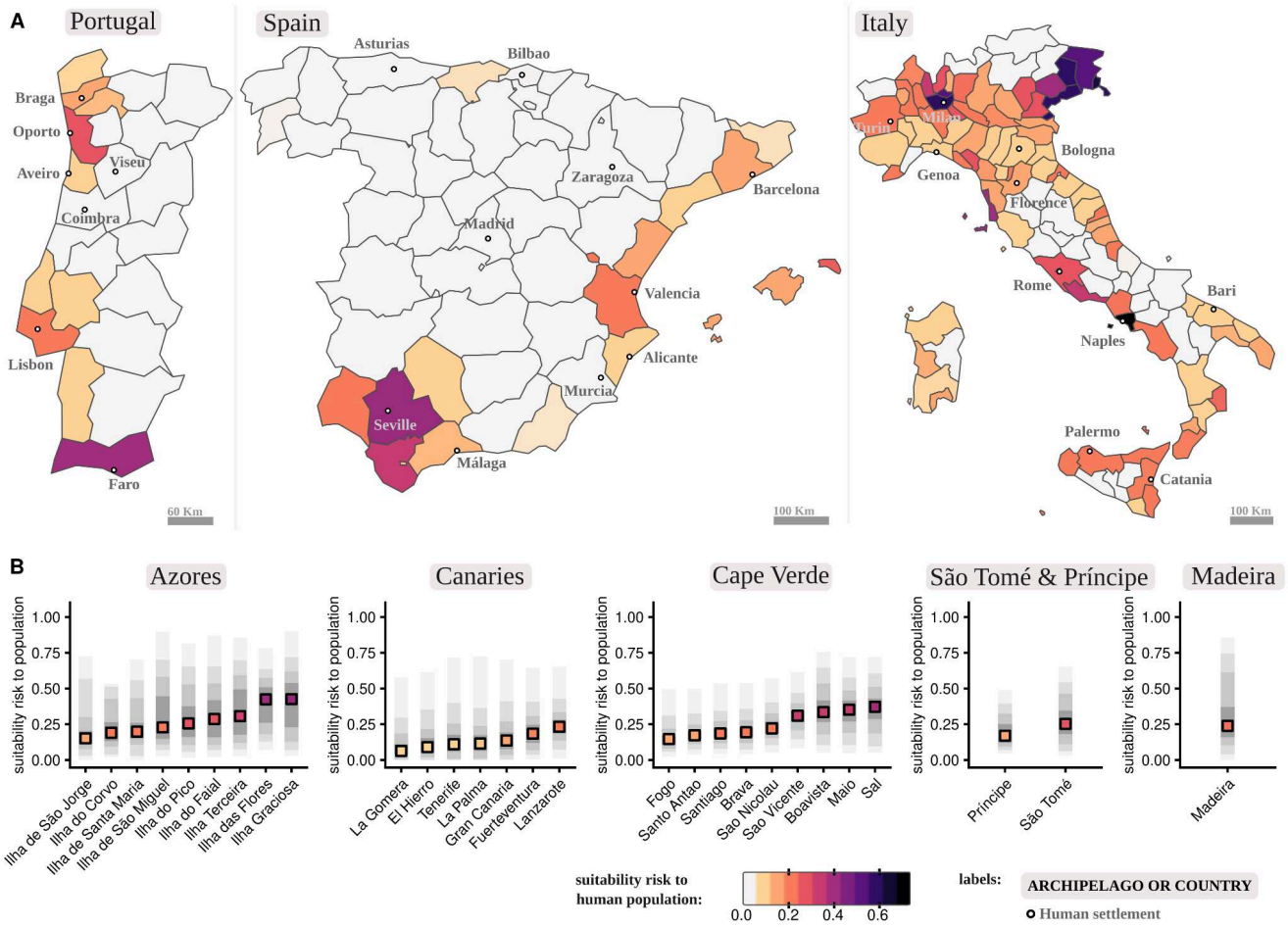

Figure 5 - Ecological suitability risk to human populations. (A) European countries (Italy, Portugal, Spain) are mapped according to NUTS III regions (Nomenclature of Territorial Units for Statistics, level 3). Regions are coloured according to the estimated median suitability risk to human populations (color scale at the bottom). (B) Archipelagos (Azores, Canaries, Cape Verde, São Tomé and Príncipe, Madeira) are presented in XY plots showing the distribution of suitability risk to human populations per island (25, 50, 75 and 95 percentiles presented as bars from darker to lighter, respectively) including the median values (squares, color scale at the bottom). The distributions for all NUTS III and islands are included in **Supplementary Figure S20,** also available as **Supplementary Table S7.**

Discussion

Driven by increased human mobility, urbanization and environmental changes, mosquito-borne viruses are emerging as global public health threats. WNV remains a well documented case [49], particularly in Europe, where its geographical range and epidemic activity have expanded significantly over the past decade. While recent awareness of the virus has led to a growing body of research, studies have remained largely focused in North America and Europe, with more recent attention to Africa. Leveraging abundant WNV occurrence data from Portugal, Spain and Italy, we aimed at estimating and better understanding the ecological suitability for WNV occurrence in Atlantic archipelagos, where competent mosquito-species are present but little is known about local transmission risk. Adding to the typical modelling output of estimating the spatial landscape of WNV suitability for the regions under study, we offer novel insights into temporal properties of seasonality and risk to the human population for both for the countries and archipelagos

In general, we find that the machine learning approach was able to replicate both the seasonal timings and spatial distribution of historical WNV occurrence in the continental territories of European countries. Consistent with other studies, the ensemble model, integrating the predictions from five

different models, outperformed all individual models. Although the modelling approach does not provide evidence of causation *per se*, results related to predictor variable importance and its relationship with estimated suitability for WNV occurrence were generally compatible with existing knowledge regarding the enzootic cycle and spillover dynamics of WNV.

Key predictor variables included altitude, mean and minimum temperature. Altitude is a known abiotic factor that affects mosquito traits (e.g. wing size [19,50]) influencing mosquito abundance [51] and consequently virus transmission potential. Several studies have shown that WNV occurrence is negatively associated with altitude (e.g. [52–54]), and accordingly, altitude showed a consistent negative association with estimated suitability for WNV occurrence in this study. Temperature is one of the most extensively studied climatic variables associated with WNV seasonality and spatial distribution. It directly affects mosquito thermal performance curves and consequently key traits [55], such as mortality rate and viral incubation period, influencing population size and vectorial capacity (i.e. viral transmission potential). For example, temperatures below 10 degree Celsius are considered unsustainable for WNV transmission by *Culex spp*. [56]. Our modelling outputs confirmed the expected positive relationship between temperature and suitability for WNV occurrence. To the best of our knowledge, wind has not commonly featured in quantitative approaches to WNV occurrence. However, it has been suggested that wind may positively influence WNV occurrence and dispersal dynamics [57], e.g. through its effect on mosquito and avian dispersal [58], although negative associations have been demonstrated e.g. in Greece [59]. In this study, wind was consistently negatively associated with suitability across Portugal, Spain and Italy. The role of precipitation on WNV occurrence remains complex, with contrasting conclusions frequently reported. While higher precipitation can theoretically increase mosquito abundance, lower precipitation can also force the accumulation of organic material that favours larval survival and development, resulting in higher larval survival and thus mosquito abundance [58]. In general, a weak negative relationship between precipitation and suitability was recovered in this study, in line with some studies (e.g. [22,23]) and in contrast with others (e.g. [57,60]). Similarly to precipitation, the current understanding of the relationship between humidity and WNV occurrence remains inconclusive [58], with studies e.g. reporting negative associations in Greece [59] and Romania [54], but positive association in Israel [61]. In this study, a negative association between humidity and estimated suitability was found, which was clearer than that of precipitation but weaker than all other predictor variables. Rather unique was the inclusion of the climate moisture index, which measures local balance between moisture supply (precipitation) and demand (potential evapotranspiration). Overall, the relationship of the index with estimated suitability for WNV occurrence was negative, with a clear trend for Italy compared to Portugal and Spain. It had a higher predictive value than both humidity and precipitation, suggesting its usefulness in future predictive modelling. Regarding land use, estimated suitability typically had a consistent negative association with the proportion of natural cover, and a positive association with the proportion of crop and mixed covers. These observations were in accordance with various sources of evidence, suggesting a link between WNV occurrence and land associated with agriculture [51,62].

From the model's potential to estimate time-varying outputs, both the absolute suitability levels and the proportion of suitable land within a region presented relevant seasonal patterns. Three general behaviors emerged from WNV suitability. Temperate regions (Portugal, Spain and Italy) had short seasonal windows peaking in late summer and early autumn, aligning with reported WNV seasonality. Subtropical archipelagos (Azores, Canaries and Madeira), had longer seasonal windows with peaks distributed across most of the year except spring and early summer. Tropical archipelagos (Cape Verde, São Tomé and Príncipe), showed minimal seasonal variation with weak or no clear troughs and peaks. Regarding the seasonality of the proportion of land deemed suitable, similar conclusions

were reached across study regions, albeit with Cape Verde behaving more like subtropical regions despite its tropical climate. In general, these results highlighted that WNV seasonality, both spatial and temporal, generally weakens as climates shift from temperate, to subtropical to tropical.

WNV is maintained in a zoonotic cycle dependent on avian and mosquito species. Within this cycle, some *Culex spp.* involved in mammalian transmission are less anthropophilic than *Aedes spp*. which are key vectors for other arboviruses. It is thus tempting to associate the human risk for WNV transmission to areas with smaller or less dense human populations where avian and *Culex spp.* more likely have better established population distributions. This association, however, has had contrasting evidence, with WNV occurrence being associated with agricultural land cover in certain regions (e.g. [9,62]) and associated with urban land cover in others (e.g. [62,63]). Differences between studies in the type of WNV occurrence data used (i.e. unique or combinations of human, equine, mosquito and avian sources) likely contribute to such contrasting evidence. As highlighted in the context of the 2020 large WNV outbreak in Spain, other factors may contribute to discrepancies [9]. For example, that transmission is likely much wider than is reflected by limited data sources whose information is itself influenced by constant avian movement between urban and non-urban areas, or that there is varying avian biodiversity of importance for WNV transmission between closely located regions, and that there is uneven contribution of mosquito species with slightly different environmental preferences, susceptibility, infectivity and biting habits. Similar to some studies and in contrast to others, the current study found that agriculture-related land cover was most informative under a positive association with estimated suitability for WNV occurrence.

When analyzing the number of months in a year that locations remain suitable for WNV occurrence, a striking positive association with local human population size was observed across all study regions (except for Cape Verde). When weighting local estimated suitability by community size as a proxy for risk to human populations, we were able to describe the spatial heterogeneity of risk across subregions of the countries and islands of the archipelagos. For countries, as expected, many subregions with large human populations were identified as having relevant risk levels, but other subregions with smaller populations were revealed as having higher risk than expected from solely considering suitability. This reiterated the conclusions from some of the intermediate exercises performed in this study, which revealed that locations deemed suitable for WNV occurrence for longer periods of time were seemingly associated with larger local human populations. In turn, this highlighted the importance of exploring the actual association between estimations of pathogen transmission potential and the distribution of relevant hosts, since e.g. regions with higher estimated transmission potential do not necessarily overlap with a significant presence of hosts relevant for public health (and vice-versa).

Limitations of this work include e.g. those related to data sources. Namely, available satellite data at adequate spatial resolution for archipelago modelling included climatic variables representative of monthly averages for the period between 1981 and 2010 and snapshots for particular years regarding land types. As such the data used for training and projection did not specifically represent the dates of WNV occurrences, and allowed only to perform suitability projections per typical month of the year (Jan-Dec) rather than for every day, month and year included in the WNV occurrence data. While this allowed us to estimate monthly spatial landscapes of suitability and generate novel insights into the expected variation of seasonality within a typical year, future research should implement higher temporal resolution outputs once satellite data is available at better spatio-temporal resolutions, specially for the archipelagos. Furthermore, while the WNV occurrence data used for model training from the three European countries included mosquito, human, equine and avian sources, it was nonetheless enriched in human and equine sources. As such, the resulting suitability estimations

could potentially be biased to represent a summary measure of spillover potential; i.e. outputs are potentially more informative towards a better understanding of the landscape of spillover risk to humans and equines rather than viral maintenance in the natural avian-mosquito reservoir. Another limitation is the inability to infer causation, such that all outputs, specifically those regarding predictor variables, should be interpreted purely as informative associations. This, however, is a general limitation of machine learning approaches and is not specific to the current study. A final limitation is that while we have previously shown that avian biodiversity is informative to predict the WNV occurrence spatial landscape in Portugal, and others have shown that mosquito distributions play a role in observed WNV occurrence spatial landscapes elsewhere, such mosquito and avian data was not included in the current study. The reason for this was a lack of available data sources, especially for the archipelagos (that is, even collating such data for the European training regions would not suffice since model projections for archipelagos would require such data to also be available for all islands). A possible future venue is to pursue reanalyses of archipelago suitabilities where and when such data becomes available.

In summary, we have developed a machine learning approach trained on European data to project WNV ecological suitability in several Atlantic archipelagos where competent mosquito-species are present but WNV transmission potential remains largely unknown. Through ecological suitability analyses, unique quantitative and dynamic insights are provided related to the spatio-temporal suitability for WNV occurrence and risk to the human population across Portugal, Italy, Spain, Madeira, Azores, Canaries, Cape Verde and São Tomé and Príncipe. Towards capacity building, this work also produces unique open-access resources. For example, we provide an in depth review of the literature on existing historical evidence on WNV and mosquito-species of interest per archipelago, as well as datasets with estimated spatio-temporal ecological suitability and human-related risk estimates per country subregion and per island across the archipelagos. These materials can serve as resources for researchers and policy makers focusing on the studied countries and archipelagos, towards supporting local preparedness, surveillance and control initiatives. In the context of the archipelagos, these resources are novel and unique.

Data availability

Ecological suitability for WNV occurrence is made available within a Figshare repository (DOI:10.6084/m9.figshare.c.7697918) in GeoTiff format (*.tif*), which is compatible with the Terra R-package [64]. Curated WNV occurrence data is also provided in the same Figshare repository. Data otherwise presented in Figures is provided in table format in **Supplementary Text**.

Authors' contributions

MAG: Data Curation, Methodology, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing. **JL:** Data Curation, Resources, Methodology, Conceptualization, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Supervision. **MG:** Conceptualization, Investigation, Writing - Original Draft, Writing - Review & Editing, Supervision. **MVC:** Resources, Conceptualization, Investigation, Writing - Original Draft, Writing - Review & Editing, Supervision.

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Conflict of interest

The authors declare no conflict of interest.

Supplementary Information

Supplementary Text File, including review of literature, additional methodological details and modelling outputs, **Supplementary Tables S1-7** and **Figures S1-20**.

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