Climate change impacts on West Nile virus transmission in a global context

Shlomit Paz

Department of Geography and Environmental Studies, University of Haifa, Israel

West Nile virus (WNV), the most widely distributed virus of the encephalitic flaviviruses, is a vector-borne pathogen of global importance. The transmission cycle exists in rural and urban areas where the virus infects birds, humans, horses and other mammals. Multiple factors impact the transmission and distribution of WNV, related to the dynamics and interactions between pathogen, vector, vertebrate hosts and environment. Hence, among other drivers, weather conditions have direct and indirect influences on vector competence (the ability to acquire, maintain and transmit the virus), on the vector population dynamic and on the virus replication rate within the mosquito, which are mostly weather dependent. The importance of climatic factors (temperature, precipitation, relative humidity and winds) as drivers in WNV epidemiology is increasing under conditions of climate change. Indeed, recent changes in climatic conditions, particularly increased ambient temperature and fluctuations in rainfall amounts, contributed to the maintenance (endemization process) of WNV in various locations in southern Europe, western Asia, the eastern Mediterranean, the Canadian Prairies, parts of the USA and Australia. As predictions show that the current trends are expected to continue, for better preparedness, any assessment of future transmission of WNV should take into consideration the impacts of climate change.

1. Climate change and vector-borne disease

Climate change is a complex phenomenon [1] that affects human health. The impacts are multifaceted and vary in scale and timing as a function of the local environmental conditions and human vulnerability. As a part of that, climatic change influences the emergence of vector-borne diseases such as malaria, dengue and West Nile virus (WNV) by altering their rates, ranges, distribution and seasonality [2–7]. Vector-borne diseases are dynamic systems with complex ecology, which tend to adjust continually to environmental changes in multifaceted ways. Although climate is one of several factors that influence the distribution of these diseases, it is known to be a major environmental driver influencing their epidemiology. Weather conditions (in particular temperature, precipitation and humidity) affect the survival and reproduction rates of the vectors, their habitat suitability, distribution and abundance. Additionally, climatic factors impact the intensity and temporal activity of the vector throughout the year and affect the rates of development, reproduction and survival of pathogens within the vectors [5,8].

The Intergovernmental Panel on Climate Change (IPCC) [9] lists vector-borne diseases among the consequences most likely to change due to global warming. Moreover, as these diseases are particularly sensitive to climatic fluctuations, they might serve as an alert to focus attention on climate change threats [10,11].

The aim of this review is to examine and integrate the up-to-date knowledge on the impacts of climate change on WNV transmission in a global context. All available peer-reviewed studies that deal with linkages between climatic factors and WNV have been collected for this paper, and most of them are mentioned below. Special attention has been paid to recent publications that highlight regional climatic change impacts on vector population dynamics and on disease transmission.
2. West Nile virus

West Nile virus is one of more than 70 viruses of the family Flaviviridae of the genus Flavivirus. Serologically, it is a member of the Japanese encephalitis serocomplex. The viruses can be designated into at least five phylogenetic lineages but only lineages 1 and 2 have been associated with significant disease outbreaks in humans [12,13]. The enzootic cycle is driven by continuous virus transmission to susceptible bird species through adult mosquito blood-meal feeding, which results in virus amplification. Species from the genus Culex mosquitoes (family Culicidae) are the primary amplification vectors and also act as bridge vectors. The transmission cycle exists in rural ecosystems as well as in urban areas where the virus infects birds, humans, horses and other mammals [14–23]. The distribution of WNV is dependent on the occurrence of susceptible avian reservoir hosts and competent mosquito vectors, mosquito host preference and availability of hosts [12].

Most human infections occur in the summer or early autumn [24]. West Nile fever (WNF) is a potentially serious illness for humans and approximately 1 in 150 infected people develop a serious illness with symptoms that might last for several weeks. Up to 20% of patients have milder symptoms and approximately 80% show no symptoms at all [25].

Geographically, the virus has circulated in Africa since 1937, and up until the early 1990s human outbreaks were reported in Africa and Israel, mainly associated with mild febrile illnesses. Since then, new viral strains, probably of African origin, have increased human disease incidence in parts of Russia and southern and eastern Europe, with large outbreaks of increased clinical severity occurring in Romania, Russia, Israel and Greece [12,26].

The first appearance of WNV in the western hemisphere occurred in New York City in 1999 [27]. The virus had spread to the Pacific coast by 2003 and to Argentina by 2005 [28,29]. Currently, WNV has an extensive distribution throughout Africa, the Middle East, southern and eastern Europe, western Asia and Australia, which derives from its ability to infect numerous mosquito and bird species. Today, as WNV is the most widely distributed of the encephalitic flaviviruses, it is a vector-borne pathogen of global importance [12].

3. West Nile virus and climate

Multiple factors impact the complex epidemiology of WNV besides its transmission and distribution. These factors are related to the dynamics and interactions between the pathogen, vector, vertebrate hosts and environment. Hence, among other drivers, weather conditions have direct and indirect influences on vector competence (the ability to acquire, maintain and transmit the virus), on the vector population dynamics and on the virus replication rate within the mosquito, which are mostly climate- and weather-dependent [23,30,31]. Table 1 summarizes the main impacts of climatic variables on the epidemiology of WNV.

(a) Temperature

Ambient temperature plays an important role in viral replication rates and transmission of WNV by affecting the length of extrinsic incubation, the seasonal phenology of mosquito host populations and the geographical variations in human case incidence [22,30,32–34]. Increased temperatures cause an upsurge in the growth rates of vector populations, decrease the interval between blood meals, shorten the incubation time from infection to infectiousness in mosquitoes, accelerate the virus evolution rate and increase viral transmission efficiency to birds [22,23,30,32,35,36].

Laboratory experiments demonstrated that the virus is capable of replication across a wide range of temperatures, from 14°C in poikilothermic mosquitoes [37] to 45°C in febrile avian hosts [33]. However, it was shown that the replication cycle is completed more quickly in mosquitoes at higher temperatures [38,39], while a clear association was found between extreme heat and outbreak intensity in humans [4,18,22,35,40–43]. At the same time, it is important to note that, in some cases, extremely high temperatures begin to slow down mosquito activity. For example, temperatures above 30°C reduced larval survival of Culex tarsalis [44] and slowed WNV growth in Culex univittatus [45].

In addition, the change in environmental temperatures might have an indirect impact on the spread of the virus. It is well known that the transmission cycle involves birds as the principal hosts (and mosquitoes, largely bird-feeding species, as the primary vectors) [23]. In recent years, it has been observed that several bird species have been migrating to their breeding grounds earlier as a result of an early rise of the mean spring temperatures, which is one of the effects of global warming [46–50]. This phenomenon might influence the appearance and timing of the disease in locations near or along migration routes. However, this assumption needs further investigation.

(b) Precipitation

A common dogma in epidemiology is that above-average precipitation might lead to a higher abundance of mosquitoes and increase the potential for disease outbreaks in humans [51,52]. This pattern of a positive association with rainfall in the months preceding disease outbreaks has been demonstrated for WNV [42,53]. However, the literature shows a more complex picture. Although the patterns of disease incidence can be influenced by the amount of precipitation, the response might change over large geographical regions, depending on differences in the ecology of mosquito vectors [23,52,54]. For instance, heavy rainfall increases the standing water surface which is necessary for mosquito larval development. On the other hand, heavy rainfall might dilute the nutrients for larvae, thus decreasing the development rate [55]. It might also lead to a negative association by flushing the ditches and drainage channels used by Culex larvae [56,57].

Below-average precipitation can facilitate population outbreaks of some species of mosquitoes because the drying of wetlands disrupts the aquatic food-web interactions that limit larval mosquito populations [44,56,58]. Drought leads to a close contact between avian hosts and mosquitoes around remaining water sources and therefore accelerates the epizootic cycling and amplification of WNV within these populations [59]. Furthermore, during drought conditions, standing water pools become richer in the organic material that mosquitoes need in order to thrive [22]. Such water areas might be attractive for several bird species also, which might increase the bird–mosquito interaction.
Moreover, ecological studies showed that drought conditions can facilitate population outbreaks of some species of mosquitoes in the following year [58].

(c) Relative humidity
The research regarding the role of relative humidity in WNV eruptions is very limited. Significant positive correlations were found between hospital admission dates of patients and relative humidity levels in the Tel Aviv metropolis (Israel) [4]. A study in Maryland, USA, examined the effect of off-season factors on mosquito population size. Among other variables, the average maximum relative humidity was associated with vector population dynamics [60]. A recent analysis detected correlations between morbidity in humans and weekly relative humidity in Europe and western Asia [22]. All these studies found that air temperature is a better predictor for increasing disease cases than air humidity.

(d) Wind
Wind patterns might contribute to virus spread by their impact on wind-blown mosquitoes [61]. Storm fronts have been proposed as dispersal mechanisms for mosquitoes and the arboviruses they transmit [62–64]. For example, it was shown that wind is used by *Culex tritaeniorhynchus* mosquitoes as a means of migration in China [65].

Winds might impact on WNV spreading also by affecting bird migration through changes in the patterns of storm tracks. In recent years, significant changes in the location and intensity of storms have been shown on a regional basis, as a part of climate change observations and scenarios [66]. Thus, it seems that change in storms might influence WNV dispersal by impacting the dynamics of storm-driven birds [23].

The importance of climatic factors as drivers in the epidemiology of WNV is increasing under conditions of climate change. Consequently, the aim of the following sections is to highlight the linkages between climatic change and WNV transmission in a global perspective (see also table 2).

### 4. Europe and Eurasia

(a) Main climatic change observations
Impacts of climate change vary by region, depending on the change intensity and the vulnerability rate of the area. In general, during recent decades Europe has warmed up; temperature rise was much larger than the global average, especially in the north, and larger than the European average in the mountain areas and the Mediterranean region. Over the past 50 years, more frequent and more intense hot extremes have occurred. This trend is expected to continue, while predictions suggest a further temperature increase (of between 2.5°C and 4.0°C) by the end of the century [67,68].

Changes in rainfall show more spatially variable trends across Europe. Annual precipitation changes are already exacerbating differences between the rainy northern part (an increase of 10–40% during the twentieth century) and the dry southern region (a decrease of up to 20%). Heavy rain events have increased in the past 50 years and are projected to become more frequent. Dry periods are expected to increase in length and frequency, especially in southern Europe.

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<tr>
<th>climatic variable</th>
<th>impacts on the epidemiology of WNV</th>
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<td><strong>temperature</strong></td>
<td>correlates positively with:</td>
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<td>- viral replication rates</td>
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<td>- seasonal phenology of mosquito host populations</td>
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<td>- growth rates of vector populations</td>
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<td>- viral transmission efficiency to birds</td>
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<td>- geographical variations in human case incidence</td>
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<td>correlates negatively with:</td>
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<td>- interval between blood meals</td>
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<td>- incubation time from infection to infectiousness in mosquitoes</td>
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<td><strong>precipitation</strong></td>
<td>above average, floods:</td>
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<td></td>
<td>- leads to higher mosquito abundance</td>
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<td></td>
<td>- reduces potential by flushing drainage channels used by <em>Culex</em> larvae</td>
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<td>- correlates positively with potential for disease outbreaks in humans</td>
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<td><strong>(contradictory findings)</strong></td>
<td>below average, drought:</td>
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<td>- facilitates population outbreaks of some mosquito species</td>
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<td>- ‘rich’ standing water attracts several species of mosquitoes and birds; this increases the bird–mosquito interaction and accelerates the epizootic cycling and amplification of WNV within these populations</td>
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<td><strong>wind</strong></td>
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<p>| Table 1. Impacts of climatic variables as drivers in the epidemiology of WNV. |</p>
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<tr>
<td><strong>Europe and western Asia</strong></td>
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<td>temperature increase</td>
<td>warmer conditions facilitated the establishment of WNV in new areas through an expansion of range and seasonal abundance of vector species, and by directly increasing competence for transmission</td>
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<td>increase in heat wave frequency and intensity</td>
<td>precipitation might increase standing water availability for mosquitoes (but results for rainfall are less consistent)</td>
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<td>precipitation increase in the north and decrease (with dry periods) in the south more heavy rainfall events in Eurasia and central Europe</td>
<td>increased temperature is positively correlated with the rate of virus evolution, with mosquito abundance and infection; it influences WNV distribution and plays an important role in the maintenance and amplification of human infection</td>
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<td><strong>North America</strong></td>
<td><strong>Australia</strong></td>
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<td>increased temperature is positively correlated with the rate of virus evolution, with mosquito abundance and infection; it influences WNV distribution and plays an important role in the maintenance and amplification of human infection</td>
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<td>across the USA precipitation has increased by an average of about 5% increase in water scarcity in the Canadian Prairies</td>
<td>findings are inconsistent, particularly when the analyses include different vectors: in general, human outbreaks of WNV are preceded by above average rainfall in the eastern USA and by below-average rainfall on the western side</td>
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<td><strong>Australia</strong></td>
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<td>annual average daily mean temperature has increased by 0.9°C since 1910</td>
<td>in a warmer climate, C. annulirostris populations are expected to reach high levels of abundance earlier and maintain them for longer</td>
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<tr>
<td>increased spring and summer monsoonal rainfall across northern Australia and decreased late autumn and winter rainfall across the south</td>
<td>an outbreak of equine encephalitis (WNV_kun) followed extensive flooding across eastern Australia</td>
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Observations for Eurasia and central Europe show more temperature extremes, less summer precipitation, more river floods in winter and higher water temperature [1,67,68]. The European Mediterranean region has become warmer with a significant increase in the frequency, intensity and duration of heatwaves [69,70] in parallel with a decrease in total precipitation. In this area, mutual enhancement (positive feedback) has been identified between droughts and heat waves [70].

(b) Climate change impact on West Nile virus transmission

Since the mid-1990s, outbreaks in humans and horses have been documented in Eurasia (Bucharest in Romania, the Czech Republic, Hungary, and Volgograd in Russia), western Europe (France, Italy, Spain and Portugal) and Israel. The lack of cases in humans in northern Europe is possibly attributed to the feeding behaviour of the predominant vector, Culex pipiens, as well as to other factors, especially climate [71].

In 2010, large outbreaks occurred in northern Greece (Macedonia), in Romania, Hungary, Italy and Spain, in Russia (Volgograd), Turkey and Israel. These outbreaks in humans were accompanied by infections in donkeys in Bulgaria and horses in Morocco, Portugal, southern Italy and Greece. Since then, all subsequent years (2011–2014) were characterized by the re-emergence of WNV in Europe, with human cases noted in almost all eastern, central and southern countries [23,26,72].

The unprecedented upsurge in the number of human WNF cases in summer 2010 was accompanied by extremely hot spells in southeastern Europe and Eurasia [22]. According to the World Meteorological Organization [73], this warming peaked in this past decade ending in 2010, which was also one of the three hottest years ever recorded. An analysis of the climatic drivers of the 2010 outbreak found the ambient temperature to be the most important [22]. The impact of climatic variables on the endemization of WNV in Europe and western Asia has been reviewed recently by Paz & Semenza [23]. They noted that in parts of Europe, climate change resulting in warmer conditions facilitated the establishment of WNV in new areas through an expansion of range and seasonal abundance of vector species and by directly increasing competence for transmission. These insights are reinforced by previous studies from western Asia. A research about the linkage between heatwaves and WNV upsurge in humans in Israel showed that an early extreme rise in temperature in the hot season is a good indicator of increased vector populations [4]. In addition, in their study on the outbreaks in the Volgograd Province in Russia, Platonov et al. [31] showed that the abundance of Culex mosquitoes in an epidemic season is higher in years with a mild winter and a hot summer.

Results for precipitation are less consistent. Papa et al. [74] noted that increased rainfall and humidity (together with high temperatures) have probably favoured the multiplication of Culex species, leading to the occurrence of numerous cases of WNV infection in humans in Central Macedonia in summer...
5. North America

(a) Main climatic change observations

Impacts of climate change in North America differ by region, with coastal areas, mountains and flood plains being particularly vulnerable. Generally, during the past 50 years, the average temperature across the USA has risen, while precipitation has increased by an average of about 5%. Some extreme weather events, such as heat- and cold-waves, intense precipitation events and regional droughts, have become more frequent and intense [75–77].

Northwards, Canada has already experienced warming that is disproportionate to global climate change, with average temperatures in some northern regions increasing by more than 2°C. In the Canadian Prairies (where WNV is a significant concern) increase in water scarcity has been observed in parallel with warmer and drier summers [78,79].

The IPCC projects that climatic and weather conditions in North America in the coming decades are likely to include warmer temperatures, shorter winters, increased proportion of precipitation falling as rain rather than snow, increased frequency of heavy rainfall and other extreme weather events. These changes pose risks to public health including the emergence of vector-borne diseases [1,70,77].

(b) Climate change impact on West Nile virus transmission

WNV was first reported in North America in New York City in 1999, when it infected many species of birds as well as humans and other mammals [36]. Later, the virus moved across the continent, reaching Canada and Central America by 2002 and was isolated in California in July 2003 [80]. In fact, WNV became endemic across most temperate regions of North America [12].

The effects of weather fluctuations on WNV transmission in the USA and Canada have been analysed by several researchers who showed that increased temperatures influence North American WNV distribution and play an important role in the maintenance and amplification of human infection [43,81]. Soverow et al. [42] assessed 16,298 human WNF cases from 2001 to 2005 across 17 states in the USA. They found positive associations with increasing temperature over each of the four weeks prior to symptom onset. Specifically, an increase of 5°C in the mean maximum weekly temperature was associated with a significant 32–50% higher incidence of reported WNF infection.

In a study in Georgia, temperature was found to be among the most important variables in predicting the distribution of WNV [82]. Warm temperature was associated statistically with higher human infection risk in Connecticut [83], with the virus spread into western states and with county-level mosquito infectivity in California [32].

Higher winter temperatures and a warmer spring might lead to larger summer mosquito populations [60]. In their study in Illinois, Kunkel et al. [39] showed a correlation between the number of days when daily maximum temperature exceeded a threshold, the timing of a seasonal shift to a higher proportion of *C. pipiens* among all *Culex* species, and the onset of the amplification phase of seasonal WNV transmission.

In a modelling research in the urban landscape of Chicago, spatial and statistical techniques were used to analyse and forecast fine-scale spatial and weekly patterns of WNV mosquito infection relative to changing weather conditions. The temperature was found to be the main factor that mediates the magnitude and timing of the increased minimum infection rate within the season. It was also strongly indicated as a key factor for explaining much of the observable differences between years while the effect of increased temperature on minimum infection rate was especially strong within a week [36].

Temperature has been linked to the rate of virus evolution. A more quickly replicating virus spurred by warmer conditions precedes an increase in mosquito infection [59,84]. It was detected that warmer temperatures facilitated the displacement of the WNV NY99 genotype by the WN02 genotype [30]. In a study in suburban Chicago, Bertolotti et al. [85] discovered high genetic variation of WNV at fine temporal and spatial scales, while variation in local temperature was offered as one explanation for this.

As the impact of precipitation in WNV transmission is more indirect, the findings regarding North America are inconsistent in particular when the analyses include different vectors [36,42,86]. For instance, the population size of *C. pipiens* (the primary enzootic and epidemic vector in the eastern USA north of 36°N) is often impacted negatively by large rain events due to the flushing of catch basins [57]. By contrast, the vector *C. tarsalis* generally responds positively to heavy precipitation, which provides the typical larval habitat in rural areas in the western part of the USA [87,88].

Regional trends showed that prior drought contributed to the initial USA WNV outbreak [86,89]. Drought conditions can increase the abundance of some vector populations in semi-permanent wetlands as they result in more larval breeding sites with fewer competitors and mosquito predators [58].

In Florida, spatial and temporal differences in periods of drought and rain were associated with human WNF cases and infection of sentinel chickens. Springtime drought followed by a wet summer was found to be a good predictor of WNV incidence in humans. Close proximity of birds and mosquito vectors during times of drought was detected as responsible for the increased virus transmission [56,59,84].

Using county-level precipitation and human WNV incidence data (2002–2004), Landesman et al. [52] tested the impacts of above- and below-average rainfall on the prevalence of WNF in human populations both within and between years. Although the mechanism is not fully understood, the authors found evidence that human WNV incidence is most strongly associated with annual precipitation from the preceding year and noted that human outbreaks of WNV are preceded by above-average rainfall in the eastern USA and by below-average rainfall on the western side in the previous year. In the western USA, primary vectors of WNV include species such as *C. tarsalis* [90], which are likely to undergo outbreaks following years of low rainfall as a result of changes in food-web structure. As the abundance of mosquito larvae is often limited by predators and competitors, in years following a drying event, both efficient mosquito predators and mosquito...
competing is H. virescens, the most highly endemic regions in North America [93]. In that region, the mosquito species C. tarsalis Coquillett, whose distribution is determined by temperature and precipitation [94], is the principal vector for WNV [95].

Laboratory experiments demonstrate that the temperature threshold for survival of C. tarsalis is generally between 14°C and 35°C, and within this range, temperature is positively correlated with the development rate of the vector [44,96]. In a recent study, Chen et al. [93] integrated empirically derived, biologically relevant temperature thresholds for C. tarsalis survival and WNV development, using statistical models to predict the effects of climate change on the distribution and abundance of C. tarsalis and WNV in the Canadian Prairies. Their results suggest that the predicted mean monthly temperatures will not exceed the upper threshold for survival of adult female C. tarsalis, whereas the temporal and spatial distribution of WNV will remain determined primarily by the lower temperature limitation for WNV amplification. The authors expect that elevated temperatures will increase the infection rate of WNV in C. tarsalis, especially in the southern part of the Canadian Prairies without a compensatory increase in mosquito mortality [93].

### 6. Australia

#### (a) Main climatic change observations

The Australian continent is characterized by climate variability. Overall, each decade in Australia since the 1950s has been warmer than its predecessor, while the annual average of the daily mean temperature has increased by 0.9°C since 1910. A general trend towards increased spring and summer monsoonal rainfall across northern Australia and decreased late autumn and winter rainfall across the south have been observed [97].

#### (b) Climate change impact on West Nile virus

transmission

The Kunjin virus (WNVKUN), which is spread by the bite of infected mosquitoes, is the Australian subtype of WNV. The main mosquito associated with the virus spread is *Culex annulirostris* that breeds in fresh water environments. Although only a small number of cases are reported annually, the virus is known to occur in many parts of Australia, particularly in the tropical northern regions. WNVKUN is less virulent than the current USA strain of WNV. Infection rarely causes disease in humans and most infected people do not develop any symptoms [98,99].

In 2011, a highly pathogenic strain caused an unprecedented outbreak of acute equine encephalitis leading to the isolation of the first virulent strain of WNVKUN. This eruption followed extensive flooding across eastern Australia that promoted ideal conditions for freshwater *C. annulirostris* mosquito breeding [100]. Indeed, these mosquitoes require an increase in precipitation amount to ensure larval habitat and to maintain humidity for adult survival [101].

In addition, changes in temperature affect the transmission of WNVKUN. In a warmer climate, *C. annulirostris* populations are expected to commence activity and reach high levels of abundance earlier, and maintain them longer. The season of arbovirus activity might be prolonged, with potential transmission increase [101]. Moreover, as a result of temperature increase, the vectors are expected to move further south into currently cooler regions because summer temperatures in southern areas will be more adequate for initiating and maintaining the virus amplification [102,103].

### 7. South America

The recent IPCC report [1] indicated an overall increase in warm days and heatwaves in South America, and more regions where more precipitation increase than decrease was observed, with spatially varying trends. However, owing to lack of data and studies in South America, there is medium to low confidence regarding climate change observations in the continent [104].

Studies on the impact of climate change on WNV spreading in South America are limited. The southward dissemination of WNV into the Caribbean and Central and South America is attributed to migratory birds. WNV was first detected in 2001 in Jamaica and the Cayman Islands. Cross-reactive WNV antibodies in humans have been detected in Mexico, the Bahamas and Cuba [105]. In 2006, four serologically confirmed human WNV encephalitis cases were reported in Argentina [106]. Serologic evidence of WNV infection in horses was reported in Guadaloupe, Mexico, Puerto Rico and Colombia. Resident birds tested positive for antibodies to WNV in the Dominican Republic and Venezuela [108]. Recently, WNV antibodies were identified in several horses and birds in Brazil [107]. Although extensive, the spread has not been accompanied by notable avian mortality or disease in humans or horses in Latin America and the Caribbean [71], although the main concern is the absence of data on the disease burden in people, horses or birds [108].
8. Discussion

The recent Fifth Assessment Report of the IPCC [1] presents stronger evidence than previously that multiple components of the Earth’s climate system are changing. Global average air temperature has risen by around 0.85°C since 1880 and each decade has been warmer than its predecessor [1]. Although climate change impacts vary by region, it is well established that it influences the distribution of vectors, pathogens of vector-borne diseases and the habitat suitability for vectors. Climate change also contributes to the expansion and shifting of endemic regions [10,109].

WNV is the most widely distributed known arbovirus in the world. The factors that explain this extensive distribution are complex and include the interactions between the vector, virus and host as well as climatic factors. Changes in climatic patterns affect WNV transmission directly through relations between the pathogen, host and vector (e.g. virus replication rate within the mosquito), and indirectly via changes in ecosystem characteristics (such as water temperature).

According to Reisen et al. [32], WNV tended to disperse into new areas during years with above-normal summer temperatures while the amplification during the following year occurred in summers with above-normal or normal temperatures. This insight was evidenced recently in Europe and western Asia, when the outbreaks in the summers of 2011–2013 occurred in most of the same disease locations as in 2010, which was an extremely hot year [22,72]. Another example appeared in the northern USA when the increasing occurrences of warmer weather patterns lead to increased incidence of WNV infections [110].

Based on the above review, it is suggested that recent variations in climatic conditions, particularly increased ambient temperatures and fluctuations in rainfall amounts, contributed to the maintenance (endemization process) of WNV in various locations in southern Europe, western Asia, the eastern Mediterranean, the Canadian Prairies, parts of the USA and Australia. Limited knowledge is available regarding climatic changes in South America and Africa. However, based on the aforementioned insights, it is reasonable to expect that global and continental warming will contribute to the risk of WNV outbreaks in these continents also.

Despite the existence of surveillance systems in several countries, outbreaks appear to be temporally and spatially unpredictable [55]. The prediction of WNV spread and eruption is challenging as it propagates via a complex of interrelationships. This notwithstanding, several statistical and mathematical models have recently attempted to predict
the risk of WNV transmission. Many of them used climatic factors (parameters of temperature and/or rainfall) in their analysis (table 3 summarizes the main recent statistical models that aim to predict WNV transmission/dynamics based on climatic predictors). For instance, a dynamic hydrology model used for predicting mosquito abundance showed that local surface wetness was correlated with the subsequent abundance of mosquito species [56]. A pair of Poisson regression models was developed to examine the extent to which off-season factors, in particular, temperature variables, predict mosquito population size [60]. In a prediction model in the province of Saskatchewan, Canada, precipitation and temperature were important in the prediction of risk of WNV in humans, while decreasing rainfall into July and higher temperatures overall were associated with high-risk areas [111]. In a recent study, Chen et al. [93] used statistical models to predict the effects of climate change on the distribution and abundance of C. tarsalis and WNV in the Canadian Prairies. Indeed, when using epidemiological prediction models, more attention should be paid to the impacts of the changing climate on future transmission of WNV. In a new study, Tran et al. [112] used logistic regression models to analyse the status of infection by WNV in Europe and its neighbouring countries in relation to environmental and climatic risk factors. Temperature, remotely sensed Normalized Difference Vegetation Index and Modified Normalized Difference Water Index (MNDWI) anomalies, as well as population, birds’ migratory routes and presence of wetlands were considered as explanatory variables. The anomalies of temperature in July, of MNDWI in early June, the presence of wetlands, the location under migratory routes and the occurrence of a WNF outbreak in the previous year were considered as risk factors. This suggested model can be used for direct surveillance activities and public health interventions in preparation for potential outbreaks in Europe and Eurasia.

Open questions remain regarding upcoming impacts of the altering climate on the ecology of WNV, such as adaptation to changing local environments, the ability of hosts to migrate, evolutionary change and disease control efforts [10,113]. These efforts target mainly the protection of human and horse populations, while in most cases they do not impact the WNV ecology such as the bird–vector cycle. Although several studies mentioned in the above review are based on case incidence in human or equine populations, WNV circulation occurs in the bird–mosquito system and in fact, the virus does not require human or equine populations for circulation.

Apart from climatic factors, other drivers contribute to the geographical spread of WNV, such as landscape features and land use, bird migration patterns, the caged bird trade and mosquitoes spread by international transportation. All of these factors and others play an important role in the worldwide dispersion of the pathogen and vector [23,114]. Nevertheless, as climatic factors have significant direct and indirect influences on the WNV endemization, the impacts of the changing climate have to be taken into account in any evaluation of WNV transmission in the coming years.

9. Conclusion

Recent climatic changes, particularly the increase in ambient temperature and fluctuation in rainfall amounts, have contributed to the endemization of WNV in various locations around the world. As predictions show that the current trends are expected to continue, for better preparedness, any assessment of future transmission of WNV should take into consideration the impacts of climate change.

References

6. Tabachnick W. 2010 Challenges in predicting climate and environmental effects on vector-borne disease epistems in a changing world.


