

SCOPING REVIEW

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Impact of climate change on the global circulation of West Nile virus and adaptation responses: a scoping review

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Abstract

Background West Nile virus (WNV), the most widely distributed flavivirus causing encephalitis globally, is a vector-borne pathogen of global importance. The changing climate is poised to reshape the landscape of various infectious diseases, particularly vector-borne ones like WNV. Understanding the anticipated geographical and range shifts in disease transmission due to climate change, alongside effective adaptation strategies, is critical for mitigating future public health impacts. This scoping review aims to consolidate evidence on the impact of climate change on WNV and to identify a spectrum of applicable adaptation strategies.

Main body We systematically analyzed research articles from PubMed, Web of Science, Scopus, and EBSCOhost. Our criteria included English-language research articles published between 2007 and 2023, focusing on the impacts of climate change on WNV and related adaptation strategies. We extracted data concerning study objectives, populations, geographical focus, and specific findings. Literature was categorized into two primary themes: 1) climate-WNV associations, and 2) climate change impacts on WNV transmission, providing a clear understanding. Out of 2168 articles reviewed, 120 met our criteria. Most evidence originated from North America (59.2%) and Europe (28.3%), with a primary focus on human cases (31.7%). Studies on climate-WNV correlations ($n=83$) highlighted temperature (67.5%) as a pivotal climate factor. In the analysis of climate change impacts on WNV ($n=37$), most evidence suggested that climate change may affect the transmission and distribution of WNV, with the extent of the impact depending on local and regional conditions. Although few studies directly addressed the implementation of adaptation strategies for climate-induced disease transmission, the proposed strategies ($n=49$) fell into six categories: 1) surveillance and monitoring (38.8%), 2) predictive modeling (18.4%), 3) cross-disciplinary collaboration (16.3%), 4) environmental management (12.2%), 5) public education (8.2%), and 6) health system readiness (6.1%). Additionally, we developed an accessible online platform to summarize the evidence on climate change impacts on WNV transmission (<https://2xz12o-neaop.shinyapps.io/WNVScopingReview/>).

Conclusions This review reveals that climate change may affect the transmission and distribution of WNV, but the literature reflects only a small share of the global WNV dynamics. There is an urgent need for adaptive responses to anticipate and respond to the climate-driven spread of WNV. Nevertheless, studies focusing on these adaptation responses are sparse compared to those examining the impacts of climate change. Further research on the impacts of climate change and adaptation strategies for vector-borne diseases, along with more comprehensive evidence synthesis, is needed to inform effective policy responses tailored to local contexts.

Keywords West Nile virus, Climate change, Adaptation, Vector-borne pathogens

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Background

West Nile virus (WNV), the most widely distributed flavivirus globally, is a significant mosquito-borne virus [1]. It was first isolated in 1937 from the blood of a febrile woman in the West Nile region of Uganda. The earliest reported outbreaks occurred in the 1950s near Haifa, Israel [2]. Since the 1950s, WNV outbreaks have primarily occurred in Israel and various African countries [3, 4]. However, the epidemiology of WNV appears to have shifted since the 1990s due to the globalization of human trade and travel [1]. WNV was first detected in New York City in 1999 and subsequently spread rapidly throughout the entire Western Hemisphere, including the United States (US), Canada, and Argentina [5–7]. Concurrently, epidemic activity increased in Europe, the Middle East, and Russia [3, 4, 8]. In 2018, Europe experienced an unprecedented WNV epidemic, with human cases exceeding 1900, seven times higher than in previous seasons [9]. In 2020, locally transmitted human cases of WNV were reported for the first time in the Netherlands and Germany [10, 11]. Evidence suggests interactive WNV cycles on all continents except Antarctica [1].

The establishment of ongoing WNV transmission relies on the interactions among the virus, vectors, hosts, and environmental factors [12]. WNV can infect a wide range of vertebrate species, including most mammals, birds, and some reptiles and amphibians [13, 14]. Birds, serving as the primary amplifying hosts, play a crucial role in WNV proliferation. While humans and horses are susceptible to WNV, they are considered dead-end hosts [15]. In humans, WNV often results in asymptomatic or mild illness, but approximately 1 in 150 cases progress to neuroinvasive disease, potentially leading to encephalitis or death [16]. The primary vectors for WNV transmission are mosquitoes, particularly those belonging to the *Culex* genus. Mosquito bites are responsible for the vast majority of human WNV infections, although the virus can also spread through blood transfusions, organ transplantations, and potentially breastfeeding [17]. Given that WNV is transmitted by mosquitoes, its distribution depends on environmental conditions and is susceptible to the impacts of climate change [18]. For example, higher temperatures can accelerate viral replication, shorten the extrinsic incubation period in mosquitoes, promote vector abundance, enhance transmission efficiency, expand the suitability of vector habitats, and increase the probability of avian migration across regions [19, 20]. Additionally, precipitation patterns have a significant impact on mosquito breeding and abundance, thus affecting the spread and geographical distribution of WNV [18].

The current body of evidence strongly indicates that climate change directly impacts the spread and proliferation of vector-borne illnesses, including WNV [21]. Numerous studies have demonstrated that areas vulnerable to WNV transmission could expand or shift due to climate elements. This encompasses projecting future global climate change scenarios, examining how vector species respond to environmental shifts in laboratory settings, and conducting field research in regions where outbreaks occur. There is some evidence of WNV emerging or re-emerging in high-latitude regions and at the edges of current endemic zones [22–26]. For example, in North America, the suitable range for WNV is projected to extend northward and to higher altitudes by 2050 and 2080, potentially leading to new infections in both native and non-native species [22]. In Europe, increased WNV cases and new outbreak locations are predicted under future climate scenarios, especially at the margin of current transmission areas [23]. In South America, high risk areas for WNV might shift between 2046–2065 and 2081–2100, with more pronounced changes under high greenhouse gas emission scenarios, potentially altering the current WNV distributions in some countries (e.g., parts of Bolivia, Paraguay, and Brazil) [24]. Moreover, existing surveillance data support the overall trend of heightened WNV risk due to climate change. For instance, in the Powder River Basin of Montana and Wyoming, US, the WNV mortality rate in the wild bird population was significantly higher in 2003 (the sixth most sweltering summer historically) than in 2004 and 2005 [25]. In Germany, the extreme heat in the summer of 2018 (the second most sweltering and desiccated summer historically) theoretically played a pivotal role in reducing the average extrinsic incubation period in mosquitoes, resulting in rapid viral amplification and increased transmission risks to vertebrate hosts [26]. However, the impact of climate change on WNV distribution may vary geographically, and some areas may see a decrease in cases. For example, while Keyel et al. predicted a general increase in WNV cases in 2021, a subsequent study indicated that future cases may decrease in areas outside the boundaries of the original study area in New York [27, 28].

While efforts to mitigate climate change are essential to reduce CO₂ emissions and lessen potential future impacts, there is an increasing need to focus on adaptation strategies as well. These include various short-term measures at different levels to address the immediate effects of climate change [29]. Adaptation approaches aim to enhance resilience in health systems, preparing them to manage and minimize the health consequences of climate change [29]. Given the commitments countries

have made to the Paris Agreement and Sustainable Development Goals, along with the growing global evidence base for climate change's impact on disease spread, nations have begun developing and implementing policy responses as components of national climate adaptation plans [30]. Insights into the expected magnitude of climate change impacts on WNV and associated adaptive responses can help inform best practices to mitigate public health impacts from the climate-induced spread of disease.

Contemporary prioritization in Canada of investigative pursuits on emerging human and animal diseases under climate change scenarios indicated that WNV is a disease requiring primary attention [31, 32]. Since the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report in 2007, the health impacts of climate change have garnered significant research focus [33]. This attention has increased further following the Fifth Assessment Report in 2014 and the 2015 Lancet Commission on Climate Change and Health, leading to a growth in the number of related publications [34, 35]. In addition to highlighting the impacts of climate change, these articles also emphasize to some degree specific interventions or policy responses within defined countries and regions. To our knowledge, a comprehensive review of the global impacts and adaptation responses related to climate change and WNV has not been conducted. Such a review is necessary to consolidate existing evidence, explore how climate change influences the spread of WNV, and identify the most effective strategies for developing adaptation policies.

In summary, this scoping review aims to address two core questions:

- i) What types of evidence exist regarding the impact of climate change on the global transmission of WNV?
- ii) What adaptation measures have been proposed or implemented in response to climate change?

Our primary focus is to elucidate the climatic drivers of WNV to better inform these strategies. This approach is intended to serve as a foundation for future research that may delve into comprehensive public health policies and adaptation measures.

Methods

Protocol and registration

We used a scoping review methodology to select studies for inclusion in this synthesis. Our review followed an established protocol, guided by the PRISMA Scoping Review Extension (PRISMA-SCR) and published scoping review methodology [36–38]. It was registered with

the OSF Registries (<https://osf.io/9j2as>) on December 25, 2023, to ensure transparency [39, 40].

Search strategy

We conducted systematic searches across four databases—PubMed (MEDLINE), Web of Science, Scopus, and EBSCOhost—to identify relevant peer-reviewed publications on climate change and WNV between January 2007 and December 2023 without imposing language restrictions. Our literature searches employed terminology related to climate change and the diseases of interest. Terms for climate change were taken from the search strategy used in Sweileh's (2020) bibliometric analysis of climate change and health publications: "climat* Change" OR "global warming" OR "changing climate" OR "climate variability" OR "greenhouse gas" OR "rising temperature" OR "extreme weather" OR "greenhouse effect" [41]. Disease-specific terms included were: "West Nile virus" OR "WNV host" OR "WNV vector". Full search strategies for each database are provided in supplementary materials (Additional file 1).

This search strategy was designed to comprehensively capture all original studies examining the associations between meteorological, climatological, ecological, or environmental change factors and the transmission dynamics, outbreaks, risks, or adaptations of WNV. By conducting systematic searches across key databases, supplemented by targeted topic strings, our strategy ensures reproducibility and effectively summarizes contemporary evidence illuminating the connections between WNV and climate amidst escalating changes.

Eligibility criteria

The criteria for including and excluding articles in our analysis are outlined in Table 1. We examined literature since 2007 to capture research conducted after the IPCC Fourth Assessment Report's release, representing a milestone driving expanded climate-health investigations [33, 41]. Focusing on this period enhances relevance and rigor by concentrating on studies consciously examining climate-related impacts during intensifying change. Further augmenting stringency, we concentrated solely on original quantitative and qualitative investigations published in English-language peer-reviewed academic journals. Together these boundaries help systematically extract recent high-quality evidence elucidating shifting WNV transmission dynamics amidst climate change while delineating adaptations instituted since an authoritative global assessment.

Screening and study selection

We used the systematic review software NoteExpress 3.8.0.9455 (Beijing Aegean Sea Software Company,

Table 1 Criteria for inclusion and exclusion

Category	Inclusion	Exclusion
Concept	Articles on climate or climate change impacts on disease emergence, transmission or spread Interventions or climate change adaptation measures related to disease emergence, transmission or spread Articles on West Nile virus	Articles on disease prevention and control interventions for West Nile virus that are not explicitly related to climate change Articles on climate impacts or interventions related to mosquito species with no mention of implications for WNV emergence, transmission or spread
Type of evidence sources	Original research studies	Review, thesis, conference, etc
Language	Articles in English	Other languages
Timeframe	Articles published between 2007 and 2023	Articles published prior to 2007
Publication status	Articles published or in press	Pre-print articles

Beijing, China) to implement standardized screening and selection procedures. Two independent reviewers carried out an initial screening of titles and abstracts to filter articles that met basic eligibility criteria, with a third reviewer resolving any discrepancies. Subsequently, these two reviewers conducted full-text evaluations of the retained articles to ensure compliance with all inclusion criteria as outlined in the predefined protocol. Any disputes again triggered third-reviewer arbitration to achieve consensus.

Data extraction

We used a predefined evidence data extraction framework to systematically characterize key article features including 1) identifiers like title, author(s), and year; 2) specific objectives, study populations, WNV research priority (primary/secondary), and geographic focus; and 3) findings of the paper, such as nature of the evidence for climate change impacts on disease emergence, transmission or spread and/or policy responses, interventions or adaptations [42, 43].

We categorized the geographic focus of articles into six regions: North America, South America, Europe, Africa, Asia, and Oceania, with multi-regional studies classified as global. The study populations analyzed included humans, mosquitoes, birds, and horses. Investigations encompassing more than one species were labeled as 'multiple species', and studies that did not specify their focus were marked as 'unspecified'. The central disease under investigation in all articles was WNV. Articles primarily focused on WNV dynamics were categorized under 'primary' interest level, while those analyzing WNV in conjunction with other vector-borne diseases were deemed of 'secondary' interest.

The findings of the paper regarding evidence or arguments presented on the impacts of climate change (including extreme weather, rising temperatures, and/or climate variability) on WNV emergence, transmission, or spread were recorded. To clearly understand the impacts of climate change on WNV, articles were grouped into

two main categories: 1) climate-WNV associations, and 2) climate change impacts on WNV, as categorized by Kulkarni et al. in their study of the impact of climate change on global malaria and dengue fever [38]. The articles defined as climate-WNV associations mainly refer to the impacts of climatic and seasonal factors (e.g. temperature, precipitation, and seasonal variations) on WNV transmission and spread within a certain time frame. Articles defined as climate change impacts on WNV are further categorized into two types: those with clear evidence of climate change or climate anomalies during the study period affecting WNV transmission and spread, and those with projections of future WNV transmission and spread under climate change scenarios.

The findings of the paper pertaining to evidence for policy responses, interventions, or adaptive measures addressing the impacts of climate change on disease emergence, transmission, or spread were documented. Specifically, the nature of the evidence or arguments presented regarding policy measures, interventions, and/or adaptations to mitigate the effects of climate change on the emergence, propagation, or spread of WNV were recorded. The United Nations Environmental Program (UNEP) handbook on methodologies for assessing climate change impacts and adaptation strategies outlines a typology of adaptation measures to safeguard human health from climate change [44]. These encompassed five categories of measures: (1) surveillance and monitoring, (2) infrastructure development, (3) public education, (4) technology or engineering strategies, and (5) medical interventions. The content of the article on adaptation strategies is categorized according to the UNEP manual and in the context of the WNV case.

Quality assessment of included literature

The quality of the included articles was assessed using the Joanna Briggs Institute Prevalence Critical Appraisal Tool [45]. All selected studies were scored using the 10 quality control items suggested by the tool. A score of

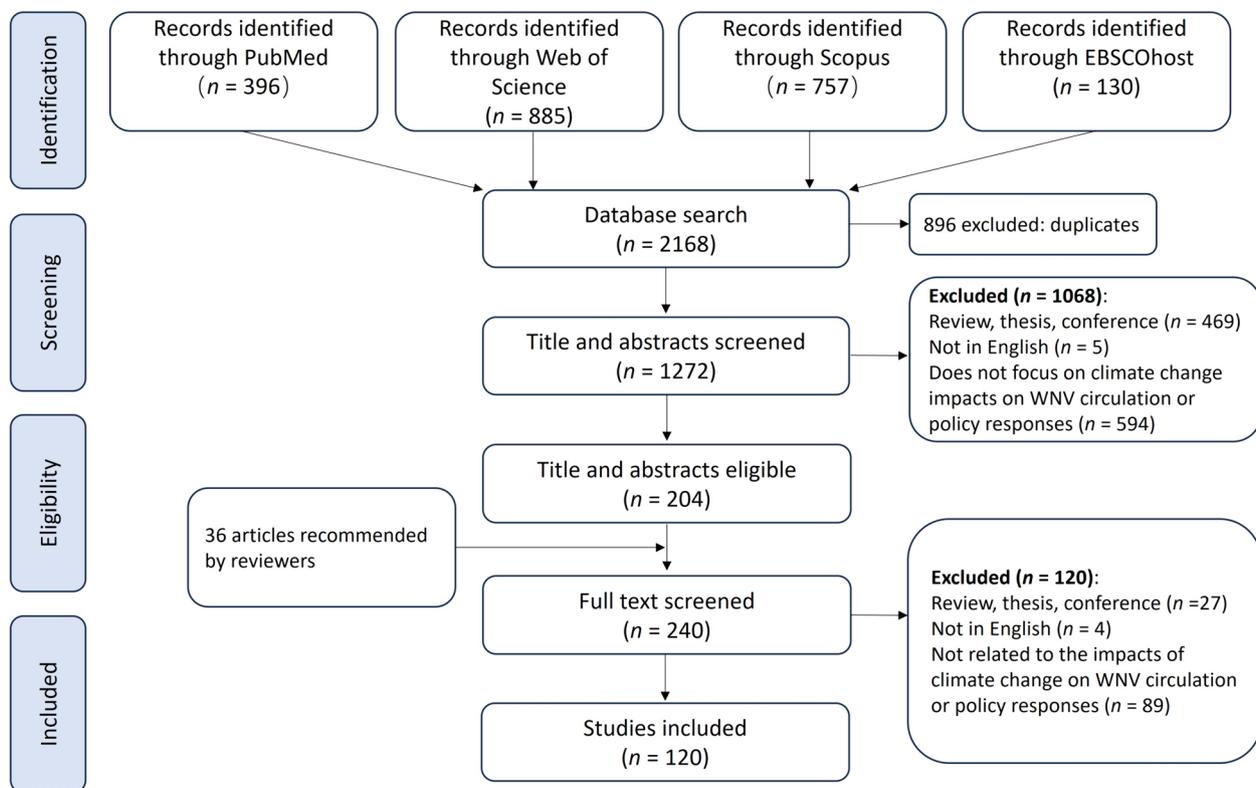


Fig. 1 Flowchart diagram illustrating the article search and selection process

one was awarded for each item fulfilled while a zero score was awarded for each unmet item. Score aggregates were generated and studies were classified as either low (0–3), moderate (4–6), or high (7–10) quality.

Web development

Most reviews traditionally present evidence in a tabular format, which consumes a considerable portion of the article's space and often hinders easy navigation through the key information [36, 38]. In this study, we used the R Shiny interactive web application framework to develop an online-accessible website that presents evidence on the impact of climate change on WNV transmission and dissemination [46]. This website allows visitors to query and download information on the effects of climate change on WNV transmission and spread at any time and from any location. This method provides a novel way to access and understand the synthesized evidence in a clearer and more convenient manner.

Results

Characteristics of included studies

Initially, 2168 articles were retrieved from four databases: Web of Science, PubMed, Scopus, and EBSCOhost. After removing 896 duplicates, 1272 articles remained (Fig. 1).

Following title and abstract screening, 1068 articles were excluded as irrelevant, leaving 204 for full-text review. This resulted in 105 articles meeting inclusion criteria, focusing on the association between climate/weather and WNV or its transmission due to climate changes.

To comprehensively cover literature on the impact of climate change on WNV, we used specific search terms based on key themes from prior studies [37, 38]. Although these terms helped in retrieving targeted and relevant literature, their specificity might have restricted the scope, possibly excluding significant studies that broader terms could have included. Hence, the reviewers recommended 36 relevant articles, which we screened and retained 15 articles according to the inclusion criteria.

The comprehensive review included 120 studies divided into two categories: 83 studies focused on the associations between climate/weather and WNV, and 37 studies examined the impacts of climate change on WNV transmission. All the reviewed evidence and related adaptation responses are available for exploration and download through a dedicated Shiny web application (<https://2xzl2o-neaop.shinyapps.io/WNVScopingReview/>).

Publication year

The number of published studies on climate change and WNV has increased over time, with a sharp rise observed

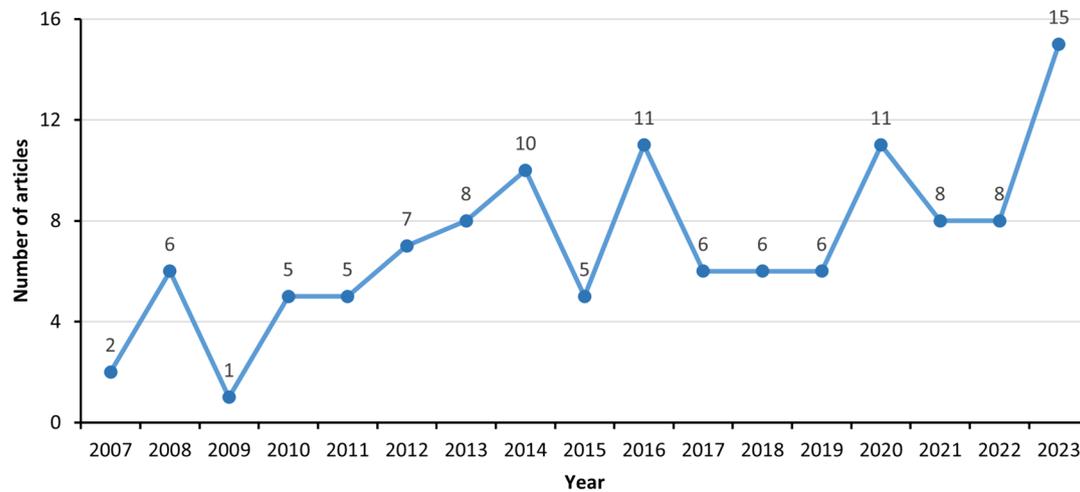


Fig. 2 Distribution of the publication years in all articles included from 2007 to 2023

after 2013 (Fig. 2). Regarding the temporal distribution of relevant literature, two key observations can be made.

First, only 26 articles were published between 2007 and 2012, of which 21 articles focused on the associations between climate/weather [47–67] and 5 articles examined the impacts of climate change on WNV [25, 68–71]. The earliest study on climate/weather factors and WNV, published in 2007, analyzed the association between precipitation and human WNV incidence in the US during 2002–2004. The first article on the impacts of climate change on WNV, published in 2007, investigated WNV prevalence in wild Greater Sage-Grouse populations across Montana and Wyoming during 2003–2005. The relatively small number of studies before 2013 indicates that relevant research was still in its infancy stage.

Second, most studies on this topic ($n=94$) emerged after 2013, corresponding to the release of the IPCC Fifth Assessment Report in 2014 and the Lancet Commission on Climate and Health in 2015 [34, 35]. As authoritative reviews synthesizing the state-of-the-art science on anthropogenic climate change and its health consequences, these landmark reports have stimulated new research assessing climate impacts on infectious diseases like WNV.

Study location

The geographical distribution of study locations examined in the articles is shown in Fig. 3. The most frequently studied region was North America, representing 59.2% of articles ($n=71$). Within North America, 53 articles focused on the US [25, 27, 28, 47–62, 68, 72–104], 17 on Canada [31, 32, 63, 64, 69, 105–116], and 1 covered the

entire continent [22]. Europe was the second most studied region, accounting for 28.3% of articles ($n=34$) [23, 26, 65, 70, 71, 117–145]. The other world regions assessed were Asia ($n=4$; 3.3%) [66, 146–148], Africa ($n=4$; 3.3%) [67, 149–151], South America ($n=2$; 1.7%) [24, 152], and Oceania ($n=1$; 0.8%) [153]. Only 4 articles (3.3%) [51, 154–156] included multiple global regions and were classified as the “global” studies.

Research on WNV has focused on two regions, North America and Europe, which corresponds to the high incidence and disease burden from epidemics reported in these two regions over the past two decades. In the US, between 2007 and 2022, there were 32,600 confirmed or suspected human WNV cases reported to the Centers for Disease Control and Prevention, particularly concentrated in California, Colorado, and Texas [157]. WNV remains the leading cause of mosquito-borne disease in the US, accounting for 83.0% of the reported cases in 2020 [158]. In Canada, since the virus’s emergence in 2001, there have been over 5000 lab-confirmed human cases, with around 20.0% of patients experiencing neurological complications [159, 160]. Additionally, it is estimated that up to 27,000 cases may have gone unreported, given the largely asymptomatic nature of WNV infection [160]. Similarly severe WNV outbreaks have hit Europe in recent years — its 2018 epidemic exceeded 1900 confirmed human cases, surpassing all previous years in scale and distribution [161]. The heavy health and economic toll has reasonably triggered intensive research interests in examining environmental risk factors such as climate change. Study interests and public health priorities understandably tend to align with acute epidemic events and tangible disease burden.

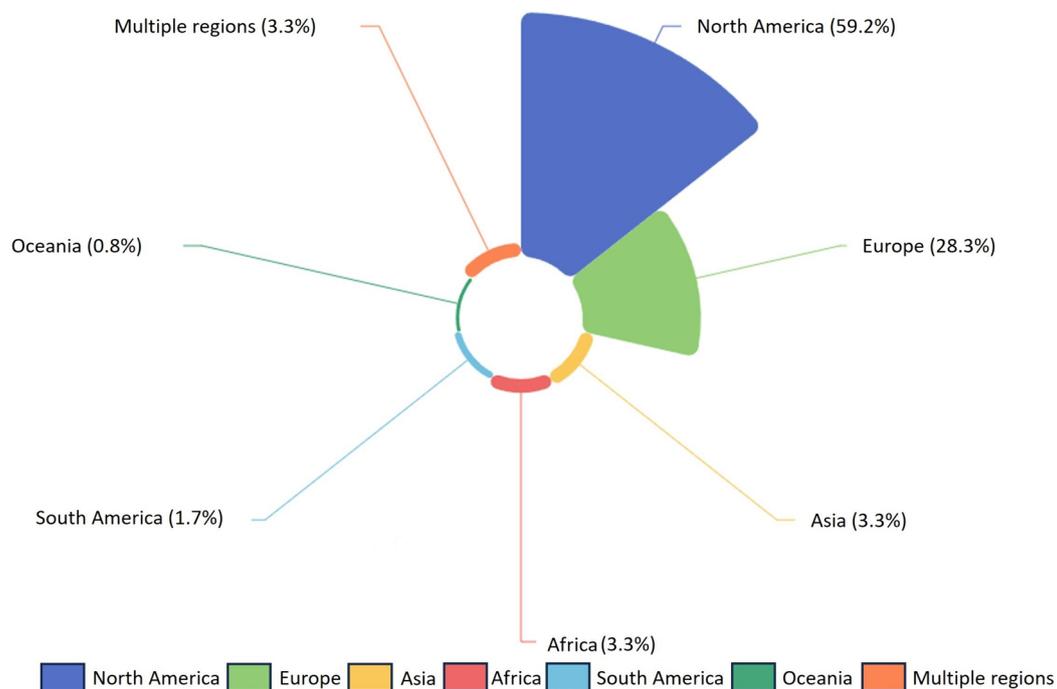


Fig. 3 Geographical distribution of the study areas in all articles included from 2007 to 2023

Research on WNV in regions like Asia, Africa, South America, and Oceania has been comparatively sparse. This imbalance may stem from various factors, such as a lower prioritization due to limited epidemiological data and clinical cases, often attributed to suboptimal surveillance systems. Additionally, the allocation of public health resources in these regions might be challenged by competing health issues, alongside barriers to conducting coordinated multi-national research. For example, in South America, inconsistencies between actual and reported WNV cases arise from symptomatic similarity with other arboviruses and limitations in differential laboratory diagnostics [24]. Moreover, mild and self-resolving cases may remain undocumented. Meanwhile, more severe cases can also be under-diagnosed, owing to a lack of accessible healthcare facilities and logistical constraints on sample transportation and testing [12].

Regional differences in climate, vector ecology, and host community characteristics contribute to variations in WNV transmission patterns and health impacts. For example, the primary vectors of WNV display distinct seasonality under varying climatic conditions [68]. Furthermore, viral strains may evolve different levels of pathogenicity in diverse host species and environmental settings [84]. Consequently, collaborative multi-regional research is essential to formulate prevention policies that are specifically tailored to different regions. Additionally, integrating knowledge and assessment tools is crucial to

further understand the environmental and social factors driving WNV transmission.

Study population

The majority of research articles ($n=103$; 85.8%) focused exclusively on WNV, its vectors, or hosts. The remaining 17 articles (14.2%) examined WNV in conjunction with other mosquito-borne diseases, such as dengue fever and Rift Valley fever. The most studied subject was human WNV cases (Fig. 4), examined in 31.7% of articles ($n=38$) [23, 27, 47, 48, 52–54, 56, 58, 59, 62, 66, 71, 73, 78, 82, 83, 90, 96, 98, 102, 109, 118, 122, 124–126, 128, 130–135, 140, 143, 145, 148]. Mosquito vectors [49, 55, 57, 61, 65, 68, 69, 72, 74, 80, 84, 87, 88, 91–93, 95, 97, 101, 103, 105, 107, 108, 110, 111, 116, 121, 127, 129, 136, 139, 144, 150, 152, 153, 155] and multi-species [22, 26, 28, 51, 60, 64, 67, 70, 75–77, 79, 81, 86, 94, 99, 100, 106, 117, 119, 123, 141, 142, 146] were investigated in 36 (30.0%) and 24 (20.0%) studies, respectively. A smaller percentage of articles ($n=10$, 8.3%) failed to specify the study population [24, 31, 32, 51, 112, 113, 120, 151, 154, 156]. Limited studies focused solely on bird hosts ($n=7$, 5.8%) [25, 50, 89, 104, 114, 115, 138] or equine hosts ($n=5$, 4.2%) [63, 85, 137, 147, 149].

The majority of WNV research has focused on human infection. It's estimated that about 1 in 150 infected individuals develop a severe, long-lasting illness [162]. High

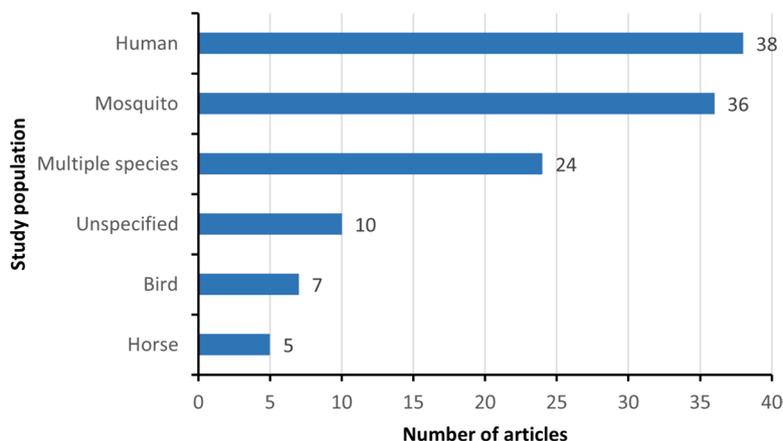


Fig. 4 Distribution of the study populations in all articles included from 2007 to 2023

incidence rates in humans have been linked to environmental factors such as extensive irrigated croplands and rural settings [54]. Mosquito vectors, particularly *Culex* species, play a crucial role in WNV transmission cycles, with their abundance influenced by factors like the urban heat island effect, the presence of water bodies, and the extent of irrigated farmland [54, 129].

However, there is a significant gap in the number of animal-focused studies compared to human studies. In North America, over 28,000 equine cases of WNV have been reported since 1999 [163]. Additionally, in the US alone, the virus has impacted over 300 bird species, with estimated deaths in the millions [164]. Juvenile dispersing birds have been demonstrated to play a vital role in the long-distance dispersal and rapid spatial spread of introduced WNV strains across North America [165]. Given the importance of the role of animals in the transmission and evolution of WNV, there is a need to strengthen research on the impacts of climate change on the transmission and spread of WNV in animals.

Climate-WNV associations

Among the 83 articles examining climate/weather associations with WNV, temperature was the most studied factor ($n=56$, 67.5%) [28, 47, 49, 51, 52, 54, 55, 58–61, 63, 64, 66, 72, 75, 76, 79–82, 84, 86–89, 92–94, 98, 105, 107–110, 117–130, 132, 134, 137–139, 147, 150]. All these studies showed increased WNV transmission probabilities or cases within certain temperature ranges. Precipitation was assessed in 34 studies (41.0%), with 13 showing a positive correlation, 13 indicating a negative correlation, 7 revealing mixed positive/negative correlations, and 1 indicating no correlation with WNV risk [28, 47, 48, 52–55, 58, 63, 67, 72, 77, 79, 81, 82, 86–88, 92, 93, 98, 105, 109, 110, 125, 126, 128, 131, 136, 137, 139, 146, 149, 150]. Drought events and warmer winters

were investigated less frequently, in 8 (9.7%) [28, 56, 72, 74, 85, 119, 126, 146] and 5 (6.0%) [50, 65, 83, 92, 106] studies, respectively. Four articles (4.8%) showed a correlation between humidity and WNV risk, with 3 [47, 80, 91] showing a positive correlation and 1 [119] showing a negative correlation. Nine studies (10.8%) found links between WNV activity and climate-driven seasonal shifts [57, 61, 62, 73, 78, 90, 95, 96, 133], while 2 (2.4%) reported increased transmission associated with flooding events [135, 153]. Three studies (3.6%) reported the correlation between WNV risk and winds/hurricanes [91, 97, 119].

Temperature and WNV

Ambient temperature is a critical driver influencing WNV transmission through direct and indirect impacts on vectors and hosts [49, 71]. Specifically, higher temperatures accelerate viral replication and shorten the incubation period in mosquitoes, fuel vector population growth, increase transmission efficiency, and expand vector habitat suitability [49]. In Israel, positive temperature anomalies were linked to greater mosquito abundance and ensuing human cases [66]. Similarly in Canada, higher mean temperatures are associated with increased *Culex* populations and elevated WNV infections [129]. Moreover, there is a trend towards increased risk around large metropolitan areas characterized by urban heat islands, for example in the United Kingdom [129]. Phenomena such as warm winters and hot summers due to increased temperatures have also contributed to the rise in WNV infection rates [50, 65, 83, 106]. The mean temperature is a strong predictor of the presence of WNV in *Culex* mosquitoes, and this relationship is unimodal [76]. The optimal temperature range for WNV transmission is identified as 22.7–30.2 °C [75]. Outside this range, particularly at temperatures below 17.0 °C, vector competence significantly declines, reaching a relative risk near

zero [76]. It is important to note that this lower temperature threshold can vary among different vector species. Moreover, extreme heat events may further amplify outbreak magnitude [65, 66]. However, it is important to note that an increase in temperature does not necessarily mean an increase in disease incidence altogether. For example, temperatures above 30 °C reduced survival of *Culex tarsalis* and slowed the growth of WNV in *Culex* mosquito [166].

In addition, ambient temperature rise under climate change may indirectly alter WNV transmission by shifting bird host ecology and associated vector exposures. Models project warming could expand bird infection prevalence to higher latitudes as longer activity seasons enable more transmission events [114]. While temperature alone allows increased vector habitat suitability and viral replication at mid-range optima, cascading impacts on avian immunity, migration timing, vector-host overlaps, and habitat ranges could potentially override direct effects. For instance, warmer climates have prompted earlier nesting in British birds, potentially leading to offspring hatching during peak mosquito seasons, increasing young birds' exposure to vectors [167]. This phenomenon is exemplified in Caillouët et al.'s study, which demonstrates how the end of the nesting season aligns with higher mosquito populations, potentially escalating WNV transmission risks during these periods [168].

Precipitation and WNV

The positive correlation between elevated rainfall pre-outbreak and intensified WNV vector abundance/infection has been well documented [47, 125, 126]. For example, a 10 cm rise in summer precipitation was associated with 0.39 more WNV-positive *Culex* mosquitoes per 1000 tested in South Africa [67]. In the US, every 1 cm precipitation increase was linked to a 15% greater WNV incidence [86]. In Australia and Srpska, flooding due to extreme precipitation events creates favorable conditions for WNV transmission, as waterlogged environments can support larger populations of waterbirds and mosquitoes, increasing the likelihood of virus spread [135, 153]. However, precipitation effects on WNV vary across regions and timescales, likely due to place-based differences in viral strain, vector, and host ecology. For example, a negative correlation between total monthly precipitation and the number of WNV cases was observed in Europe [128]. Similarly, in years of increased human WNV incidence in Israel, there was a significant decrease in spring precipitation [146]. In America, extreme drought caused by extremely low precipitation is a potential amplifier of WNV virus transmission and can further increase the risk of WNV transmission [56, 85].

The cause of this phenomenon may be related to the fact that below-average precipitation creates limited water resources for mosquitoes, thereby increasing close contact between hosts and infected mosquitoes at remaining water sources [169]. In addition, both positive and negative correlations of precipitation on WNV incidence have been observed in the eastern and western parts of the US at different time scales [53, 82].

Humidity, wind speed and WNV

Humidity and wind speed play important and complex roles in WNV transmission dynamics, but the impacts vary widely across ecosystems. For instance, higher humidity increased the probability of human infection with WNV in the US [47], and positive correlations were found between soil moisture and vector indices [80]. However, a Greek study conversely found negative relative humidity-WNV case correlations [119]. A study in New York and Connecticut showed an inverse U-shaped relationship between soil moisture and WNV-infected mosquitoes, with high infection associated with drought, but also an increase associated with wetter conditions—both patterns can be present at the same time [27]. Meanwhile, wind may impact disease transmission by influencing mosquito movement. For example, low wind speeds were found to be associated with the capture of WNV-infected mosquitoes during the same week that human cases of WNV emerged in Greece [119]. This may be related to the fact that high wind speeds reduce the chances of a mosquito blood meal, thus reducing the chances of human WNV cases [119]. Additional hypotheses, including storm roles in bird migration contributing to WNV transmission [170], require further investigation.

Climate-driven seasonal shifts and WNV

Climate-driven seasonal shifts are also important factors influencing WNV spread and outbreak magnitudes. For example, Texan counties experience major spikes following wet springs and hot, dry summers [73]. In Suffolk County, warm and dry conditions in early spring have been shown to increase WNV infection in *Culex* mosquitoes [74]. Patterns of dry, hot temperatures following wet years also increase WNV infections [78]. Broader European analyses suggest that anomalous seasonal temperatures and dry winters exacerbate seasonal amplification and drive WNV outbreaks [133]. These climate-mediated seasonal effects likely arise through multiple mechanisms affecting vector reproduction, host immunity, viral replication rates, and transmission efficiency at different phases [170]. As climate change intensifies precipitation variability and seasonal temperature extremes, such seasonal shift tipping points may become more

frequent. Therefore, improved surveillance programs that are responsive to emerging seasonal shifts remain essential for predicting and mitigating transmission at fine geographic and temporal scales.

Summary

While climatic factors have a significant impact on the spread and transmission of WNV, many other factors also influence the complexity of the transmission dynamics. Land use, global trade, bird migration patterns, landscape features, and socioeconomics also partially determine the geographic distribution of infections [50, 80, 86]. For example, areas with older infrastructure, lower incomes, high percentages of cropland, and large rural populations have more landscape features and environmental conditions favorable to vector habitat, which increases local WNV risk [54, 80]. Therefore, operationalizing the “One Health” paradigm through collaborative surveillance, modeling, and mitigation across veterinary, human, wild-life and environmental health remains imperative for fully anticipating and responding to shifting WNV.

Climate change impacts on WNV

Among the 37 articles examining climate change impacts on WNV, the majority ($n=28$; 75.7%) predicted the impact of climate change on WNV [22–24, 27, 31, 32, 69, 70, 99–104, 111–116, 141–143, 145, 151, 152, 155, 156]. Specifically, high latitude regions, areas with immunocompromised populations, locations prone to extreme weather events, and marginalized communities were expected to be more affected [22, 24, 103]. Additionally, 8 articles (21.6%) provided substantial evidence that climatic variability phenomena have already affected the transmission and distribution of WNV during recent outbreaks [25, 26, 68, 71, 140, 144, 148, 154]. Only 1 article (2.7%) focused on developing a national indicator framework for monitoring climate change impacts on infectious diseases [51].

Evidence of future climate change impacts on WNV

In the review, most evidence predicts that future climate change may affect the spread and distribution of WNV [22–24, 111, 114, 151, 155, 156]. In North America, the projected climatic suitability range for WNV in 2050 and 2080 is expected to expand northward and into high-altitude areas, potentially leading to infections in novel and native hosts [22]. In Europe, studies project heightened WNV infection rates and new endemic areas under future climate scenarios, particularly at the margin of current transmission zones (e.g., eastern Croatia, northeastern and northwestern Turkey) [23].

Notably, recent evidence also confirms local transmissions as far north as Germany and the Netherlands, indicating an expansion of risk areas beyond those previously identified [10, 11]. In South America, high-risk areas for WNV may shift between 2046–2065 and 2081–2100, becoming more pronounced under high greenhouse gas emission scenarios, potentially altering the current WNV distribution in some countries (e.g. parts of Bolivia, Paraguay, and Brazil) [24]. In Morocco, the suitable habitat range for *Cx. pipiens* is projected to expand into new central and southeastern areas by 2050, increasing the risk of WNV transmission [151].

Current evidence of climate change impacts on WNV

In addition to predictive studies on the future, existing evidence also demonstrates that climatic variability phenomena have already affected the transmission and distribution of WNV in some regions [25, 26, 144, 148]. In the Powder River Basin of Montana and Wyoming in the US, WNV-related mortality rates in bird populations were significantly higher in 2003, the sixth warmest summer on record, than in 2004 and 2005, the 86th and 41st warmest, respectively [25]. Although this increase in mortality coincided with higher temperatures, it is crucial to consider that 2003 also marked a period of the virus’s initial introduction into the region. This introduction likely contributed significantly to the observed mortality rates, as populations are often most vulnerable when a pathogen first emerges. In Germany, the extreme heat of the summer of 2018 (the second hottest and most arid summer on record locally) was speculated to be an important reason for the decreased mean extrinsic incubation period values in mosquitoes, leading to rapid viral amplification and increased risk of transmission to vertebrate hosts [26]. Additionally, the detection of WNV-infected *Uranotaenia unguiculata* in northern Germany in 2016 presents another case of climate change driving the northward spread of mosquito species and WNV [144]. In Israel, an intense heat wave and a spike in summer temperatures were observed during WNV outbreaks [148].

Summary

The extent of climate change impacts on WNV transmission depends on local regional conditions, including population immunity levels and vector abundance [99, 101, 103]. In areas where comprehensive vaccination programs for animals susceptible to WNV, such as horses, are in place, alongside robust public health infrastructure and strong vector monitoring and control systems, the impact of WNV may be significantly mitigated or even negligible [103]. For example, predictions for the island scrub-jay in California showed that vaccinating ≥ 60

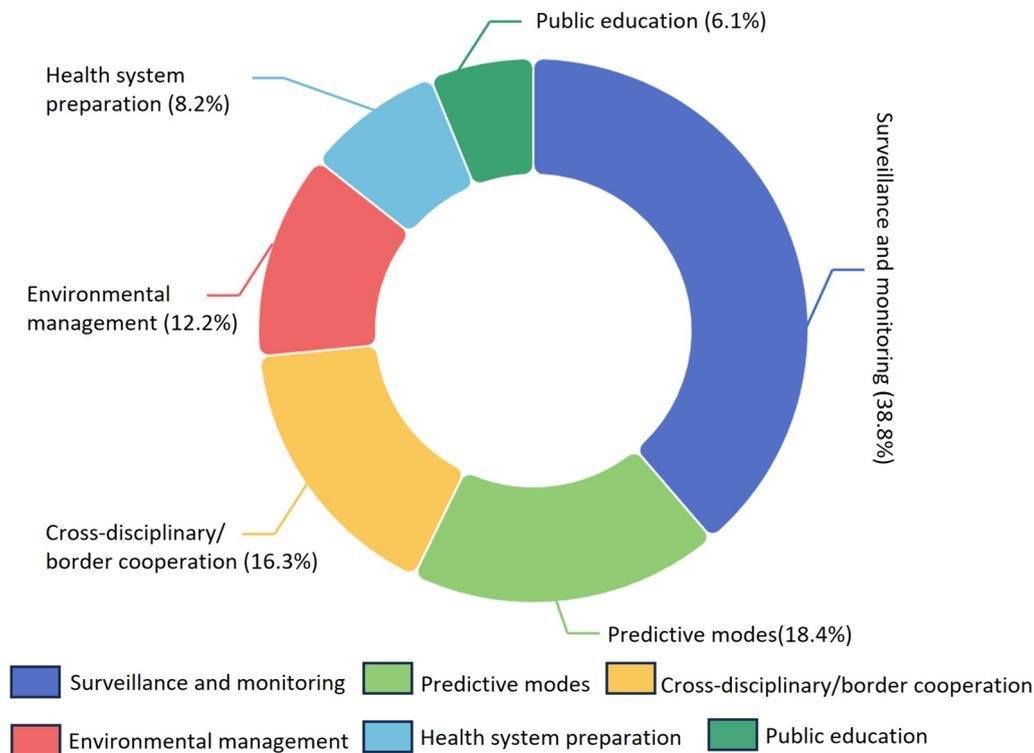


Fig. 5 Classification of 49 articles that proposed or discussed adaptive strategies against West Nile virus risks in response to climate change, divided into six categories based on United Nations Environmental Program criteria

individuals during WNV outbreaks could decrease the risk from $\geq 22\%$ to $\leq 5\%$ [104]. Undoubtedly, strengthening broad-spectrum socioecological resilience through surveillance, preparedness, vector management, and medical capacity building remains paramount for sustainable health amidst climate and global change [101]. However, these anthropogenic measures require considerable regional coordination and resource mobilization, frequently lacking in disproportionately impacted communities. Therefore, actualizing equitable and adaptive WNV resilience necessitates comprehensively integrating climatological, environmental, veterinary, wildlife, genetic, immunological, and public health data into prediction frameworks and response protocols prioritizing vulnerable populations. International organizations must lead in facilitating such collaborative resilience measures globally.

Adaptation strategies to address climate-driven WNV transmission and spread

Among all 120 reviewed articles, 49 proposed or discussed adaptive strategies against WNV risks in response to climate change. These measures were categorized into six groups based on UNEP criteria and the case of WNV (Fig. 5) [44]: surveillance and monitoring ($n=19$; 38.8%)

[22, 23, 56, 65, 69, 75, 85, 92, 99–101, 106, 117, 120, 123, 135, 148, 151, 152]; predictive models ($n=9$; 18.4%) [49, 70, 74, 81, 84, 98, 103, 105, 111]; cross-disciplinary/border cooperation ($n=8$; 16.3%) [24, 51, 80, 126, 131, 133, 141, 156]; environmental management ($n=6$; 12.2%) [25, 87, 95, 104, 142, 145]; health system preparation ($n=4$; 8.2%) [27, 57, 102, 121]; and public education ($n=3$; 6.1%) [86, 113, 118]. A brief overview table of identified adaptation strategies is provided (Additional file 2), with details accessible on the project website under “Detailed adaptation strategies”.

Monitoring and surveillance

Most studies reviewed highlight that monitoring and surveillance are the most critical means of preventing and controlling the spread of WNV under climate change scenarios. Specifically, surveillance should concentrate on high-risk populations, vector populations, wildlife and domestic animals, migrating birds, and neglected areas. As Skaff et al. noted, identifying consistencies between highly susceptible communities and local climates approaching critical thermal thresholds can enhance infectious disease prevention efficacy amidst climate change [75]. Additionally, Semenza et al. recommended fortifying epidemiological monitoring for neuroinvasive

diseases potentially indicative of WNV to expand health-care provider awareness of clinical manifestations and strengthen diagnostic testing capabilities [23]. They also advised augmenting blood donation screening and transportation safeguards while at the same time accounting for climate change in formulating robust WNV contamination prevention protocols [23]. Moreover, numerous studies have suggested that a more granular analysis of meteorological and entomological factors could improve comprehension of intricate WNV transmission dynamics [31, 56, 65, 101, 106, 151, 152]. Concurrently, research and control programs must localize to maximize relevance for regional climate change impacts [101]. Furthermore, public health agencies and vector control teams should amplify efforts to continuously track distributions to minimize human infection risks [151, 152]. Meanwhile, WNV surveillance systems should be strengthened with host monitoring and regular risk assessment, especially for rural livestock, long-distance migratory birds, and wildlife with high mobility [117, 123]. Domestic livestock, particularly horses in high-risk areas, should be vaccinated to enhance their immunity and prevent mortality and morbidity [85]. Routine surveillance should also be conducted in neglected areas (e.g., areas thought not to be transmitted zones and poor areas) [22]. Based on the results of data analysis from surveillance and monitoring, preventive and control strategies need to be adjusted accordingly to cope with changing infectious diseases.

Predictive models

Beyond intensifying surveillance, advancing predictive models and early warning systems remain vital for honing outbreak preparedness and rapid response. Sophisticated predictive tools enabling localized risk projections and efficient resource allocation can dramatically amplify intervention impact [38]. Ideally, such systems would synthesize meteorological, biological, genetic, ecological, entomological, and epidemiological data for accurate emergence prediction across scales [49, 70, 74, 81, 84, 103, 105, 111]. Developing predictive models by linking laboratory-observed environmental transmission patterns to actual transmission patterns is crucial to accurately predicting the impact of climate change on WNV and other vector-borne pathogens [49]. Most importantly, next-generation frameworks must address substantial knowledge gaps around viral evolution, vector-host mutations, species migration and adaptation capacity, infection-recovery dynamics, and anthropogenic environmental change impacts on virus shifting dynamics [70, 103, 111]. Advancing models encompassing this intrinsic biocomplexity and policy-environment feedback remains essential to preempt unprecedented

post-climate change outbreaks through context-specific preparation and response. International alliances should prioritize pioneering these innovations in prediction science alongside flexible surveillance strengthening for integrated epidemic resilience. Beyond informing ongoing emergence, these efforts will uncover complex ecological interconnectivity in the face of convergence across climate and global changes.

Cross-disciplinary/border cooperation

As climate change accelerates, advanced WNV prevention and control requires integrating “One Health” approaches across human, veterinary, wildlife, and environmental health sectors. Multidisciplinary collaboration enables the holistic elucidation of shifting transmission dynamics for accurate risk prediction, alert activation, and adaptive response [126, 133]. Specifically, increased data sharing between public health, vector control, and meteorological agencies, coupled with artificial intelligence integration, can exponentially improve monitoring sensitivity, early warning trigger development, and outbreak interception agility [24, 80]. Additionally, trans-regional information exchange and coordination remain imperative for refining control strategies and resource allocation amidst climate and global change [156]. The 2018 European WNV emergency exemplified the superiority of integrated “One Health” surveillance, ensuring targeted data-driven countermeasures, bridging counties halted uncontrolled cross-border transmission [141]. Given the existential threat of vector-borne diseases necessitates all governmental and international institutions prioritizing and operationalizing such interdisciplinary preparedness and response architectures. This obligation will grow increasingly urgent as environments continue transforming unprecedentedly.

Other adaptive strategies

Of all the studies reviewed, there are fewer strategies related to public education, environmental management, and health system preparedness. However, adapting to the growing threat of WNV under climate change will require multifaceted strategies across environmental management, public awareness-raising, and health system preparedness. Effective environmental management to suppress vector populations, including the elimination of mosquito breeding grounds and the establishment of secondary conserved populations for possible vaccination, forms a crucial first line of defense against WNV [25, 104, 142]. However, this must be coupled with sustained public education campaigns to promote protective behaviors among individuals and vigilant surveillance efforts to enable early response [86, 113, 118]. Finally,

health systems must enhance their capacity for detecting WNV outbreaks in vectors and hosts, allowing timely intervention measures, as well as boosting clinical diagnosis and treatment capacity [102, 121].

Future work

While this review concentrated on the climatic aspects of WNV transmission, it sets the stage for subsequent in-depth analyses of adaptation strategies within the public health domain. Future studies could adopt a One Health approach or leverage the UNEP framework to explore diverse responses to WNV, thereby enriching the dialogue between climate science and public health policy.

Conclusions

Climate change may affect the transmission and distribution of WNV, with the extent of the impact depending on local and regional conditions. Surveillance and monitoring stand out as the most recommended adaptation tactics to address the spread of WNV under climate change scenarios. However, far fewer studies have explicitly focused on adaptation strategies than have investigated the impacts of climate change. Further research on the impacts of climate change and adaptation strategies for vector-borne diseases, as well as more comprehensive evidence synthesis, are needed to inform effective policy responses tailored to local contexts.

Our findings highlight the significant role of climate factors in the transmission dynamics of WNV. However, acknowledging the limitations of our focus, we propose future research to extensively explore adaptation strategies that address these climatic challenges. Such efforts would provide comprehensive insights that are crucial for the development of robust public health policies.

Abbreviations

WNV	West Nile virus
IPCC	Intergovernmental Panel on Climate Change
UNEP	United Nations Environmental Program

Supplementary Information

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Supplementary Material 1.

Supplementary Material 2.

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Authors' contributions

HRW participated in the design, study selection, data extraction and analysis, and write-up of this study. TL, XG, and HBW participated in the design of this study and revised the manuscript. JHX participated in the revision of the manuscript. All authors approved the final version.

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Competing interests

The authors declare that they have no competing interests.

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