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West Nile and Usutu viruses: current spreading and future threats in a warming northern Europe

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Climate change heavily threatens planetary and human health. Arboviral infections are best studied using the One Health concept, due to their reliance on complex interactions between environmental factors, arthropod vectors and vertebrate hosts. This review focuses on two arboviruses, namely West Nile Virus (WNV) and Usutu Virus (USUV), both causing emerging public health issues in northern Europe. They are both maintained in an enzootic cycle involving birds and *Culex spp* mosquitoes. WNV has demonstrated its sensitivity to the consequences of climate change and there is already evidence that global warming contributes to its expansion in Europe. Future WNV indigenous transmission in northern Europe is therefore plausible. Usutu is a lesser known arbovirosis, sharing similar vectors and hosts as WNV. USUV has a similar geographic expansion to WNV, exhibiting some level of co-circulation. It is therefore crucial to monitor these viruses in the hitherto relatively spared regions of northern Europe.

KEYWORDS

arbovirosis, West Nile virus, Usutu, zoonosis, One Health, climate change, Europe

1 Introduction

The climate is changing (1). While it is still of crucial importance to mitigate these changes, it is also increasingly recognized that it cannot be avoided and have now to be taken into account (2).

Human health, in particular, is heavily threatened by future and current climate changes (2). One of the domains in which global change impacts human public health is related to infectious diseases (3). Among these, some are of particular interest in the OneHealth perspective: arboviral zoonoses. Arboviruses – arthropod-borne viruses – depend on the biology of arthropods, which are ectothermic animals, whose physiology is therefore largely driven by the abiotic parameters controlled by the local and global climate (4). Therefore, arboviruses are extremely influenced by the climate changes (4, 5). Most of arboviral diseases are zoonotic, and the implication of non-human hosts, often acting like reservoirs, increases the complexity of the epidemiology and the difficulty to control the associated diseases (6).

In this review, we focus on two arboviruses, namely the West Nile and Usutu viruses, to illustrate zoonose cases.

2 West Nile virus

2.1 Virus and cycle

West Nile Virus (WNV), a member of the Flaviviridae family, was first isolated in 1937 in Uganda (7). If the strains were originally grouped into two lineages, today 7 of them are recognized, among which the most common in Europe are lineage 1a and lineage 2 (8).

The main cycle (illustrated in Figure 1) of this WNV is sylvatic and involves birds, mainly passerines, and several species of mosquitoes, mostly belonging to the *Culex* genus (10). Mammals, especially humans and horses, can be infected, but usually constitute dead-end hosts, meaning they do not develop sufficient viremia to infect mosquitoes during a blood meal (11). Other uncommon hosts are reptiles and amphibians, with diverse levels of viraemia and altogether only an anecdotical contribution to the overall viral circulation and impact (12). West Nile Virus can also, even rarely, be transmitted via transfusion of infected blood products (13). Congenital infection has also, albeit uncommonly, been reported (14). Occupational exposure can occur among workers in close contact with animals or in a laboratory facility (15).

In Europe, *Cx pipiens* and *Cx modestus* are the main proved competent vectors for the transmission of the WNV (16–18). The first is the most common, widely present in all Europe, with a well-known competence as an arboviral vector. Two distinct forms (or biotypes) are described. *Culex pipiens f. pipiens* is mostly ornithophilic, capable of diapause and found in open urban and peri-urban habitats (19, 20) while *Cx pipiens f. molestus* is mostly found in underground urban areas, do not enter diapause, mate in confined space and bite mammals (19, 20). A certain degree of hybridization is found to occur in zones of sympatry and the hybrids *Cx pipiens pipiens x molestus* feed on both avian and mammal species, constituting a potential bridge vector (20–22).

Culex modestus, firstly described in 1889 in Italy, is historically found in central and southern Europe, where it breeds in permanent water bodies in rural zones (23). In recent years, it has been found to be established in ever northern parts of the European continent (24), including in Denmark since 2011 (25), in United Kingdom since 2010 (26) and in Belgium since 2018 (27). The hypothesis of a recent introduction in United Kingdom (the alternative being an only recent correct identification of a long-established population) is supported by an analysis of genetic diversity in Europe (28). In addition to what seems to be an expansion of its geographical range, *Cx modestus* also shows an increase in abundance in its historical endemic zone in central and southern Europe (29, 30). Its competence as a WNV vector has been proven both in laboratory and in-field conditions (23, 31). *Culex modestus* is considered a bridge vector, as it feeds on avian population and on humans (23). Also, *Ae. albopictus*, the tiger mosquito, demonstrates its

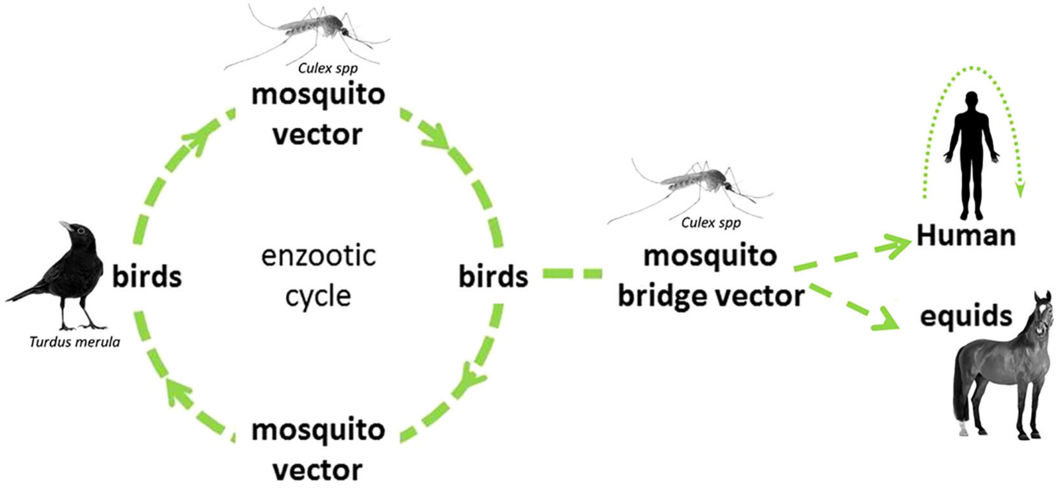

FIGURE 1
WNV cycle, with an illustration of most common hosts in Europe. Modified from ECDC (9).

competence for the transmission of WNV under laboratory condition. Its role in the circulation of the virus is likely limited due to its feeding preference for mammals, which constitute dead-end hosts (16, 18, 32).

2.2 Clinical manifestations

Birds, as the main reservoir of WNV, are to variable degrees affected by the disease. Birds species more commonly affected by WNV are passerines species (33, 34). Strains belonging to the lineage 1 of WNV, and in particular NY, the strain introduced in North America in 1999, show higher virulence among avian species (34). Variants in non-structural proteins of the virus constitute some of the determinants of this higher virulence (35, 36). Mortality from WNV infection in birds is most often related to a multisystemic disease, with a particular tropism of the lesions for cerebral and cardiac tissues (37). Infected birds can show an alteration of general condition as well as diverse neurological signs (38).

Human WNV infection is most often asymptomatic. It is responsible for a mild flu-like disease, with fever and headache in 20% of cases (39). However, it also causes a potentially severe neuroinvasive disease (meningitis, encephalitis or flaccid paralysis) in less than 1% of the cases (39, 40). Risk factors for severe disease include older age, male gender and the presence of comorbidities (41, 42). The mortality rate of the neuroinvasive WNV disease is close to 10%, with high variability depending on the syndrome (flaccid paralysis being the most fatal) (43, 44). In 50% of cases, survivors present long-term after-effects (mainly motor and neuropsychological) (44).

The West Nile Virus also affects horses. The proportion of neurological manifestations is higher, reaching 20% and mortality rate is around 30% (45–47). Neurological manifestations in horses are diverse, with ataxia as the most common finding (48, 49). As in birds, NY99 is suspected to show a higher virulence towards equine species (49).

2.3 Current distribution

WNV is historically enzootic in the Old World, particularly in Africa and a southeastern part of Europe (50). Its human circulation in Europe remained limited to sporadic cases and limited outbreaks in the south of the territory until 1990s (51). In 1999, the virus was imported to the USA, where it colonized the territory with astonishing speed, until becoming endemic (32). In the 1990s, WNV was also caused its first major epidemics in Eastern Europe (50). The West Nile Virus spreads to new territories mainly occurs via infected birds (migratory or passively imported), leading to potential establishment if a suitable vector and a reservoir host are present (8). The WNV circulation can remain unnoticed, within an enzootic cycle, for months or even years before the occurrence of a human case (8). The virus is currently circulating in Europe mainly around the Mediterranean basin and in the southeastern part of the territory (notably in certain regions of France, Germany, Italy, Austria, Spain, Greece), where it is considered endemic (8, 52–54).

The 2018 year was an exceptional time in terms of cases number in Europe, with 2083 indigenous infections, which was more than the cumulative numbers of cases since 2010 (55). Even if the yearly number of human indigenous infections in Europe has dropped during the years after this exceptional season, the pattern of geographical expansion, especially towards northern European countries, persists (56). In 2023, human cases were reported in 11 European countries (57).

The Netherlands case exemplifies the way this geographical expansion can be observed, with first cases of birds (common whitethroat) and mosquitoes indigenous infection by WNV reported in August 2020, in the region of Utrecht, with a rapid subsequent information given to healthcare providers (58). In October of the same year, the first human indigenous case was diagnosed in the same region, leading to 5 more retrospective diagnoses among patients with unexplained encephalitis and their relatives (59). These successful early detections, contributing to the global knowledge of the underlying mechanisms of the geographical colonization of WNV, took place in the context of a national monitoring of arbovirosus with a structural One Health approach (60).

Before 2010, the main lineage identified during outbreaks in Europe was Lineage 1a. A shift has occurred and since 2013, Lineage 2 is the dominant lineage (61). This lineage shift is associated with the northward expansion and overwintering capacity of the virus (61).

2.4 Impact of climate change

Climate change involves an increase in average as well as extreme temperatures, and altered rainfall, leading to an increased risk of both flooding and drought episodes.

Life history traits of *Cx. pipiens* are heavily altered by increasing mean temperatures, with an increase in development rate (especially below 24°C) and an increase in mortality (especially above 28°C) (62). Models integrating these effects associated to field studies showed that the maximum biting adult population is reached for a mean temperature around 25°C (63). This optimal temperature could even be higher for southern populations of *Cx. pipiens* (64). Temporality of the exposure to higher temperature also plays a role, with high temperatures in spring resulting in an earlier onset of the breeding season and an increase in the total number of biting mosquitoes while high summer temperatures results in an increase of adult mortality (65).

Increase of temperature causes a shortening of the incubation period and an increase in infectivity for WNV in the mosquito (66, 67). Depending on the strain, the effect of the temperature could even be non-linear (68). The environmental factors that best predict a WNV outbreak include high summer and annual temperature, low precipitation and the presence of wetlands (69–73). A particularly mild winter could also be a factor involved (74).

Rainfall regimen has also a strong impact on mosquitoes' population. An increase in (early) spring precipitation increases the summer population of *Cx. pipiens* (65). On the opposite, drought during the summer seems to maintain suitable larval habitats undisturbed during the breeding season and then to promote mosquitoes proliferation (75). Drought also increases the density of contacts between the vectors and the birds, favoring the WNV circulation (76, 77).

Another complex and less-known impact of climatic and global change on the distribution and outbreaks of WNV is thought to happen via their effect on the population of birds (71). Migratory routes are altered by climatic change (78), and migratory birds have been observed to reach their breeding locations earlier as an effect of rising temperatures (79, 80). This could have an effect on the timing, location and intensity of the introductions of WNV in Europe. Moreover, there is a concern that highly-vulnerable birds, in response to the loss and fragmentation of their habitat, thrive in a more urban habitat, closer to human populations (81). It is still difficult to assess precisely the part of endemicity and the part of annual reintroduction via migratory birds, stressing the importance of a deeper understanding of the complex interactions between the changing climate, the avian populations, the mosquito vectors and human health (82).

It is therefore not a surprise if the environmental factors that best predict a WNV human outbreak include mild winter, hot summer and warm annual temperature, low precipitation and the presence of wetlands (69–74, 83, 84). In northern Europe, epidemics could happen following an introduction of the virus during late Spring (85). They would be best predicted by high summer temperatures (86).

Aside from climate changes, other human-related global changes are proven to have a high impact on infectious, especially arboviral and zoonotic, diseases (87, 88). In particular, globalization and introduction of invasive species are well-known factors driving the colonization of already climatically-suitable habitats (88, 89). Reduction of biodiversity and wildlife could lead to a decrease in non-amplifying hosts, decreasing their dilution effect and increasing the circulation of the virus (90). Changes in agricultural methods towards deforestation, intensification and increased irrigation causes an increase of the interfaces between different species with an increased risk of spillover, a reduction of biodiversity and the creation of habitats suitable for the breeding of mosquitoes (91–93). Urbanization, human population growth and migration also contribute to the fragmentation of habitats, the reduction of biodiversity and to an increase of the human population at risk (87).

There is already evidence that global change contributes to the current increase of incidence and the geographical expansion of WNV in Europe (94–96). Projections predict an increase in WNV transmission in Europe, even in the northern regions, during the next decades (97, 98). In North America, an expansion of the range of the disease is also predicted at the continental scale by the end of the century (99). It therefore seems plausible that in the short-term autochthonous cases of WNV will be observed in Northern Europe.

3 Usutu

3.1 Virus and cycle

Usutu virus (USUV) is an *Orthoflavivirus*, first isolated in 1958 in South Africa from a *Culex neavei* mosquito (100). It is closely related to WNV and undergoes a sylvatic cycle involving several species of birds (the predominant host being blackbirds) and mosquitoes (100–102). Mosquito vectors appear to belong mostly to the *Culex* genus, with *Cx. pipiens* as a proven competent vector in Europe (103, 104). It could also play a role in the virus winter persistence (in female overwintering mosquitoes and by vertical transmission) (105). *Culex modestus* could also support the spread of the virus and act as a bridge vector (106, 107). The competence of *Ae. albopictus* for Usutu transmission is still discussed, with contradictory results between experimental infections and in-field contaminations (104, 108). Interestingly, co-circulation of both viruses is widely demonstrated in Europe (109–112). Like for WNV, humans (and to a lesser extent, other mammals species such as horses) are accidental, dead-end hosts of Usutu (101, 113).

Until the beginning of the century, USUV infections had never been reported outside the African continent, where only two (mild) human cases have been observed (114). In 2001, a significant mortality excess among avian populations in Austria highlighted the USUV circulation on the European continent (100). Retrospectively, evidence of its presence was found already in 1996 in Tuscany, Italy (115). Phylogenetic studies have since concluded that USUV was introduced several times from Africa to Spain, Austria and Germany during the last century, but started to spread in the European continent after 2000 (116, 117). After 2001, the similarities with the spectacular spread of WNV in the USA, highlighted by a massive die-off of local birds, have attracted attention and a surveillance network was put in place. Circulation of the virus has since been observed in many European countries (118). Northwestern European countries are not spared, with human as well as bird cases reported in Germany, France and the Netherlands (54, 118–120) (see also Figure 2). In Belgium and Luxembourg, to date no human case has been reported, but the virus has been identified in birds (118, 121). Epizootics affecting several countries in Northern Europe were recorded in 2016 and 2018 (101, 122).

3.2 Clinical manifestations and detection

Usutu virus is a common cause of disease and death in reservoirs birds, mainly passerines and raptors. Clinical syndromes caused by the virus are still poorly understood but

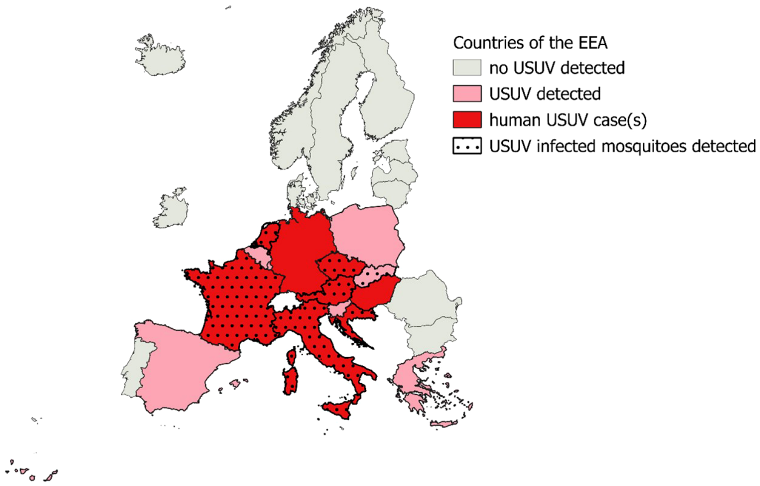

FIGURE 2
Detection in mosquitoes or vertebrate hosts of Usutu Virus in countries of the European Environment Agency 2012-2021. Data from the ECDC (118).

include neurological involvement (torticollis, seizures, opistothonos, inability to fly) as well as unspecific signs (apathy, anorexia) (122, 123)

The exact human pathogenicity of the Usutu virus remains unknown. In 2012, a seroprevalence study on blood from donors in Italy and Germany demonstrated the silent circulation of the virus in the human population (124, 125). Two first cases of neuroinvasive syndrome were demonstrated in 2009 in Italy, in two severely immunocompromised patients (126, 127). Since then, several neuroinvasive syndromes (mainly encephalitis and meningoencephalitis) have been reported in Europe, some in immunocompetent patients (111, 112, 128–131). Mild symptomatic flu-like cases have also been identified, but the proportion is difficult to assess in such a small sample (around 100 cases in Europe) (128, 131).

To date, no clinical cases of USUV infection have been described in equids, which can present a subclinical seroconversion and serve as a sentinel species to detect the circulation of the virus (132, 133).

The large co-circulation between USUV and the closely related flavivirus WNV adds another layer of complexity to the already difficult detection of this virus (134). The similarities of surface proteins of the two viruses causes a cross-reactivity of antibodies and makes it difficult to distinguish between the serological response against WNV and USUV (135). Even when using the virus neutralization test, a cross-neutralization occurs with a certain level of asymmetry at the expense of USUV detection (136).

3.3 Impact of climate change

Since the emergence of USUV in Europe, the impact of climate change on the intensification and spreading of the circulation of the virus has been questioned. There is a suspected association between climatic factors (abnormally high temperatures), the local abundance of the vector and significant circulation of the virus (120). A model developed in Austria in 2009, based on different climatic change scenarios showed a high risk of endemicity of USUV in Central Europe (137).

This climate change susceptibility, together with the current increase of the geographical range of the USUV and the probable underestimation of its current circulation suggest a current and future impact of this virus on human health in northern European countries and strongly advocate for a better surveillance of the circulation of this virus.

4 Conclusions

West Nile and Usutu viruses are closely related and ecologically similar Orthoflaviviruses, transmitted by *Culex spp* for which birds are amplifying hosts and humans are dead-end, accidental hosts. They both have a recent history of rapid expansion to ever more northern regions of Europe and of a dramatic global increase in the number of human cases. They show a large co-circulation and important antigenic similarities making their discrimination difficult.

Their reliance on an ectothermic vector is a key – but not unique – factor of the observed and predicted impact of climate change on the distribution of the diseases they cause. Aside for anthropogenic climate change, human actions have multiple direct and indirect impacts on their circulation. Modelization and observational data converge to identify Northern Europe as a territory at risk for future outbreaks and establishment of USUV and WNV.

The complexity and multiplicity of anthropogenic changes and their effects on per se complex cycles of transmission make it illusory to try to identify predictive factors for the transmission of the virus by focusing only on one aspect of its circulation. It is therefore a subject whose importance in terms of public and global health and whose multi-disciplinary nature - requiring the collaboration of specialists in climatology, virology, entomology, human and veterinary medicine - strongly advocate a One Health approach.

Author contributions

JL: Conceptualization, Writing – original draft, Writing – review & editing. HA: Writing – review & editing. PB: Writing – review & editing. DD: Writing – review & editing. FF: Writing – review & editing. M-MG: Writing – review & editing. M-PH: Writing – review & editing. AL: Writing – review & editing. GD: Methodology, Supervision, Writing – review & editing.

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