Seasonal variations in dengue virus transmission suitability in the Americas

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Abstract

Dengue fever (DF) is associated with significant morbidity across the tropics and sub-tropics. Here, we used a temperature-based model of the extrinsic incubation period (EIP) and a temperature and humidity-based model for adult mosquito survival to explore the relationship between seasonal climate variability and DF in Brazil from 2014 to 2019. We found that municipalities with higher mosquito survival probabilities and shorter EIPs were more likely to be associated with DF case reports, but with significant intra-annual variability. A 0.012 or above probability of Aedes aegypti surviving the EIP was associated with a greater than 50% probability of DF being reported in the municipality. We extrapolated these results to the Americas using climate data over the last decade (2010–2019) to map the seasonal change in the range of areas suitable for dengue virus transmission and the magnitude of the population living in those areas. Areas near the Equator exhibited high suitability throughout the year whereas suitability in the subtropics and temperate regions varied seasonally, especially moving poleward. Strengthening our understanding of DF seasonality is essential to mitigating risks, particularly as the Americas experience the impacts of climate change.

1. Introduction

Dengue fever (DF) is a mosquito-transmitted disease that results from infection by one of four serotypes of the dengue virus (DENV) and causes considerable morbidity across the tropical and sub-tropical regions of the world. Bhatt et al (2013) estimated an annual global burden of 390 million viral infections, with 96 million resulting in symptomatic cases of DF. Although symptoms can be mild, they may also progress into dengue hemorrhagic fever or dengue shock syndrome that can be fatal and are most common in repeat infections (Wang et al 2020). DENV is vectored by Aedes genus mosquitoes, with Aedes aegypti being the most common. In 2019, countries in the Americas recorded the largest numbers of cases of DF, with over three million cases, including 1538 deaths; this was a 30% increase over the period 2015–2016 (PAHO/WHO).

DF has a long history in the Americas, but with an increase in the burden and geographic range in recent decades. This was due to many factors, including growing urbanization, reductions or cessations of vector control programs, population growth, and increased travel. DF has been recorded in Brazil since at least 1845, with considerable public and private efforts to control its spread (Fares et al 2015). However, these efforts have been broadly unsuccessful, with dengue spread largely uncontained throughout much of the country (Barreto et al 2011). Brazil’s health system is insufficiently equipped to handle dengue outbreaks, which disproportionately affects poorer Brazilians (Ladner et al 2015). The challenge of adequately caring for dengue patients has become significantly greater as a result of Brazil’s poor handling of the COVID-19 outbreak (Lorenz et al 2020). Additionally, high DF burdens are associated with unplanned urbanization (slums), which are common throughout Brazilian metropolises (Kikuti et al 2015). Because the Aedes mosquitoes that spread DENV develop in stagnant water, including wastewater, government efforts to provide universal water
and sanitation coverage (in turn decreasing informal forms of water provision and human waste disposal) are likely to reduce sources for mosquitoes in the coming years. However, progress on these efforts remains slow (Queiroz et al 2020).

Because weather and climate can impact mosquito ecology and the DENV incubation period, climate change has been implicated in recent DF epidemics and range expansion by altering spatial and temporal patterns of virus transmission suitability (Morin et al 2013, Ebi and Neilson 2016). Numerous studies have sought to determine the current and future range of DENV transmission suitability (Cattarino et al 2020, Xu et al 2020), including by modeling not only weather/climate variables, but also demographic and socioeconomic factors (Messina et al 2019). These studies provide important information for planning and preparing for the incursion of DENV into novel locations and changes to its intensity in locations where the disease is either endemic or sporadic.

While identifying the current geographic range and projecting future changes in the DENV transmission suitability range is useful, it is important to note that suitability in most locations will vary greatly over the course of the year. A greater understanding of this variability would increase the effectiveness of interventions by appropriate targeting. The current study maps the seasonal suitability for DENV transmission over the Americas and estimates changes in the population at risk throughout the year, focusing specifically on seasonal temperature and humidity variation. Suitability is estimated using a temperature-based model of the extrinsic incubation period (EIP) and a temperature and humidity-based model for adult mosquito survival. Dengue data from Brazil were used to determine the suitability limits for transmission. The results of this study could serve as guidance for public health professionals on where and when control measures should be implemented.

2. Methods

2.1. Data

Dengue data for the study were obtained from the Brazil Ministry of Health’s Notifiable Diseases Information System (Sistema de Informação de Agravos de Notificação (SINAN) (http://tabnet.datasus.gov.br/cgi/tabcgi.exe?sinanet/cnv/denguebr.def)). Health providers are mandated to report all DF cases to SINAN; however, SINAN is a passive surveillance system that does not cover cases where individuals did not seek medical care. The data cover calendar years 2014–2019 and provide the number of reported probable dengue cases for each municipality of Brazil during each epidemiological week. Brazil was chosen as the location for this analysis because it is a large, environmentally diverse country with data available at appropriate temporal (weekly) and spatial (municipality) resolution. Brazil has 5570 municipalities, but we limited the study to those with a population over 200 000 in 2014 leaving 145 municipalities included in the analysis. This allowed us to analyze a manageable number of municipalities representing most of the climate zones in Brazil (figure 1) while focusing on high population density areas where DF is most common. The DF count data were converted to weekly incidence (new cases per 100 000 population). It is important to note that reported cases may not have contracted the virus in the municipality where it was reported.

While SINAN data are the most comprehensive DF surveillance data available nationally in Brazil, counts are likely to be significantly underreported, particularly during periods of low transmission, because laboratory testing to confirm DF infection is often not conducted (Silva et al 2016, Angelo et al 2020). Underreporting DF cases in national passive surveillance systems is common throughout Latin America and the Caribbean; and makes estimating the true burden of DF challenging (Shankar et al 2018, Carabali et al 2021).

The municipality populations for each year were obtained from the Brazilian Institute of Geography and Statistics (www.ibge.gov.br/en/home-eng.html) and were used to calculate the DF case incidence for each municipality. Gridded population data were obtained from the Gridded Population of the World dataset (https://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-count-adjusted-to-2015-unwpp-country-totals-rev11). We used the United Nations World Population Prospects-Adjusted Population Count estimates for the year 2020 to determine the current intra-annual variability of the population in areas suitable for dengue transmission (described later).

Climate data for the study were obtained from the NASA Global Land Data Assimilation System (GLDAS, https://ldas.gsfc.nasa.gov/gldas). GLDAS is a global reanalysis dataset that incorporates land and satellite observation data. The data we used were from the NOAH Land Surface Model with a $0.25^\circ \times 0.25^\circ$ spatial resolution and a three hourly temporal resolution and covered the period from 2010 to 2019. We extracted air temperature, surface air pressure, and specific humidity. Additionally, we converted specific humidity to relative humidity from these variables. The data were then averaged weekly to match the epidemiological weeks. Although precipitation is also important because it can provide the necessary water required for immature mosquitoes, the association with dengue is complicated because many water sources are available independent of precipitation (e.g. irrigation, water storage, sanitation, etc) and therefore was not included in our model.
2.2. Modeled suitability

Environmental suitability for dengue transmission was calculated using a sub-model for the EIP and another sub-model for adult mosquito survival. The EIP is the period from when a mosquito takes an infected blood meal to when it is able to retransmit the virus through a subsequent blood meal. It is sensitive to temperature (Watts et al. 1987) with EIP length decreasing at warmer temperatures. Tjaden et al. (2013) collected data from three studies measuring EIP length at various temperatures. We used these data to generate a regression model for calculating the EIP length at a given temperature. We only used data from studies that demonstrated transmission of the virus to animals through mosquito feeding. We did not include data from studies that based the EIP length on detection of virus in the mosquito salivary glands because these studies do not fully demonstrate transmission of the virus to a new host. Tjaden et al. (2013) noted that including these data led to a reduction in the estimated length of the EIP, especially at lower temperatures. Their recommendations to use or not use data are context dependent. Because we chose not to include it, our results provide a more conservative estimate of DENV transmission suitability.

Adult mosquito survival is regulated by both temperature and relative humidity (Schmidt et al. 2018). We used a model based on Schmidt et al. (2018) to calculate the daily survival suitability at a given temperature and relative humidity. From the EIP and daily mosquito survival probability (MSP) we calculated the probability that a mosquito survives the EIP (PSE) under particular climate conditions (equation (1), figure 2):

\[
PSE = MSP^{EIP}. \tag{1}
\]

We used this as a measure of the suitability of the climate to support dengue transmission. Using the weekly aggregated gridded temperature and relative humidity data, we calculated the PSE over the period 2010–2019. The gridded PSE data was then averaged over each municipality during the period when dengue data were collected (2014–2019). The Brazil municipality shapefile used to compute the gridded mean was obtained from the GADM database of Global Administrative Areas (www.gadm.org/).

2.3. Analysis

We analyzed weekly DF incidence with the associated PSE for each municipality over the study period 2014–2019 to quantify the relationship and apply it to the wider region of the Americas. This created 45 385 data points (313 weeks × 145 municipalities) for analysis. We made the weekly dengue incidence binary (present/absent), with a value greater or equal to 0.5 new cases per 100 000 labeled as present for DENV transmission and absent for transmission otherwise. This was done so we could estimate the population in areas suitable vs not suitable for DENV transmission. Although 0.5 new cases per 100 000 is a low incidence, the actual incidence is likely higher because mild and asymptomatic cases generally go unreported. This lower value also ensured that we captured...
Figure 2. Mosquito survival though the EIP (PSE) at a range of temperature and relative humidity levels.

the minimum conditions for DENV transmission, even if it only resulted in a small number of cases.

Because the impacts of climate conditions on DF transmission are not immediate, we used the average PSE over the previous four weeks when comparing it with weekly DF presence or absence. The period of four weeks roughly approximates the lifetime of a mosquito and also the maximum length of the incubation period (Tjaden et al. 2013, Schmidt et al. 2018) including an approximately one-week latent period within the human host (plus a few days for diagnosis). Therefore, it is this period that is likely to exert the greatest impact on DENV transmission. The average PSE was calculated for each of the 145 municipalities over the 313 weeks of the study period (lagged weeks will overlap) and was used as the measure of climate suitability for DENV transmission.

Suitability for DENV transmission was determined using the created DF presence/absence data and the associated average PSE values. This was done by first dividing the calculated average PSE values for each week and municipality (145 municipalities × 313 weeks = 54,385 instances) into groups with values of 0–0.08 using intervals of 0.001. In each group, we calculated the percentage of instances categorized as present for DF (greater than 0.5 cases per 100,000). We then identified the group with the lowest average PSE value where the percent of instances classified with DF being present was greater than 50%. This PSE value was used as the threshold for creating a binary classification for DENV transmission suitability (more suitable if the PSE value is above the threshold and less suitable if the PSE value is below the threshold).

The gridded PSE data then was averaged by week over the 2010–2019 period to provide an average measure of suitability for DENV transmission over the past decade. Grid cells with an average PSE greater than the threshold value were assigned a value of 1 (more suitable) or 0 (less suitable). We then overlaid the gridded population data to determine the total population in an area labeled more suitable for DENV transmission for each week of the year across North and South America. We repeated the analysis using cutoffs of 40%, 45%, 50%, 55%, and 60% to assess the sensitivity of the analysis to our chosen threshold. These percentages approximately cover the PSE interval where the slope of the graph in figure 3 (change in the probability of reporting dengue/PSE values) transitions from steep to shallow.

3. Results

Figure 3 shows the probability of a municipality reporting DF as a function of average PSE value. An average PSE of 0.012 (red line in figure 3) and above indicated a greater than 50% probability of DF being reported and was labeled more suitable whereas those below this value were less suitable as described above. Figure 3 shows a sharp increase in probability between an average PSE of 0.0 and 0.005 followed by a shallower increase until 0.02, where it leveled off with a probability of reporting DF of 0.6 and above.
As expected, average PSE varies greatly over the course of the year and is generally higher in tropical areas and also areas further poleward during their summer months (figure 4). High average PSE values were sometimes found in areas where local DENV transmission was rarely or never reported, such as southern Texas, where locally acquired cases were rare but the PSE is relatively high during the summer months.

The number of weeks per year classified as more suitable for DENV transmission was greatest in the tropics and decreased poleward and at higher elevations (figure 5). In areas around the Equator (except at high elevations), the climate was suitable for transmission in all 52 weeks of the year. Southern Florida, which experiences small local DF outbreaks, was suitable for transmission much of the year (∼42 weeks). Further north, however, the number of weeks classified as suitable decreased quickly. The number of people living in areas that were more suitable for DENV transmission also varied over the course of the year with the highest numbers during the Northern Hemisphere’s late summer and early fall (figure 6). We used five different values for classifying a grid cell as more/less suitable (probability of a municipality reporting DF cases) with little variation between the results.

4. Discussion

Given the impacts of climate on *Ae. aegypti* and DENV, it was not surprising that equatorial regions (except for high elevation areas) were more suitable for DENV transmission and that there were a greater number of weeks throughout the year during which they were more suitable. This largely agrees with observational data (Jentes *et al* 2016). The seasonal variation, however, is critical for understanding the range of DENV transmission risk. This is important for planning the allocation of healthcare resources, as well as for understanding the risks associated with travel and large events. For example, there was considerable concern over Zika virus transmission during the 2016 Olympics (Petersen *et al* 2016). A number of risk factors for visitors and athletes were examined, including the timing (season) of the Olympics (Burattini *et al* 2016).

When considering the maximum range of suitability across all seasons, our results generally agreed with other studies that mapped the range of *Ae. aegypti* and/or DENV transmission such as Kraemer *et al* (2015), Messina *et al* (2019), and Cattarino *et al* (2020). Estimates of mosquito vector ranges are often larger because pathogen transmission is often limited by an extended EIP at cooler temperatures that can still support vector populations. For instance, the distribution of *Aedes albopictus* from Kraemer *et al* (2015) extends beyond the range of DENV transmission suitability found in this study and by Messina *et al* (2019). The distribution for *Ae. aegypti*, however, is closer to the range of suitable found in our study.

Our results also show that many locations in higher latitudes and areas that do not traditionally
report local DENV infections exhibit more suitable conditions during a portion of the year. These areas are beyond the distributions indicated by Messina et al (2019) and Cattarino et al (2020). Dick et al (2012) describes historic outbreaks of DF in the Americas including in Philadelphia, PA in the United States in 1780 and other US port cities like New Orleans and Charleston in the 19th century. Although in recent decades locally acquired DF cases in the US have been limited to Florida, Texas, and Hawaii, climate conditions could support transmission in a much wider region. Modern living conditions, improved public health practices, and limited influx of infectious travelers were likely the reasons DENV transmission does not occur in these locations. In southern Florida and Texas, however, the number of weeks when conditions were more suitable for DENV transmission is higher (figure 4) and travel to DF endemic areas was likely more frequent than in other areas of the USA.

Understanding variations in seasonality is important for evaluating introduction risks in non-endemic areas. Shang et al (2010) studied the relationship between indigenous and imported DF cases and concluded that imported cases can initiate epidemics in areas where DF is not endemic when weather and climate conditions were suitable for transmission. Chowell et al (2011) studied the difference in the seasonality of DF in Peru between the jungle and coastal regions and found mean temperature to be a large driver of the timing of the epidemics. They posited that the weather in the jungle region facilitates year-round DENV transmission and, consequently, can cause outbreaks in the coastal region when conditions permit. This indicates that evaluating potential introductions of DENV, and other vector-borne pathogens, is dependent on the transmission suitability of the local area and the area visited by travelers.

During the 2016 Zika virus (ZIKAV) pandemic, Monaghan et al (2016) used several sources of information to determine the areas in the US where a local outbreak was most likely. Southern Florida and Texas during July–September were estimated to have the highest risk due to climate conditions that supported a high Ae. aegypti population and because they are air travel hubs (Miami and Houston) from areas where the epidemic was ongoing. In July, local transmission of ZIKAV was reported in southern Florida and in southern Texas shortly thereafter (Moreno-Madrinan and Turell 2018). Monaghan et al (2016), indicated that winter transmission was unlikely because most locations could not support Ae. aegypti populations, and in those that could, the population was relatively low and the EIP would be prohibitively long. This demonstrates how understanding the seasonality in addition to the range of a vector or pathogen can enable more precise estimations of risk.

As figure 6 shows, the population in more suitable areas was largest in the Northern Hemisphere’s late summer and early fall. This was likely due to the larger population in the Northern Hemisphere, even though much of the land mass is further poleward. Many of
these areas did not report local DENV transmission, likely because they were distant from areas where transmission occurs during all or much of the year. If warming temperatures extend the seasonality of DENV transmission, however, some of the areas that were once on the margins of transmission (e.g. the southern United States) may become vulnerable to sporadic local outbreaks. Given the size of the population at this range, the future burden of DF may increase greatly in the coming decades.

There are some important limitations of the current study that warrant discussion. First, suitability in the study was based on urban areas in Brazil, a country where many areas experience year-round or a long season where DENV is transmitted. *Ae. aegypti* are generally found in urban areas, so the high population municipalities used in our sample are ideal environments for their survival. Additionally, as mentioned earlier, because many areas of Brazil experience long transmission seasons, the opportunity for reintroduction of the virus into areas with shorter transmission seasons was higher than in other areas. Also, our measure of suitability depends only on atmospheric conditions. However, simply because an area is more climatically suitable does not necessarily indicate that it is more likely to experience an outbreak, as climatic conditions are only one of several factors that affect whether an outbreak is likely to occur. Local economic conditions (Reiter *et al* 2003), among other factors, can also influence whether an

**Figure 5.** Number of weeks per year that an area was classified as more suitable for DENV transmission based on its weekly calculated PSE. The PSE was calculated using the gridded GLDAS data (averaged weekly).
outbreak occurs. Areas that have climatic conditions that support DENV transmission are unlikely to have outbreaks if there are few infected mosquitoes and/or travelers present.

The DF data we used, although extensive, has limitations. As mentioned earlier, the absence of reported DF cases is not proof of absence because surveillance is passive. Additionally, this study focused only on *Ae. aegypti*, but *Ae. albopictus* is another potentially important vector in Brazil and other regions in the Americas and its climate tolerance and juvenile habitat preference sometimes differ (Kraemer et al 2015). There is an implicit assumption that *Ae. aegypti* inhabit all of the areas categorized as more suitable for DENV transmission. However, it is possible that this may not be true in some areas, although this was likely rare because the thermal tolerance of the mosquito tends to be lower than DENV (Morin et al 2013). We also did not include precipitation in our model, which is often important for providing water for immature mosquito habitat. However, *Ae. aegypti* are notorious for their ability to find appropriate habitat even in challenging environments, especially in urban areas where human managed water sources are readily available (Johansen et al 2018).

Our results are strongly suggestive of spatial and seasonal patterns of DENV transmission. However, due to limited data availability, we are unable to demonstrate this with more sophisticated statistical methods. Our results concur with those in previous studies on this topic. Additional case data in the study region would help validate these results further.

5. Conclusion

Our results illustrate the importance of both seasonality and location when assessing the risk of DENV transmission in a region. Suitability for transmission depends both on the mosquito survival probability and the length of the EIP. As climate warms, locations experiencing local acquired DF cases are expected to increase in range, however, the initial cases will most likely be limited to the warmest periods of the year. Furthermore, areas where the disease is already endemic may experience changes in seasonality. Understanding these changes will be important for designing and implementing intervention strategies.

Future research can expand upon this work in several ways. Our study only considers climate under recent conditions; using climate change projections to identify alterations in the seasonality of DENV transmission and including other important risk factors (similar to Messina et al 2019) could provide extremely useful results to public health professionals. The inclusion of DF case data from other countries would also improve the robustness of our results. Lastly, seasonal climate forecasts could be incorporated into our model of PSE to generate DF risk forecasts that could aid in planning transmission intervention strategies.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.
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Conflict of interest

The authors declare that they have no conflict of interest.

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