GeoHealth

RESEARCH ARTICLE
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Special Section:
Climate change and infectious diseases

Key Points:

- Environmentally informed West Nile virus (WNV) forecast model
- Our forecast shows that a dry, cool winter, followed by a wet, warm spring, and a cool summer promotes WNV
- Early season forecasts are a potential decision tool to inform public health and mosquito abatement intervention

Supporting Information:

Supporting Information may be found in the online version of this article.

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A Spatially Resolved and Environmentally Informed Forecast Model of West Nile Virus in Coachella Valley, California

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Abstract West Nile virus (WNV) is the most significant arbovirus in the United States in terms of both morbidity and mortality. West Nile exists in a complex transmission cycle between avian hosts and the arthropod vector, *Culex* spp. mosquitoes. Human spillover events occur when humans are bitten by an infected mosquito and predicting these rates of infection and therefore the risk to humans may be associated with fluctuations in environmental conditions. In this study, we evaluate the hydrological and meteorological drivers associated with mosquito biology and viral development to determine if these associations can be used to forecast seasonal mosquito infection rates with WNV in the Coachella Valley of California. We developed and tested a spatially resolved ensemble forecast model of the WNV mosquito infection rate in the Coachella Valley using 17 years of mosquito surveillance data and North American Land Data Assimilation System-2 environmental data. Our multi-model inference system indicated that the combination of a cooler and dryer winter, followed by a wetter and warmer spring, and a cooler than normal summer was most predictive of the prevalence of West Nile positive mosquitoes in the Coachella Valley. The ability to make accurate early season predictions of West Nile risk has the potential to allow local abatement districts and public health entities to implement early season interventions such as targeted adulticiding and public health messaging before human transmission occurs. Such early and targeted interventions could better mitigate the risk of WNV to humans.

Plain Language Summary West Nile virus (WNV) is the most significant arbovirus in the United States and is transmitted seasonally by mosquitoes. Humans are most at risk when they are in close proximity to infected mosquitoes. Predicting the risk to humans is not straightforward. In this study, we use deviations in climate associated with mosquito biology and viral development to forecast seasonal West Nile risk in the Coachella Valley of California. We developed a statistical model of WNV transmission in the Coachella Valley using 17 years of mosquito surveillance data and environmental data. Our model indicated that the combination of a cooler and dryer winter followed by a wetter and warmer spring and a cooler than normal summer was the combination of environmental events most associated with West Nile positive mosquitoes in the Coachella Valley. The ability to make accurate early season predictions of West Nile risk could assist local public health entities implement early season interventions to better mitigate the risk of WNV to humans in the Coachella Valley.

1. Introduction

West Nile virus (WNV) was first introduced to the United States in New York in 1999 and over the following 5 years spread across the continent to the Pacific Coast (Sejvar, 2003). WNV exists in a complex transmission cycle between the mosquito vector, predominantly *Culex* spp., and avian amplifying hosts (Hayes, Komar, et al., 2005; Troupin & Colpitts, 2016). Humans, horses, and other mammals are incidentally infected as dead-end-hosts with approximately 80% of human infections not resulting in disease; however, 10%–13% of the <1% of human cases that do develop neuroinvasive disease result in death (Hayes, Sejvar, et al., 2005; Mostashari et al., 2001; Riccardo et al., 2022). WNV transmission in desert climates presents an ecology unique from other areas of high transmission, such as the Central Flyway states. Unlike these states where environmental conditions suitable to support mosquito and avian populations are more widespread, these conditions typically only exist in smaller geographic pockets in the desert Southwest of the United States. Despite this the largest county-level arboviral neuroinvasive disease outbreak ever recorded in the United States occurred in a desert climate in 2021, when

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Maricopa County reported 1,487 human WNV cases (Kretschmer et al., 2023). A total of 956 of these cases were classified as neuroinvasive and resulted in 101 deaths (Kretschmer et al., 2023). Reported cases from this outbreak were nearly the same as all neuroinvasive cases reported in Arizona between 1999 and 2016, but only represent a fraction of the overall infections (Ronca et al., 2019). However, these 1,487 cases do capture the high morbidity related to this WNV outbreak, which based on previous studies, may be estimated to have cost nearly 1 billion dollars in hospitalizations, follow-up care, and work lost (Ronca et al., 2019). The morbidity and mortality of this outbreak emphasizes how critical it is to gain a better understanding of the environmental drivers associated with the transmission cycle between avian reservoir hosts and mosquitoes, which can result in incidental zoonotic spillover to humans (Colpitts et al., 2012; Nasci & Mutebi, 2019).

WNV transmission is not only dependent on factors such as bird immunity, and mosquito feeding behavior but is also substantially driven by environmental drivers such as meteorological and hydrological conditions (Davis et al., 2017; DeFelice et al., 2017; Kilpatrick et al., 2006; Paull et al., 2017; Shaman et al., 2005; Wimberly et al., 2022). Much effort has been made to produce accurate forecast models for WNV transmission, however, there remains significant variability and little consensus between these products (Barker, 2019; DeFelice et al., 2017; Keyel et al., 2021; Little et al., 2016; Wimberly et al., 2022). Temperature, humidity, and available water affect the development and survival of WNV mosquito vectors, as well as the extrinsic incubation period (EIP) of the virus (Epstein, 2001; Reisen et al., 2008; Shaman et al., 2005; Wegbreit & Reisen, 2000). Warmer temperatures accelerate population growth by providing conditions suitable for earlier season larval development, completion of the gonotrophic cycle, and shortened EIP of the virus (Ciota & Kramer, 2013). Conversely, extreme temperature events negatively affect mosquito population growth resulting in slower development at low temperatures and significant mortality at high temperatures (Mordecai et al., 2019). Temperature driven shifts in mosquito activity and WNV infections have been observed in areas that experience seasonal temperature variations, such as coastal Los Angeles, where during the extreme hot periods of summer, WNV incidence increases in the Coastal Zones that are otherwise typically too cool for transmission during the rest of the year (Skaff et al., 2020).

Additionally, the availability of suitable aquatic breeding sites is important for mosquito population success, but it is less certain how to measure this habitat most effectively. Precipitation has been demonstrated to have contradictory associations with WNV incidence. On one hand, heavy rainfall may increase available water for mosquito larval sites, but it may also wash out more sustained habitats, such as ditches or catchment basins favored by *Culex* spp. (Koenraadt & Harrington, 2008). Conversely, drought periods increase the proximity and contact between *Culex* mosquito vectors and avian hosts, accelerating enzootic amplification of WNV throughout the mosquito population and increasing the risk of spillover to humans (Shaman et al., 2005). Using precipitation as an indicator for mosquito population success also presents a challenge in arid desert environments with little rainfall. Evapotranspiration (ET), the measure of the amount of water transferred from the ground or plants to the atmosphere, offers a unique measure of the available water in an ecosystem (Fisher et al., 2020; Shaman & Day, 2005). Actual measures of ET, opposed to potential ET, may be a better hydrological indicator of mosquito population success and viral amplification in a desert region where the availability of surface water is primarily driven by agricultural and recreational practices rather than precipitation. Additionally, ET is available at multiple scales allowing modeling efforts to be scaled appropriately for an environment where vector and transmission activity are localized around sparsely available surface water. In turn these scales can be tailored to operational capacity and to reduce the amount of wasted control efforts and excessive application of pesticides over large areas.

Warmer, wetter environments favor mosquito development, whereas dryer than usual conditions in a geographic location create island effects where mosquitoes and birds are concentrated around similar resources (Landesman et al., 2007; Roehr, 2012). This concentration of avian host and mosquito vector favors WNV amplification and transmission (Shaman et al., 2005). Additionally, the stress of drought and extreme heat events increase the susceptibility of immunologically naïve juvenile birds to WNV infection and results in higher viremias. The increased susceptibility and increased viremia make transmission to host-seeking mosquitoes more likely. However, abnormal weather patterns must happen at specific points in both the mosquito and avian populations' development to result in WNV amplification and spillover to humans. Lastly, the effect of these environmental deviations on the mosquito infection rate and therefore the potential risk of a human WNV outbreak may not be apparent until weeks or months after the environmental events. We hypothesized that extreme heat events seen in Coachella Valley during the summer months have the effect of depressing the mosquito population, thereby slowing WNV transmission, and that cooler-than-average summers lead to increased rates of WNV transmission. Additionally, we postulated that changes to the late-season climatology of the Coachella Valley may play a role in the magnitude of WNV transmission the following year.

In this study, we evaluate the hydrological and meteorological drivers associated with mosquito biology and viral amplification in a desert climate to understand if these associations may be used to forecast seasonal WNV risk. We developed and tested a spatially resolved ensemble forecast model of WNV transmission in the Coachella Valley using 17 years of mosquito surveillance data and environmental data from the North American Land Data Assimilation System (NLDAS)-2. We then cross-validated the ensemble model using a leave-1-year-out strategy and produced real-time monthly forecasts for 2022 with analyses of agreement with observations at the end of the season. Our work indicates that we can use early-season meteorological conditions to identify how annual infection rates by region will compare to a one infected mosquito per 1,000 tested threshold, defined as the 75th percentile of historical infection rates. The ability to make accurate early season predictions of West Nile infection rates has the potential to provide local public health entities a biologically informed decision support tool to help guide them through the implementation of early season interventions such as targeted adulticiding, larvaciding and public messaging before human transmission occurs.

2. Materials and Methods

2.1. Study Location

This study was carried out in the Coachella Valley, a portion of the Mojavi and Colorado deserts, located in Riverside County, California. Coachella Valley has a history of WNV outbreaks, the largest of which occurred in 2015 when Riverside County reported 127 human cases (Table S1 in Supporting Information S1). Coachella Valley has unique ecotypes that vary across a North-South gradient with the Salton Sea and its associated marshlands to the South, agricultural and recreational land along the length of the valley, and desert to the North. The center of the valley is largely agricultural with urban areas intermixed. Agriculture consists largely of dates, citrus, and grapes with various rotational row crops such as lettuce, peppers, corn, and carrots. According to the Coachella Valley Water District the Coachella Canal provides 424,000 acre-feet of water per year to the valley in addition to local wells and recycled water, with ∼60% applied as drip or other micro-irrigation and the remaining as flood or sprinkler irrigation (Crider, 2018). Unused surface water is traditionally drained to the Salton Sea (Crider, 2018). Hydrology and, by association, viable mosquito habitat, are dictated by agricultural and recreational water use. This is evident by the geographic seasonality of WNV in the Coachella Valley which has historically followed a South to North track—originating around the Salton Sea during spring months then distributing Northward along irrigated agricultural land and golf courses over the duration of the season (Figure 1).

Mosquito surveillance is substantial in Coachella Valley. Trapping is carried out weekly throughout the valley with locations rotating on a bi-weekly schedule. The number of locations has increased from 65 in 2006 to 263 in 2022 with variation between years due to reactive surveillance (Table S2 in Supporting Information S1). Similarly, the number of mosquitoes trapped has steadily increased with the increase in trapping effort from 67,321 in 2006 to 155,633 in 2022 (Table S2 in Supporting Information S1). CO_2 baited traps are most predominant, followed by gravid traps (Table S3 in Supporting Information S1).

2.2. Meteorological and Hydrological Data

We used meteorological variables from the North American Land ata Assimilation System - 2 (NLDAS) (https://ldas.gsfc.nasa.gov/nldas/nldas-get-data) for Coachella Valley (NLDAS, 2012). We aimed to find a combination of environmental variables (hydrological and meteorological conditions) that best described the complex desert environment. August and September of the year in question were omitted as by the end of August, the transmission cycle is over. Models were run using a combination of eight different environmental parameters for the 10 months (October–December of the previous year and January–July of the current year) and with a maximum of four environmental values (Table 1). Our best model results came from ET and atmospheric temperature (ATMP). We performed correlation testing of the 10 monthly estimates of environmental conditions and developed a heat map to determine what were the most appropriate environmental indicators for infectious mosquitoes (Figures S1 and S2 in Supporting Information S1). We used monthly estimates of ATMP (Kelvin, 2 m above ground level) and the Mosaic hydrology model simulation estimates of ET (kg/m^2, monthly accumulated) with a

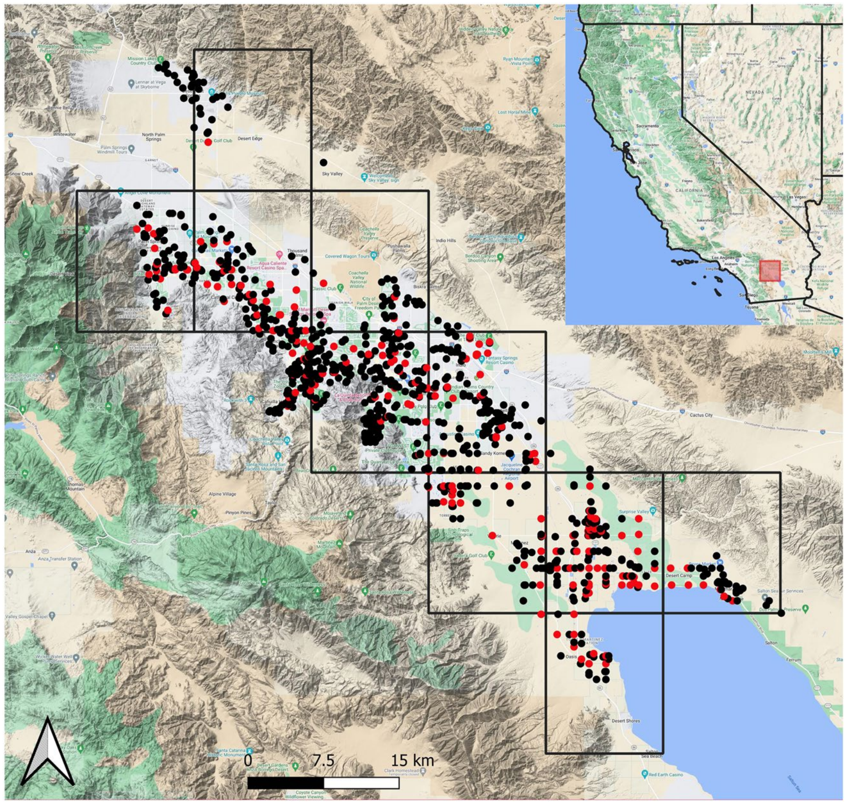

Figure 1. North American Land Data Assimilation System grid cells (0.125° or ∼13 km^2) with all historical trap locations that have ever been positive (red) and negative (black) overlaid the Coachella Valley. Inset: location of Coachella Valley within California.

spatial resolution of 0.125° (∼13 km^2 grid cells) creating 10 grid cells over Coachella Valley to forecast annual infection rates of WNV infected mosquitoes (Figure 1).

2.3. Mosquito Data

Mosquito data was obtained for 17 years (2006–2022) from the Coachella Valley Mosquito and Vector Control District. Trap data was analyzed to evaluate mosquito population abundance per trap night by Centers for Disease Control and Prevention (CDC) week. These data were averaged over the Coachella Valley. To understand the annual WNV infection rate in the mosquito population, the control district tests trapped mosquitoes in species specific pools of one - 50. These data were filtered for *Culex tarsalis* and *C. quinquefasciatus* mosquitoes, which comprised 65% and 34% of the positive samples, respectively, and are the known vector species of WNV in the Coachella Valley. Abundance was then calculated and averaged over the Coachella Valley (Table S2 in Supporting Information S1).

Table 1
Monthly North American Land Data Assimilation System (NLDAS) Environmental Variables

Environmental variable	NLDAS abbreviation	Scale/unit
Total precipitation	apcpsfc	kg/m^2
0–40 cm soil moisture	soilm40	kg/m^2
0–10 cm soil moisture	soilm10	kg/m^2
Surface pressure	pressfc	Pa
2 m above ground specific humidity	spfh2m	kg/kg
Average surface skin temperature	avsftsfc	K
2 m above ground temperature	tmp2m	K
Total evapotranspiration	evpsfc	kg/m^2

We determined infection rates of mosquitoes at the NLDAS grid cell scale (0.125° or ∼13 km^2) using the presence/absence of mosquito pools and a statistical method (maximum likelihood estimator [MLE]) to estimate the annual infection rate of mosquitoes per 1,000 mosquitoes tested ($\mathbf{I_M}$) (Ward, Sorek-Hamer, et al., 2023). The MLE was chosen because it takes advantage of changes within pool size and estimates a higher infection level by assuming that if a pool tests positive, one or more mosquitoes are WNV positive. This is a more appropriate estimate as the number of mosquitoes tested increases and the true infection rate is small (Walter et al., 1980; Ward, Sorek-Hamer, et al., 2023). All traps were assigned an NLDAS grid, all pools

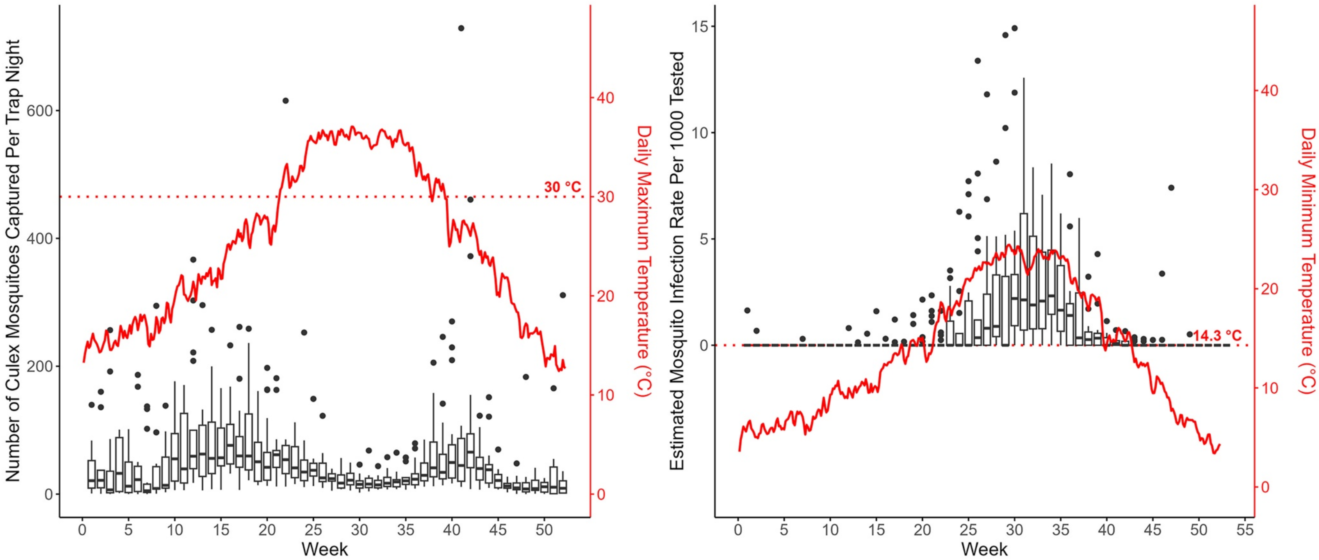

Figure 2. Historical *Culex* mosquito abundance in the Coachella Valley, number of infected mosquitoes per 1,000 tested, and atmospheric temperature (ATMP) from 2006 to 2022. Left: weekly mean number of mosquitoes trapped per night (boxplot, dots = outliers >1.5 × interquartile range [IQR] higher than the 75th percentile), maximum daily ATMP (red line), and temperature threshold for mosquito population decline (30°C, red dotted line). Right: average weekly $\mathbf{I_M}$ (boxplot, dots = outliers >1.5 × IQR higher than the 75th percentile), minimum daily ATMP (red line), and temperature threshold for viral amplification (14.3°C, red dotted line) (Reisen, Fang, Lothrop, et al., 2006).

within each grid were combined from CDC weeks 20–45, and the annual infection rate was calculated (Table S2 in Supporting Information S1). For methodology on calculating the annual $\mathbf{I_M}$ using the MLE see Ward, Sorek-Hamer, et al. (2023).

To address the uncertainty of the observed WNV mosquito infection rates, we set a threshold of a minimum of 500 mosquitoes tested within a year to establish a valid annual observation (DeFelice et al., 2017). This resulted in the inclusion of 10 NLDAS grids (Figure 1). Data were also evaluated to understand the seasonality of viral amplification before being included as a valid observation. CDC weeks 20–45 (mid-May to early-December) were included to address the seasonality of environmental conditions of WNV transmission in mosquitoes, with 97.5% of all historical positive mosquito pools in the Coachella Valley occurring within that window (Figure S3 in Supporting Information S1). These weeks also correspond to when the daily low temperature exceeds the threshold for viral amplification (14.3°C), and 3 weeks after the daily low temperature drops below this threshold (Figure 2) (Reisen, Fang, & Martinez, 2006). Annual mosquito infection rates were calculated for each of the NLDAS grids for which meteorological and hydrological data were available at the appropriate spatial scale. Aggregating mosquito data by NLDAS grid cell provided enough mosquitoes for a robust estimate of infection rate while also discounting more local scale land use conditions that bias trap collections. Thus, it allowed for analysis of how fluctuations in meteorological and hydrological conditions influence mosquito infection rates. Additionally, 13 km^2 is small enough for forecasts to be operationally useful at the abatement district level by aerial application.

2.4. Model Selection

We built a hierarchical negative binomial model with annual infection rates at the NLDAS grid cell as the outcome variable and a combination of monthly ATMP and ET as independent variables. Each NLDAS cell's monthly environmental variables were normalized to the historical observations by subtracting the mean of observations from 2006 to 2021, then dividing by the standard deviation. Monthly environmental observations were used to provide resolution to determine the effect of temperature and hydrology at the sub-seasonal temporal scale.

The hierarchical negative binomial model was chosen due to high zero-inflation within the mosquito infection rate data (Figure S4 in Supporting Information S1). We included random intercepts for each NLDAS grid cell, and the annual infection rate of mosquitoes was estimated using the MLE of all pools tested from week 20–45 within the NLDAS cell. Monthly ATMP and ET data from October to December of the prior year and January to July of the current year were used for model fitting. Each month's environmental data were treated as independent variables, yielding 20 potential predictors (10 months of ATMP and 10 months of ET). Models were fit on all possible combinations of four predictors of the possible 20 predictors, producing 4,845 candidate models for the ensemble (Equation 1). Models over four parameters were overfit and models with less than four did not provide sufficient resolution to analyze how fluctuations during the early-season meteorological and hydrological conditions influenced mosquito infection rates over time.

$$\binom{20}{4} = \frac{20!}{4! \times 16!} = 4,845 \tag{1}$$

Each candidate model was trained using environmental data from 2006 to 2018, and the parameters of these models were assessed for significant associations (p-value <0.05) with mosquito infection rate. Models, where all variables were significant, were isolated as potential models for the final ensemble. Equations 2–4 were used to identify the best combination of environmental parameters and calculate model-averaged predictions with unconditional confidence intervals. Specifically, we identified the best models using whole model goodness-of-fit estimated from the second order estimation of the Akaike Information Criterion (AIC_C) which is a better estimation of model fit when the ratio of parameters (n) to observations (k) is small ($n/k < 40$) (Burnham & Anderson, 2002). Following evaluation of numerous model structures, a mixed effects negative binomial model with grid cell as the random effect produced the best AIC_C and was used to make predictions with four environmental variables of ATMP and ET in each model.

The ensemble, defined as the weighted average of the combination of the top models, is used to improve forecast accuracy and account for the uncertainty of their competing predictions. To rank goodness-of-fit among the models tested, we calculated an AIC_C score and the weight of model i, ω_i, relative to the best model (Equation 2):

$$\omega_i = \frac{e^{-\frac{1}{2}\Delta_i}}{\sum_{i=1}^{R} e^{-\frac{1}{2}\Delta_i}} \tag{2}$$

where $\Delta_i = AICc_i - AICc_{min}$, $AICc_{min}$ is the AIC_C of the best-fit model, and R is the number of models where all parameters were statistically significant. We used a subset (N) of models whose weights summed to 0.95, and after identifying the combination of the top models, the Akaike weights were re-normalized to sum to one.

The model averaged prediction was generated from a weighted average (Equation 3):

$$\hat{\hat{\theta}} = \sum_{i=1}^{N} \tilde{\omega}_i \cdot \hat{\theta}_i \tag{3}$$

where $\hat{\theta}_i$ is the mean estimate of model i, $\tilde{\omega}_i$ is the re-normalized Akaike weight for model i in the ensemble, and $\hat{\hat{\theta}}$ is the mean ensemble prediction calculated from the N best fitting models identified in the step above. The unconditional model-averaged variance was then obtained from the weighted ensemble prediction (Equation 4):

$$\mathrm{Var} = \left[\sum_{i=1}^{N} \tilde{\omega}_i \cdot \sqrt{\mathrm{Var}\left(\hat{\theta}_i\right) + \left(\hat{\theta}_i - \hat{\hat{\theta}}\right)^2}\right]^2 \tag{4}$$

where $\mathrm{Var}\left(\hat{\theta}_i\right)$ is the variance of the prediction from model i and $\hat{\hat{\theta}}$ is defined as above.

This unconditional estimator takes into account the variation within and between each model in the model set (i.e., the model selection uncertainty) and was used to estimate unconditional confidence intervals around each model-averaged prediction.

We performed leave-one-year-out temporal cross validation analysis for each year from 2006 to 2018, with outcome data for that year excluded from the input data, and generated predictions for that year based on the ensemble model identified from the large number of candidate models. We identified an ensemble model using data from all years 2006–2018 combined, which we used to make predictions retrospectively for 2019, 2020, and

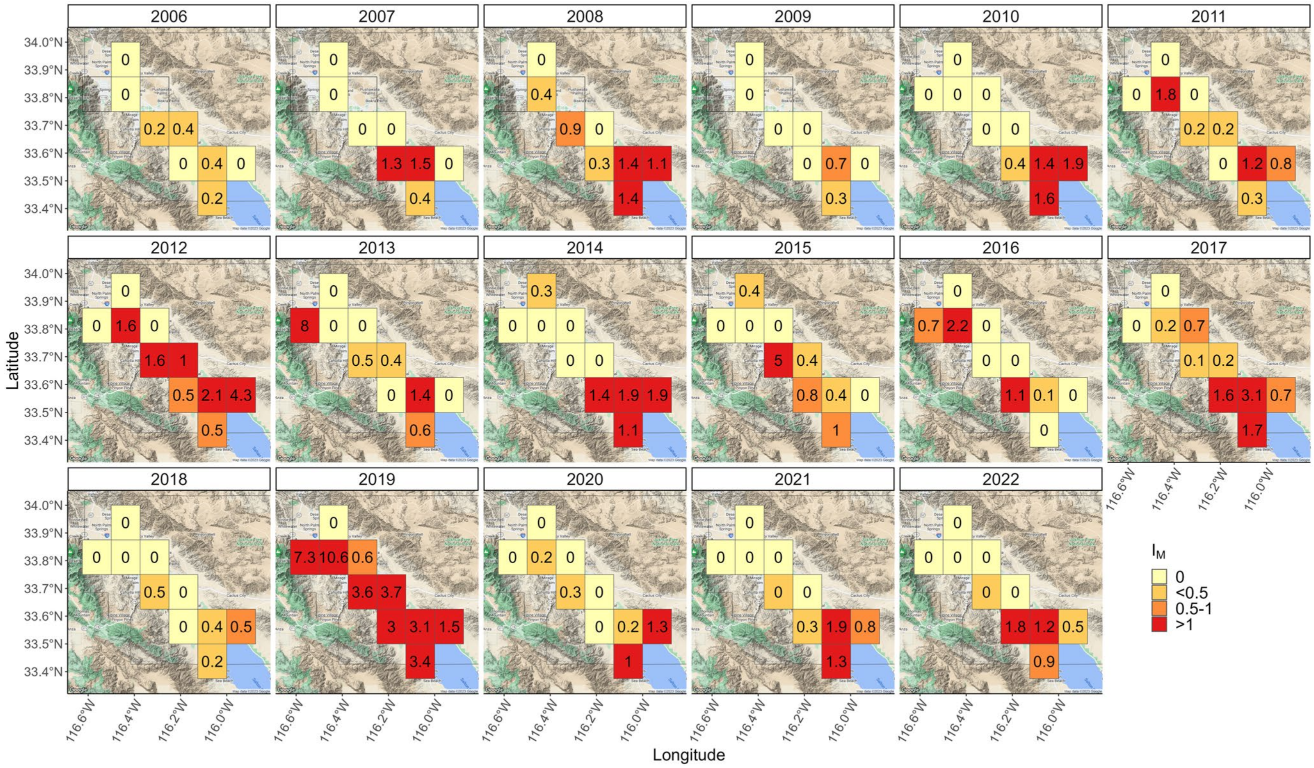

Figure 3. Annual $\mathbf{I_M}$ for Centers for Disease Control and Prevention weeks 20–45 by North American Land Data Assimilation System grid (0.125° or ~13 km^2) in the Coachella Valley from 2006 to 2022.

2021. We also applied the same methodology to data from 2006 to 2021 to develop ensemble models to produce real-time monthly predictions for 2022.

We evaluated forecast accuracy by grid cell and year for 2019 to 2021. Forecasts were deemed accurate if a prediction was above or below one infected mosquito per 1,000 tested in each grid cell. One infected mosquito per 1,000 tested annually was defined as high risk for transmission.

All analyses were conducted using the statistical software R (version 4.2.2) and the package "glmmADMB" to build the hierarchical regression models (R Core Team, 2023).

3. Results

3.1. Mosquito and Climate Data

The collected mosquito population, when normalized by trap night, and averaged across all years by week, generally exhibits a pronounced bimodal structure peaking in late spring to early summer (~CDC week 16) before drastically declining during the summer (~CDC week 30) corresponding to peak maximum daily ATMP and rebounding during the fall (~CDC week 36) (Figure 2). Conversely, the weekly average $\mathbf{I_M}$ peaks during the summer (~CDC week 30) corresponding to the peak in average minimum daily temperature (Figure 2); however, annual variability in these trends was observed (Tables S1–S3 in Supporting Information S1).

$\mathbf{I_M}$ at the NLDAS grid level for each year from 2006 to 2022 exhibited a relatively consistent pattern of WNV positive mosquitoes focused near the Salton Sea in the South in typical years with dissemination North through the valley in outbreak years such as 2019 (Figure 3).

3.2. Model Selection

Regression analysis using all combinations of four independent variables from 2006 to 2021 yielded 51 models with all parameters significant (1.053% of total models run, $N = 4{,}845$, p-value <0.05) with two models

Table 2
Significant Models With AIC_C Weights Summing to 95% Used in the Ensemble Models

Model rank	AIC_C	Weight	Ensemble weight	Temperature					Evapotranspiration		
Ensemble models 2006–2021											
1	323.39	0.668	0.680	–	April 0.57 (0.15)	–	–	July −0.36 (0.14)	January −0.51 (0.22)	February 0.99 (0.19)	–
2	324.89	0.315	0.320	December −0.27 (0.13)	April 0.75 (0.17)	–	–	July −0.59 (0.13)	–	February 0.67 (0.11)	–
Ensemble models 2006–2018											
1	251.38	0.453	0.453	–	April 0.71 (0.23)	–	–	July −0.36 (0.18)	January −0.76 (0.33)	February 1.20 (0.39)	–
2	252.82	0.220	0.220	–	–	May 0.55 (0.23)	June 0.52 (0.19)	July −0.74 (0.22)	–	February 0.60 (0.22)	–
3	252.89	0.213	0.213	December −0.29 (0.15)	April 0.61 (0.23)	–	–	July −0.50 (0.18)	–	February 0.46 (0.20)	–
4	254.13	0.115	0.115	–	–	–	June 0.44 (0.18)	–	January −0.70 (0.29)	February 0.98 (0.32)	June −0.41 (0.17)

Note. Effects of each parameter are shown, including month, parameter estimate, and the standard error of the estimate in parentheses.

comprising the ensemble with weights summing to 95% (Table 2 and Table S4 in Supporting Information S1). The same analysis performed using environmental data from 2006 to 2018 yielded four models with all parameters significant (0.083% of total models run, $N = 4{,}845$), all of which were included in the ensemble (Table 2). The ensemble of models for 2006–2021 suggests that a cooler and drier winter followed by a wetter and warmer spring and a cooler than normal summer are the set of environmental conditions most likely to influence the WNV IM in the Coachella Valley (Figure 4). For example, a one standard deviation increase in ET in February means we expect an increase of 0.89 infected mosquitoes per 1,000 tested.

3.3. Leave-1-Year-Out Cross Validation 2006–2021

We found the cross-validated model error was small comparable to the omitted years of data, with a Root Mean Square Error (RMSE) of 2.14 $\mathbf{I_M}$ (Table 3). Additionally, no single year dominated the ensemble, and the effect/contribution of the environmental parameters across years was consistent (Figure 5). The sensitivity and specificity of the ensembles' ability to predict above average years ($\mathbf{I_M} > 1$; 75th percentile) was 0.49 and 0.86, respectively, for 2006–2021 (Table 3 and Figure S4 in Supporting Information S1). This is comparable to the best model which was 0.44 and 0.86 (Table 3). When evaluating the observed versus predicted, the ensemble forecast system showed more predictive skill than the best model at identifying grid cell years having above average WNV infection rates (Figure S4 in Supporting Information S1). In comparison, the null model has lower RMSE because many NLDAS cells had zero positive mosquitoes over this period, keeping the historical average infection rate (null prediction) and the observed infection rate low (Table 3). Due to the NLDAS offset (random effect), the ensemble will not predict an infection rate of zero; thus, there will always be some error for those years when the cells have zero positive pools. However, the null model is much more susceptible to poor predictive performance during years with high WNV infection rates, as shown by the sensitivity. A paired Wilcoxon Signed-Rank test was performed to compare the predictive error of the environmentally informed ensemble model to that of the null model. For each NLDAS cell from 2006 to 2021, ensemble errors were defined as the absolute difference between the observed mosquito infection rate and the ensemble model prediction. Null model errors were defined as the absolute difference between the observed infection rate and the historical average infection rate (Table S5 in Supporting Information S1). The paired Wilcoxon test indicated that the predictive error of the ensemble model was significantly lower than that of the null model, with a p-value of 0.025.

3.4. Retrospective Forecast

Retrospectively, the ensemble forecast correctly predicted if an areas' annual mosquito infection rate was above or below one infectious mosquito per 1,000 tested 80% of the time from 2019 to 2021 using the ensemble trained on environmental data from 2006 to 2018 (Figure 6). In comparison the null model would predict high or low infection rates for the same period 50% of the time. Additionally, the ensemble performed better with environmental variables than without (Table 4 and Figure S5 in Supporting Information S1). Generally, these models indicate that a cooler drier winter followed by a wetting period and a warm spring with a cooler than normal summer, increase the risk of WNV and are the best predictors of WNV rates in the Coachella Valley.

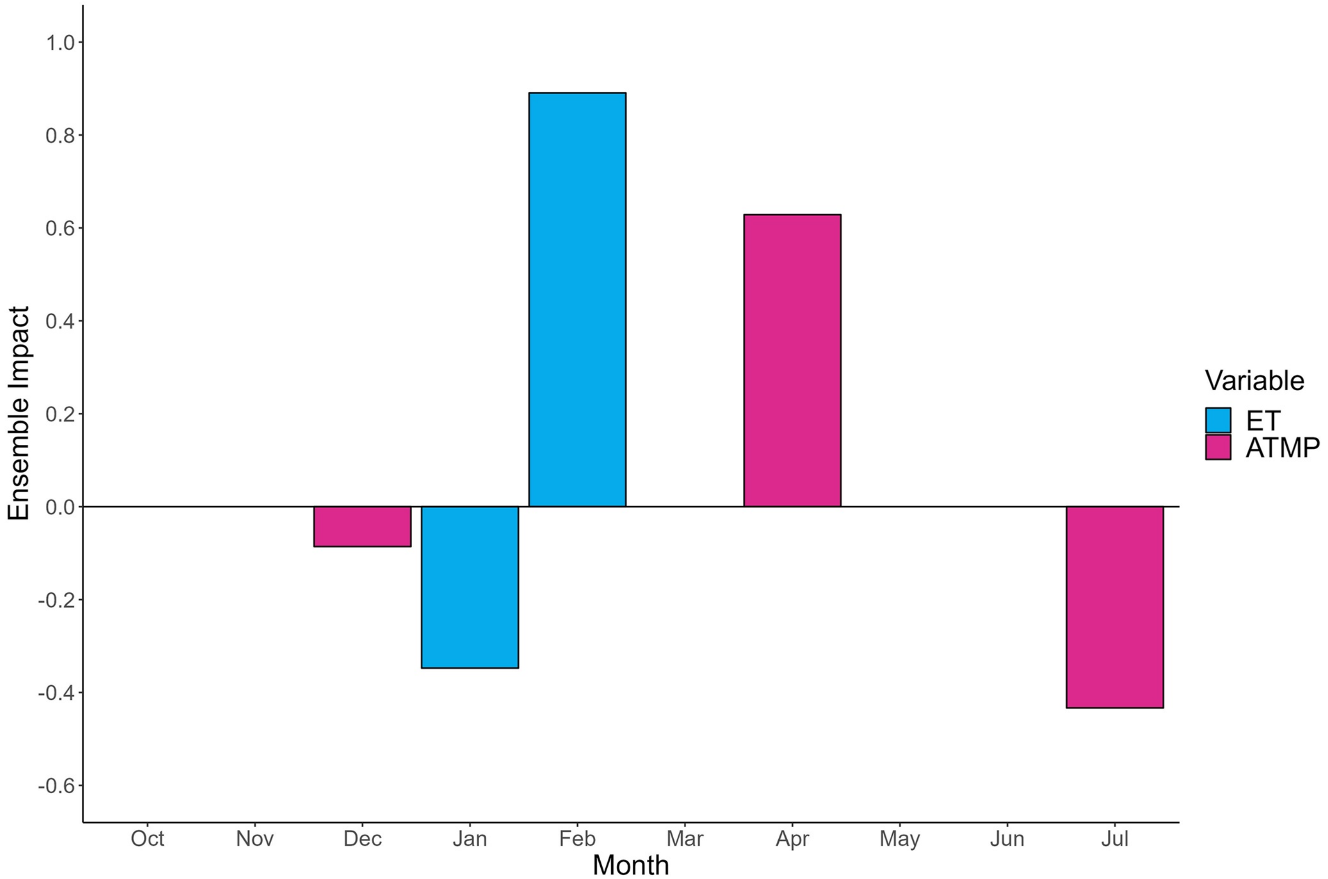

Figure 4. Effect and contribution of evapotranspiration (ET) and atmospheric temperature (ATMP) to the ensemble model associated with the estimated change of $\mathbf{I_M}$ at the monthly North American Land Data Assimilation System grid scale (0.125° or ∼13 km^2) for 2006–2021. Bars indicate the weight and direction of deviation of ATMP and ET in the ensemble from the average that increases $\mathbf{I_M}$ ($^{+\mathrm{Blue}}/_{-\mathrm{Red}}$).

3.5. Real-Time Forecast 2022

We conducted real-time monthly forecasting between March and August 2022 using our four—predictor ensemble model based on data from 2006 to 2021 at the NLDAS grid scale. In 2022, infected mosquito pools were identified in only four grids with three of the four grids becoming positive in July and August (Figure 7, Row 2). For predictions where environmental data were not yet available, the missing data were filled with the historical means from 2006 to 2021, which were then standardized to zero prior to generating the forecast. Our ensemble model predicted $\mathbf{I_M}$ changed in May and August as additional environmental data were added to the system. These predictions agreed with the observed values 80% of the time early in the season (Figure 7, Row 4). Furthermore, our model correctly predicted when $\mathbf{I_M}$ was greater than one for a 13 km^2 NLDAS grid cell for 50% of the cells that were identified as having WNV during the 2022 season. Lastly, the RMSE of our 2022 forecast including environmental variables was 0.534 $\mathbf{I_M}$ compared to 0.541 $\mathbf{I_M}$ without environmental contribution, demonstrating how model accuracy improved as observations of ET and ATMP were integrated into the model.

Table 3
Sensitivity and Specificity of Observed Versus Predictions for the Best Model, Null Model, and the Ensemble Model for 2006–2021

Observed versus	Sensitivity	Specificity	RMSE (I_M)
Ensemble	0.49	0.86	1.66
Best model	0.44	0.86	2.14
Null model[a]	0.31	0.74	1.51

[a]Null model prediction defined as historical average infection rate.

4. Discussion

This study aimed to describe how fluctuations in hydrological and meteorological conditions in the desert climate are associated with annual mosquito WNV infection rates in the Coachella Valley of California. Our multi-model inference system trained on 13 years of data was able to retrospectively predict $\mathbf{I_M}$ above or below one for an NLDAS grid cell (0.125° or ∼13 km^2)

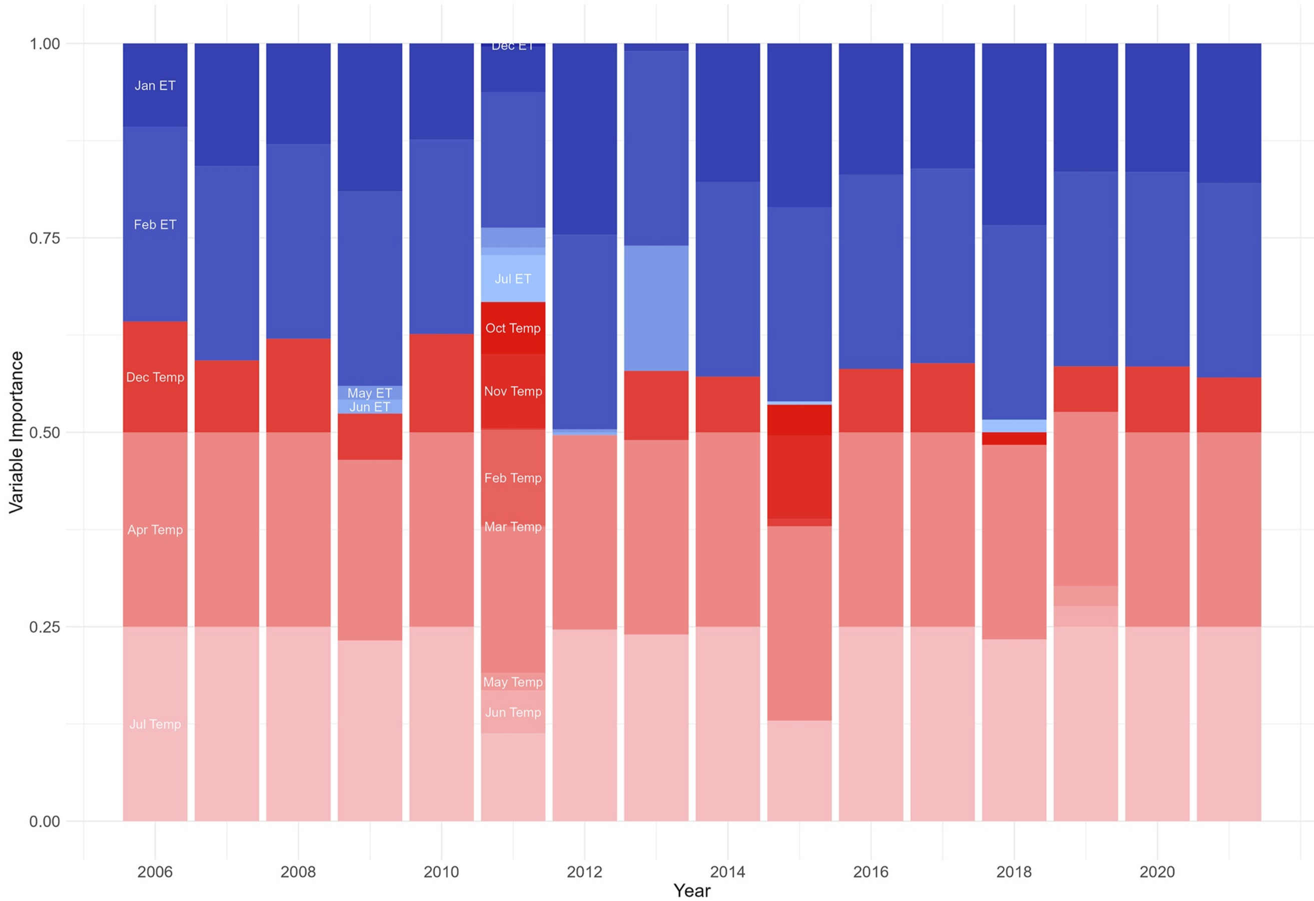

Figure 5. Variable weights contributing to cross-validated models for 2006–2021 (red = atmospheric temperature and blue = evapotranspiration [ET]). Year is the annual data removed from the cross-validated model.

80% of the time (2019–2021); and in real-time for 2022 trained on 16 years of data, was able to predict correctly eight out of 10 grid cells as of 4 March 2022. This multi-model inference system indicated that the combination of a cooler and dryer winter followed by a wetter and warmer spring and a cooler than normal summer was the combination of environmental changes that were most predictive of an increase in the rate of mosquitoes infected with WNV in the Coachella Valley.

Multiple strategies have been employed for WNV forecast models to deal with both spatial and temporal differences. Numerous other studies have presented forecast models of WNV over multiple geographies and ecosystems. Most models focus on forecasting human disease or risk at the county level or larger. The process of integrating these models into the real-time framework of public health decision making framework is underway but challenges are acknowledged (Barker, 2019; DeFelice et al., 2019; Keyel et al., 2021). These structures require incorporating human case data in real or near real-time and have shown promise in terms of understanding the relationship between infected mosquitoes and human cases (DeFelice et al., 2019). For example, a study utilized a compartmental model integrating mosquito infection rates and human WNV cases with an ensemble adjusted Kalman filter to accurately forecast peak timing and peak magnitude of infectious mosquitoes along with human WNV cases. This forecast utilized mosquito infection data and was able to accurately predict the total number of human WNV cases >74% of the time prior to when 50% of human cases were reported and 9 weeks prior to the end of transmission (DeFelice et al., 2017, 2018). However, the downside of human case data is that substantial lags exist between the onset of human disease and case confirmation, making real-time forecasting dependent on contemporary data streams difficult (DeFelice et al., 2019). Additionally, county level forecasts provide only a temporal trajectory rather than a spatially refined estimate of infection or spillover risk. Spatially refined forecasts at scales below the county level would provide districts with analytics to potentially guide the decision-making process around proactively spraying potential transmission foci and reducing the risk of spillover to humans.

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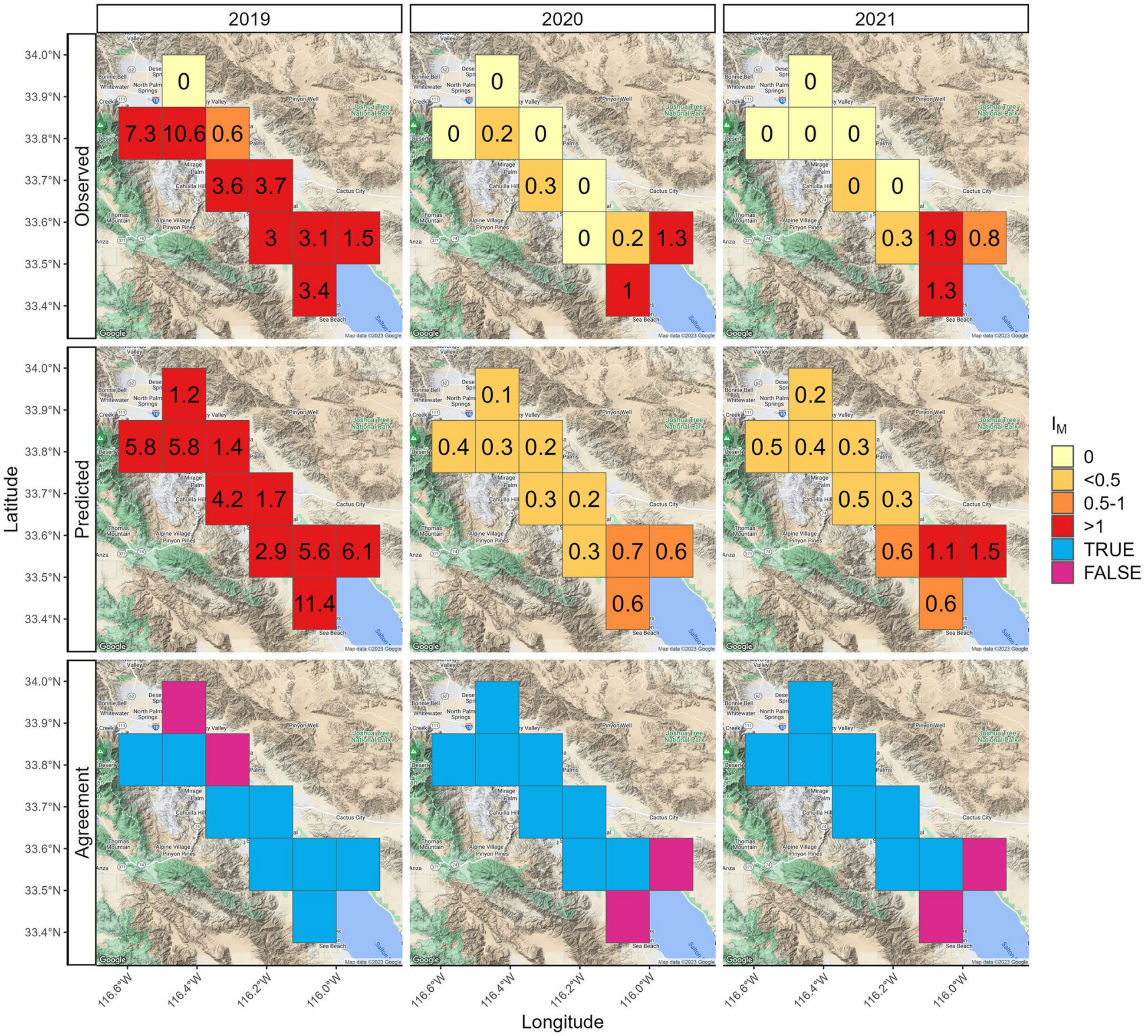

Figure 6. Agreement between observed and predicted $\mathbf{I_M}$ stratified by North American Land Data Assimilation System grid (0.125° or ∼13 km^2) in the Coachella Valley for 2019–2021. Row 1: observed $\mathbf{I_M}$ in 2019, 2020, and 2021. Row 2: predicted $\mathbf{I_M}$ in 2019, 2020, and 2021 using a four-predictor ensemble model trained on years 2006–2018. Row 3: cells where observed, and ensemble model predicted infection rates are in agreement based on the threshold of one infected mosquito per 1,000 tested.

Table 4
Performance of Retrospective Ensemble Forecasts With and Without Environmental Data

	RMSE		
Year	Ensemble w/ET and ATMP	Ensemble w/o ET and ATMP	Null model
2019	3.51	4.30	4.25
2020	0.36	0.46	0.54
2021	0.51	0.52	0.50

As a result of the difficulties with human case data, other forecast models have focused on mosquito infection rates. Like our model, these focus on forecasting mosquito infection rates allowing for early decision making to prevent human cases. For example, a study in Harris County, TX, used a seasonally auto-regressive forced linear model for time-series analysis of the correlation of weather, vegetation, mosquito abundance and infection rates and found that increased variability in temperature and rainfall during the winter was correlated with increased summer mosquito abundance while warmer winter temperatures related to increased mosquito infection rates 8 months later (Poh et al., 2019). Similar to our study, Little et al. demonstrated that meteorologic and hydrologic data can be used to predict WNV

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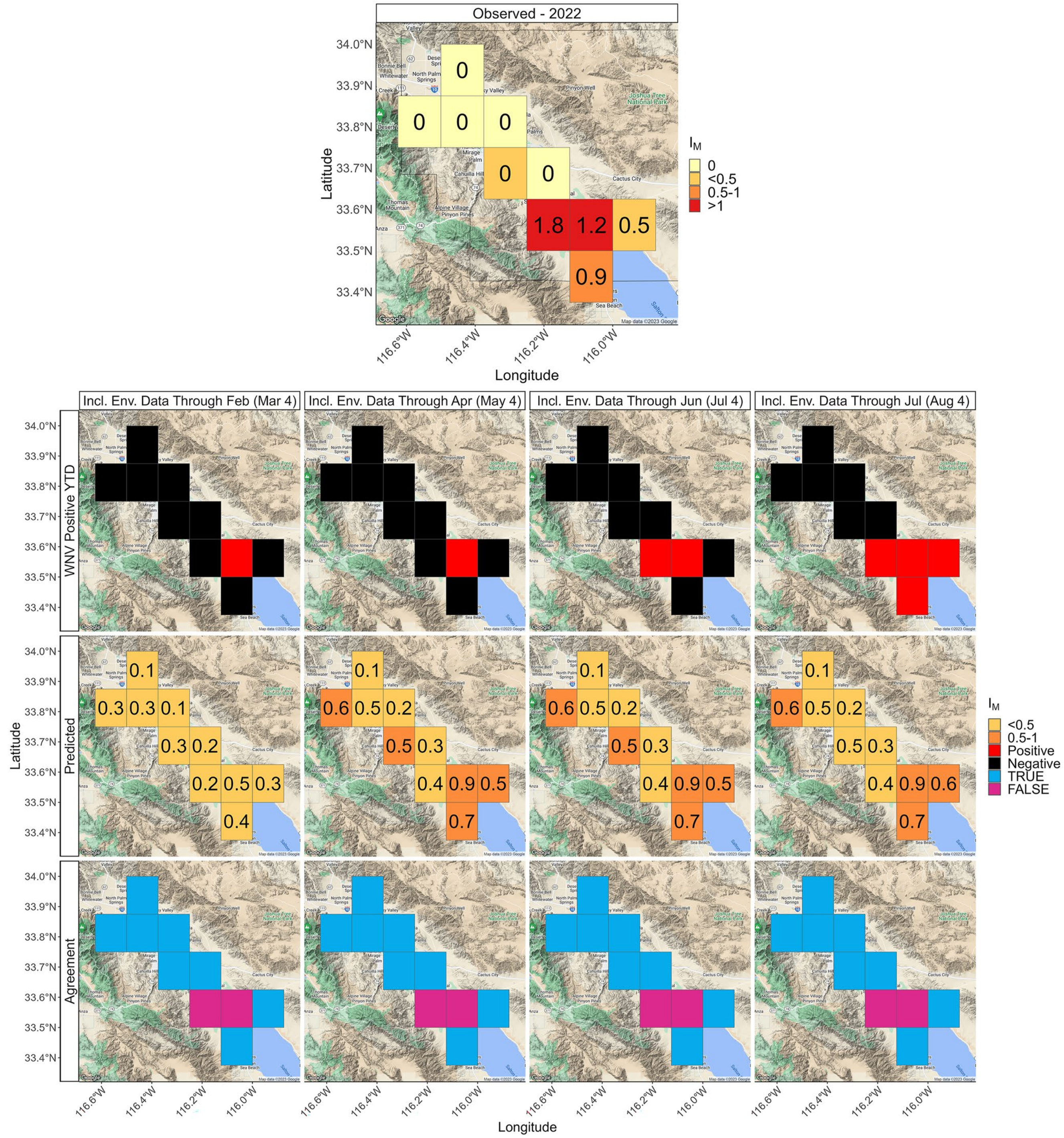

Figure 7. Real-time forecasting of West Nile virus (WNV)-infected mosquito pools from March, May, July, and August of 2022 using available North American Land Data Assimilation System environmental data (13 km^2) and the parsimonious hierarchical negative binomial ensemble model. Row 1: observed annual $\mathbf{I_M}$ in 2022. Row 2: grid cells in which WNV was identified in the Coachella Valley mosquito population year to date (red = WNV+ and black = WNV not identified). Row 3: predicted annual $\mathbf{I_M}$ in 2022 using all environmental data prior to parenthesized forecast date. Row 4: cells where observed, and ensemble model predicted infection rates are in agreement based on the one infected mosquito per 1,000 tested threshold.

mosquito infection rates prior to their seasonal peaks. They utilized a multi-model inference system and negative binomial models to determine that a warm and dry, early spring correlated to an increase in WNV infection rates in *Culex* mosquitoes in Suffolk County, NY (Little et al., 2016). In contrast, we focus on mosquito ecology in a desert climate and demonstrate that a dryer and cooler than normal winter followed by a warming and wetting period and a cooler than usual summer are ideal for WNV amplification in the desert. Additionally, our model forecasts at the NLDAS grid scale (0.125° or ~13 km^2) making it a more operationally useful spatial scale than models at the county level. Aggregating mosquito data by NLDAS grid cell provided enough mosquitoes for adequate signal and a better representation of the mosquito infection rate. It also reduced local scale error characteristic of individual trap collections resulting from localized environmental factors or land use characteristics. This allowed for determining how climate affects relative mosquito infection rates. Lastly, this scale allowed us to produce more spatially resolved risk maps than models at the county or state level (Figure 6).

Desert climates such as those of Southern California or the U.S. Southwest pose unique challenges for arthropods with aquatic larval stages such as mosquitoes. These challenges drive mosquito populations in desert climates to have unique ecologies and population dynamics (Reisen et al., 1992). While mosquitoes benefit from relatively mild desert winters compared to populations at more northern latitudes, they must weather extreme heat and drought events during the summer months. The natural hydrology of the desert means there is far less larval habitat available, and populations are restricted to areas with sufficient available water for larval development (Chew & Gunstream, 1970; Reisen et al., 1992). In Coachella this hydrology is almost exclusively driven by agricultural activity, especially during the warmest periods of the year when more water is used to keep crops healthy. Additionally, mosquito populations are further geographically restricted to areas with sufficient blood meals to facilitate egg development. Paradoxically, this geographic restriction concentrates both mosquito and avian hosts in the same location facilitating transmission of WNV between birds and mosquito, and viral amplification in both populations. However, if the summer is too warm, such as is often the case in Coachella, it is detrimental to the mosquito population, causing die offs. During these years we see average or even below average annual $\mathbf{I_M}$ in the Coachella Valley. Conversely, and as demonstrated by our model, during years where the average temperature during the typically warmest months of the year (July–August) are slightly cooler than normal, mosquito populations are less stressed, and transmission and amplification more readily occurs leading to increased annual $\mathbf{I_M}$ in the Coachella Valley.

Additionally, in desert climates such as the Coachella Valley, where winters are mild compared to other regions of the United States, the magnitude of WNV transmission the previous year may have a residual effect on the following season (Chew & Gunstream, 1970; Reisen et al., 1992). For instance, in the Coachella Valley the mosquito population exhibits a substantial drop during the hottest part of the summer that is usually followed by a rebound period in the fall going into the winter months (Figure 2). *C. quinquefasciatus* and *C. tarsalis* are the known vectors of WNV in the Coachella Valley, making up 34% and 65% of positive WNV pools respectively, however they have differing overwintering strategies. *C. quinquefasciatus* do not diapause, but rather enter a state of slowed metabolism as adults or embryos called quiescence triggered by adverse environmental conditions (Diniz et al., 2017). In contrast, *C. tarsalis* diapause primarily as nulliparous adult females (females which have not laid eggs) in response to shorter days and cooler temperatures (Harwood & Halfhill, 1964). This analysis suggests there are two complimentary modes of persistence of WNV in a region: (a) virus overwintering in mosquitoes, and (b) virus is maintained in the avian amplifying hosts (Goddard et al., 2003; Reisen, Fang, Lothrop, et al., 2006).

Considering the overwintering strategies of the vectors in Coachella Valley, cooler than normal winters, such as indicated by our model, likely increase the rate of *C. quinquefasciatus* entering quiescence as well as increase the success of *C. tarsalis* overwintering by diapause. The more successful each species is at overwintering, the greater number of mosquitoes remaining in the population at the beginning of the next spring. This greater than normal starting value could then result in more rapid population growth especially if there are more larval resources and a warmer spring as indicated by our model. This growth produces more mosquitoes with the potential to become infected with WNV after feeding on an infected bird. Similarly, greater numbers of successfully overwintering adult female mosquitoes increase the potential that some of those mosquitoes are already infected with WNV and thus able to transmit the virus to naive birds earlier in the season (Farajollahi et al., 2005; Goddard et al., 2003; Kampen et al., 2021; Nasci et al., 2001; Reisen, Fang, Lothrop, et al., 2006). These factors may be especially important should environmental conditions be ideal for rapid spring mosquito population growth within the desert, as indicated by our model.

Successful overwintering has been shown in other studies to enhance WNV transmission the following year. One study which found that the number of days of harsh winter conditions in Texas and along the Central Flyway, such as hard-freeze or colder winters with deep snow, were negatively correlated with WNV incidence the following season (Chung et al., 2013; Hort et al., 2023). While Coachella Valley rarely has hard-freezes the significance of ideal overwintering conditions is just as important. Additionally, the association with a wetter and warmer spring and increased WNV transmission is consistent with other studies in the Midwest, Great Plains and Europe (Chuang & Wimberly, 2012; Chuang et al., 2012, 2013; Paz et al., 2013; Ruiz et al., 2010). Less than ideal winter conditions for *Culex* spp. mosquitoes means the population likely takes longer to rebound, and therefore there are less mosquitoes to transmit or become infected with WNV earlier in the season. Mosquitoes in Coachella overwinter better when temperatures are cooler than normal-keeping in mind that average daily low temperature in the desert ecosystem usually does not go below 10°C or 50°F, with temperatures dropping below 0°C or 32°F less than 1% of our study period (NLDAS-2). Successful overwintering combined with a wetter and warmer than usual spring creates optimal conditions for observed mosquito WNV infections in the Coachella Valley. Whether these trends continue as global temperatures rise remains to be seen. Genotyping late season and the following early season WNV from positive mosquitoes could inform on the inter-annual persistence of WNV in the Coachella Valley (Hepp et al., 2018; Kampen et al., 2021).

Average temperatures in Riverside County are projected to rise between 1.5 and 2.6°C by mid-century, depending on the emission scenarios (IPCC, 2023; Maizlish et al., 2017; O'Neill et al., 2016). These projected changes in temperature show an increase in both winter and summer, with the average mid-century winter and summer temperatures estimated to be the second warmest winter and the hottest summer Coachella Valley has had in the last 16 years (NLDAS-2). Such dramatic increases in temperature will likely result in dramatic changes to *Culex* spp. ecology as well as vector–virus–host interactions in the Coachella Valley (Couper et al., 2021). In addition to the increased average temperatures, it is likely that hydrology and land use patterns will change as agricultural practices adapt to the warmer climate, potentially increasing resources for juvenile mosquito life stages. However, even though Coachella has one of the oldest water rights to the Colorado River system (Crider, 2018), as drought conditions continue to shrink the volume of water in the California's river systems, underground aquifers continue to be depleted, and temperatures continue to rise, it is reasonable to conclude that water use may shift from agricultural and recreational to municipal use. This shift will likely mean less surface water available for juvenile mosquitoes, further restricting mosquito populations. Given, it is well known that warmer winter temperatures reduce overwintering success and extreme summer temperatures cause declines in adult mosquitoes, these combined with reduced surface water, make it difficult to project the long-term impacts of WNV in this desert ecosystem.

Mosquito control intervention in the Coachella Valley is predominantly aerial application of adulticide. If going forward our inference system proves insightful on how environmental conditions influence WNV mosquito infection rates at the beginning of May, 4 months before the historical peak of spillover events in Coachella (July–August), they may provide a valuable additional decision-making tool for local public health entities and mosquito control districts. More years of testing are needed, but the forecast model presented here may provide the abatement district with further spatially refined information on how changes in meteorological and hydrological conditions early in the year may lead to higher WNV $\mathbf{I_M}$. Additionally, it could provide empirical data to support early targeted adulticide applications to mitigate WNV amplification and transmission in the valley while reducing the overall use of pesticides. Furthermore, early season forecasts could provide public health agencies with the information necessary to target messaging to at-risk populations. This may be especially important because mosquito populations are paradoxically at their lowest when infection rates are at their highest. This lower population may skew people's perception resulting in a perception of lower risk due to fewer nuisance biting mosquitoes. This, in turn, may reduce the proclivity to take protective measures, such as wearing repellant or long clothes, at these times when mosquito infection rates are highest. Early season messaging may help avoid this, but caution must be used, too not over-saturate residents and cause message fatigue; whereby residents become desensitized to risk-related messaging (Eppler & Mengis, 2004; So et al., 2017).

A major component of industry in the Coachella Valley is agriculture which requires laborers to work outdoors, potentially in proximity to WNV hot spots. Spatially resolved forecasts, such as our multi-model inference system, provide local public health entities additional information on where and when to target educational outreach and risk reduction efforts such as signage, collaborating with local farm-worker organizations, and providing protective measures such as DEET products to those at risk. Additionally, due to migrant status and other social-economic factors such as barriers to care or accessing care in Mexico, it is likely that many, if not a majority of non-neuroinvasive WNV cases go unreported in migrant farm-worker populations (Horton &

Cole, 2011; Seid et al., 2003; Villarejo, 2003). Early season, targeted outreach could aid in closing this reporting gap by increasing knowledge about WNV and care-seeking behaviors, while decreasing barriers to care.

Ensemble forecast modeling has advantages over more traditional regression analysis or using only the best model in that it provides an aggregation of the top significant models. This theoretically provides a more accurate estimate of the true state (Burnham & Anderson, 2002). As demonstrated, we saw improvements of our parsimonious ensemble over the best model with a 5% improvement in sensitivity. However, it is still dependent on the availability and quality of the data going into the models, and sensitivity and specificity improve as more environmental and WNV data is incorporated. Additionally, NLDAS data have both advantages and disadvantages. First, NLDAS data are freely downloadable and easily accessible; therefore, this model and ensemble strategy could be applied to other geographical regions. However, data sets of this scale and complexity do require a computational skillset to manipulate and make full use of mosquito trapping data. Additionally, an advantage of NLDAS is its scale. At 13 km^2, the grid cells are suitably large to not only potentially match the scale of aerial abatement interventions but are also large enough to capture the effects of meteorology on infection rates over the background of land use, which is essential for a climatically driven model. Future years will need to be analyzed to evaluate this system's overall predictive accuracy.

5. Conclusions

This study showed the potential for accurate prediction of the annual mosquito infection rates of WNV in Coachella Valley at the NLDAS scale utilizing a parsimonious multimodel ensemble inference system and freely available meteorological data. This ensemble system improved forecasting ability over the best-model. The results emphasize the unique ecology of WNV in this extreme desert climate. Our inference system for the deserts of Southern California predicted a combination of a cooler and dryer than usual winter followed by a wetter and warmer spring with a cooler than usual summer as the sequence of conditions best supporting WNV amplification in *Culex* mosquitoes. Through this model, we have a greater understanding of the biological characteristics that lead to WNV amplification. Thus, using early season meteorological and hydrological conditions improved our ability to identify areas of concern applicable for targeted early season interventions. Thereby better mitigating the risk of WNV to humans in the Coachella Valley before transmission occurs.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

NLDAS data is freely available from NASA (NLDAS, 2012). Our code, figures, data, and methodology can be accessed via (Ward, Patel, & DeFelice, 2023), and the statistical software R and cited packages can be obtained from the R Project for Statistical Computing (R Core Team, 2023). Mosquito data supporting this research are available from the Coachella Valley Mosquito and Vector Control District through VectorSurv under memorandum of understanding and are not accessible to the public or research community without prior approval (VectorSurv [Database]. https://vectorsurv.org/starting/). To gain access to this data researchers should contact the Coachella Valley Mosquito and Vector Control District directly.

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