

## ARTICLE

## Disease Ecology

## Spatial modeling of two mosquito vectors of West Nile virus using integrated nested Laplace approximations

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## Abstract

The abundance of *Culex restuans* and *Culex pipiens* in relation to ecological predictors is poorly understood in regions of the United States where their ranges overlap. It is suspected that these species play different roles in spreading West Nile virus (WNV) in these regions, but few studies have modeled these species separately or accounted for spatial correlation using Bayesian methods. We used mosquito surveillance data collected by the Pennsylvania Department of Environmental Protection from 2002 to 2016 and integrated nested Laplace approximations with the stochastic partial differential equation approach to predict *C. restuans* and *C. pipiens* abundance in relation to several ecological predictors. We then made a predictive risk surface of abundance for each species at locations that were not sampled. Explanatory variables in the models included ecological variables previously described to be important predictors of the abundance of these mosquito species. Developed habitat, temperature, and precipitation were important predictor variables for the abundance of *C. restuans*, whereas developed habitat, snow water equivalent, and normalized difference water index were important predictor variables for the abundance of *C. pipiens*. The abundance of *C. restuans* had a negative relationship with developed habitat in contrast to *C. pipiens* abundance, which had a positive relationship with developed habitat. Julian date was modeled as a temporal trend for both species and showed *C. restuans* to be more abundant from late April through late June and *C. pipiens* to be more abundant from July through September. A seasonal crossover was observed between these two species on Julian day 185, 4 July. We observed different spatial patterns of abundance in the predictive risk maps of each of the species. Our results indicate that modeling the abundance of these species spatially and separately in regions where these two mosquito vectors coexist can help gain further insight into understanding the epidemiology of WNV in human and susceptible animal populations.

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## KEYWORDS

Bayesian hierarchical model, *Culex pipiens*, *Culex restuans*, ecology, epidemiology, mosquito, Pennsylvania, R-INLA, spatial model, stochastic partial differential equations (SPDEs), West Nile virus

## INTRODUCTION

West Nile virus (WNV; family *Flaviviridae*, genus *Flavivirus*) was first detected in North America in 1999 (Nash et al., 2001) and has become endemic throughout the United States and Canada. The virus, which can cause morbidity and mortality in humans, equines, and several avian species, has become a global threat to human and animal health (Gray & Webb, 2014). The transmission cycle of WNV alternates between multiple wild bird reservoirs and mosquito vectors, both of which vary regionally (Kramer et al., 2008; Reisen, 2013). Human and animal infections of WNV are clustered in space and time (Mostashari et al., 2003; Sugumaran et al., 2009). To help predict WNV transmission cycles and implement targeted surveillance and control measures, the spatial and temporal distributions of mosquito communities and population dynamics must be understood (Sallam et al., 2017).

Epidemiologically, the abundance and reproductive rate of mosquitoes determine the frequency of host contact, the rate of pathogen transmission, and subsequently the risk of infection in humans and other animals (Smith, 1987). Thus, in areas where mosquito-borne viruses are known to occur widely and reservoirs are present, mosquito abundance can be used to identify areas at risk for disease transmission (Cleckner et al., 2011). Determining the spatial and temporal distribution of mosquito vectors could help predict the areas at risk of mosquito-related diseases, especially during outbreaks (Sallam et al., 2017). In addition, risk maps generated from distribution models can help in understanding the geographic distribution range of unsampled areas, which is needed to target mosquito surveillance and control efforts in these areas (Sallam et al., 2017).

Further understanding the spatial epidemiology, ecology, and distribution of *Culex pipiens* and *Culex restuans* is of particular interest to human and animal health because it has been estimated that these two mosquito vectors are responsible for up to 80% of human WNV cases in the northeastern United States (Kilpatrick et al., 2005). In addition, several avian species, including American crows (*Corvus brachyrhynchos*) and ruffed grouse (*Bonasa umbellus*), have been documented to be vulnerable to

WNV-associated population declines in this region (George et al., 2015; LaDeau et al., 2007; Stauffer et al., 2018). In the northeastern United States, *C. restuans* and *C. pipiens* are abundant and have been suggested to be maintenance vectors of WNV (Turell et al., 2005). Although both of these species primarily feed on blood from avian hosts (Molaei et al., 2006), they have ecological differences, including *C. restuans* being endemic and generally inhabiting rural and undeveloped sites (Ebel et al., 2005; Johnson et al., 2015) and *C. pipiens* being invasive and predominantly found in urban areas and other anthropogenic habitats (Fonseca et al., 2004). *C. restuans* is considered to be an early season vector of WNV, whereas *C. pipiens* has been identified to play a greater role in amplifying the virus later in the season (Andreadis et al., 2001; Johnson et al., 2015). This difference is suspected to be due to the abundances of the two mosquito species shifting seasonally (Kunkel et al., 2006; Lampman et al., 2006).

In regions where these two mosquito species coexist, the epidemiology of WNV remains unclear (Johnson et al., 2015). Due to *C. restuans* and *C. pipiens* being similar in appearance and difficult to separate, some authors do not differentiate between the two species and subsequently classify them to be *C. pipiens/restuans* (Ebel et al., 2005). Thus, the two species are often pooled together (Harrington & Poulson, 2008), which makes it difficult, if not impossible, to use commonly collected mosquito surveillance data to determine the epidemiology of WNV (Ebel et al., 2005; Johnson et al., 2015). From 2002 to 2016, the Pennsylvania Department of Environmental Protection (DEP) conducted mosquito surveillance for WNV statewide and distinguished between *C. restuans* and *C. pipiens* when determining the abundance of these vector species. Our objectives were: (1) to use integrated nested Laplace approximations (INLA) spatial models to understand the relationship of ecological variables (e.g., temperature, precipitation, developed, and agriculture) to the abundance of each of *C. restuans* and *C. pipiens*, and (2) to make a predictive risk map for the abundance of each species at a large extent (e.g., state and provincial levels), but with fine resolution (meters–kilometers), to further understand the ecology and spatial distribution of these species in regions where they coexist.

## METHODS

### Study area

Our study area consists of the entire state of Pennsylvania, USA, which is centered at 41.203323 latitude and  $-77.194527$  longitude. Pennsylvania has a diverse landscape, including the Appalachian Mountains in the interior, agricultural areas, and large metropolitan areas (Frankson et al., 2017). The climate throughout the state generally has a humid continental climate with hot and humid summers and cold winters (Frankson et al., 2017). The climatic patterns in Pennsylvania depend on elevation, latitude, and proximity to large water bodies (Gelber, 2002). The Appalachian Mountains cause higher elevations to receive more precipitation than other regions, and southeastern Pennsylvania has less rain and snow and milder winters than the northern and western regions of the state (Gelber, 2002). The Atlantic Ocean and Lake Erie moderate the climate of coastal areas and the northwestern region, respectively (Frankson et al., 2017).

### Mosquito surveillance

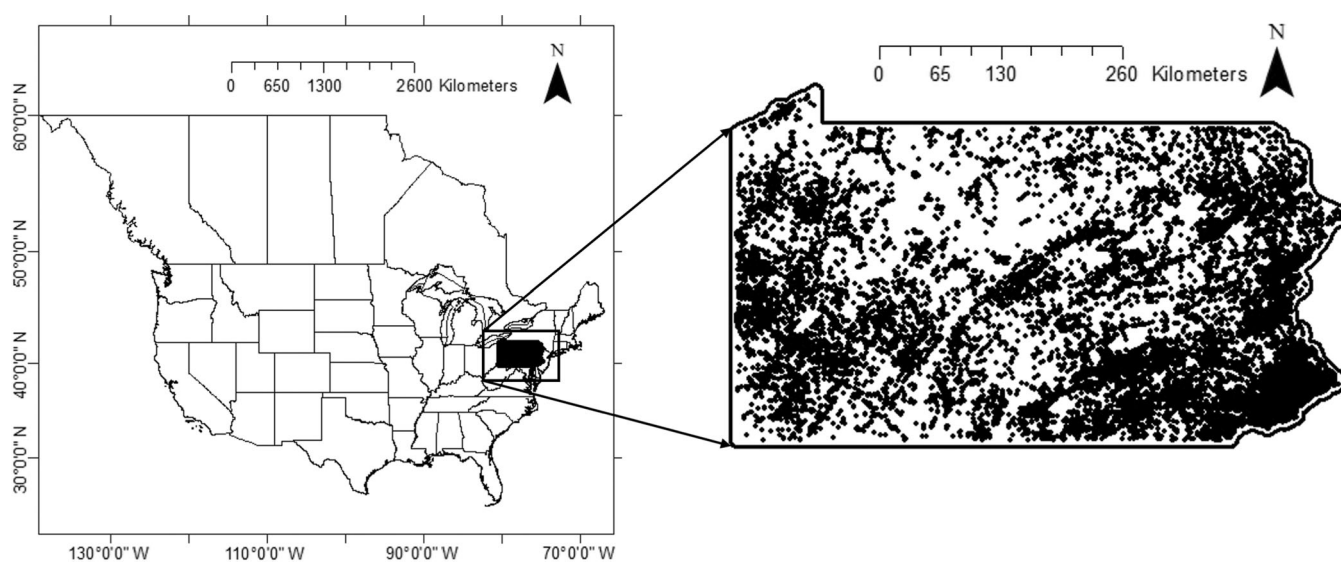
The DEP conducted surveillance of WNV in mosquitoes from 2002 to 2016 by setting gravid traps from April to September statewide. Data collected from these efforts included mosquito abundance by vector species. Traps were set to include one overnight and two crepuscular periods, which typically represented 18–24 h of capture

effort. Only one gravid trap was placed at each site within a given 24-h period; however, some sites were surveyed more routinely within and across years due to the local prevalence of WNV and public requests.

Upon collection, samples were immediately shipped to the DEP using dry ice, which helped maintain sample integrity for identification. Gravid *C. restuans* and *C. pipiens* mosquitoes were identified to species using morphological characteristics (Darsie & Hutchinson, 2009; Darsie & Ward, 2005). If species could not be distinguished between *C. restuans* and *C. pipiens* in a trap, we excluded those observations. Some sites had multiple mosquito counts recorded on a given day, so we also excluded these observations to prevent errors from being incorporated into our dataset. Surveillance data that met our criteria resulted in 187,390 samples containing *C. restuans* and/or *C. pipiens* distributed throughout Pennsylvania (Figure 1). Of the data meeting our criteria, the mean number of traps set per year was  $12,493 \pm 3624$  SD. The number of unique sites sampled ranged from approximately 3000–6600 per year. The number of traps set ranged from 5745 to 9337 per year from 2002 to 2005, and from 10,494 to 14,473 per year from 2006 to 2016.

### Ecological variables

We considered ecological variables that have been associated with *C. restuans* and/or *C. pipiens* abundance in previous studies (Lebl et al., 2013; Rosà et al., 2014; Yu et al., 2018) and were known or hypothesized to impact their physiology, reproduction, and survival



**FIGURE 1** The distribution of the trapping locations of gravid traps used for mosquito surveillance of West Nile virus by the Pennsylvania Department of Environmental Protection throughout the state of Pennsylvania, USA, from 2002 to 2016.

(Table 1). These variables were available in raster format for the duration of the dataset (2002–2016) that included temperature, precipitation, snow water equivalent, normalized difference water index (NDWI), elevation, agriculture, developed, and forest (Appendix S1: Table S1). We downloaded files for precipitation, snow water equivalent, and temperature from Daymet (Thornton et al., 2014). Precipitation and snow water equivalent were generated from raw files, whereas temperature was generated by averaging the daily maximum and minimum temperature files. We generated NDWI from MODIS band 4 and band 6 following Xu (2006). We then generated a 5-km resolution raster for each of these variables by resampling the original raster with a template of the study area, which had a 5-km resolution containing 5545 cells with a boundary that extended 5 km outside the study area. The resampling was conducted using bilinear interpolation in the raster package in R (Hijmans, 2016; R Core Team, 2021). We linked the variables for temperature, precipitation, snow water equivalent, and NDWI to each mosquito

trap observation. We then included time lags for each of these variables that we determined by using cross-correlation maps (Curriero et al., 2005) and taking into account time lags that were found to be important in previous research (Chuang et al., 2012; Rosà et al., 2014).

Cross-correlation maps are a graphical method that allows for the visualization of the effects of variables over intervals of time and are a generalization of cross-correlation plots, which are commonly used to display lag associations at single points in time (Curriero et al., 2005). We derived cross-correlation maps separately for *C. restuans* and *C. pipiens*. Except for NDWI, we averaged the daily values of each predictor as a single daily mean and averaged the log of abundance across the traps set in the same day. This allowed us to visualize the correlation between the log abundance at day  $t$  and the mean value of each variable during day  $t - x_1$  and  $t - x_2$ , with  $x_1 \geq x_2$  (Curriero et al., 2005). The cross-correlation maps were built using the daily averages from day 1 to 120 days prior to day  $t$ . We used the

**TABLE 1** Ecological variables considered that could impact *Culex restuans* and *Culex pipiens* abundance through physiology, reproduction, and/or survival.

Variable	Importance to <i>Culex restuans</i> and <i>Culex pipiens</i> population abundance	References
Temperature	Affects most biological rates, including blood feeding, reproduction, development of eggs, larvae, and pupae, and survival rates of immatures and adults.	Madder et al. (1983); Wilton and Smith (1985); Wang et al. (2011); Ciota et al. (2014)
Precipitation	Rainfall may increase quantity and quality of larval sites.	Chaves and Kitron (2011); Chuang et al. (2012)
Snow water equivalent	When and how fast snow melts can influence quantity and quality of larval sites.	Reisen et al. (2008)
Elevation	Mosquitoes may be less abundant at higher elevations due to cooler temperatures. They may be more abundant at lower elevations due to preferred host species and favorable larval habitats being more available.	Bravo-Barriga et al. (2017)
Proportion developed	Urban infrastructure can provide larval habitats in the forms of stagnant water and artificial containers.	Trawinski and Mackay (2010); Deichmeister and Telang (2011)
Proportion forested	Vegetation density is positively correlated with preferred avian host species and trees may offer resting habitats and sugar sources.	Brown et al. (2008); Gardner et al. (2013)
Proportion agriculture	Artificial containers on agricultural sites could facilitate mosquito breeding. Livestock kept outdoors at night could provide feeding opportunities.	Kaufman et al. (2005); Bravo-Barriga et al. (2017)
Normalized difference water index	Higher values early in the season have been associated with an earlier start and duration of mosquito breeding. Index might be indicative of the level of moisture in the soil, which would facilitate formation and persistence of mosquito breeding sites.	McFeeters (2013); Rosà et al. (2014); Sriwongsitanon et al. (2015)
Julian date	Seasonal cycles create periods of year with favorable conditions for reproduction and growth.	Reisen et al. (2008)
Year	Variation among years determines interannual changes in population size.	Reisen et al. (2008)



120-day (approximately 17 week) time period because this period was used to create cross-correlation maps of these species in a previous study that found this time period to be a better predictor of mosquito abundance than approximately 4 weeks, which represents the lifetime of a mosquito, including the aquatic stages (Lebl et al., 2013). The time lags we used included: temperature averaged 3–7 days prior to trapping; precipitation averaged 1–40 days prior to trapping; snow water equivalent averaged 90–120 days prior to trapping; and NDWI averaged 1–17 weeks prior to trapping. For NDWI, we used weekly averages because daily averages were not available for this variable.

Using the same methods as described previously, we derived elevation by aggregating 10-m original files to the template of the study area, which had a 5-km resolution. We then assigned an elevation value to each trap, which was based on the 5-km grid cell in which each trap fell. We used the US National Land Cover Database (NLCD) to estimate the proportion of three landscape features (developed, agriculture, and forest) in each 5-km grid cell (Homer et al., 2015). For developed, we combined open space with low, medium, and high-intensity developed categories. For agriculture, we combined pasture-hay and cultivated crop categories. For forest, we combined deciduous, evergreen, and mixed forest categories. To generate the developed, agriculture, and forest values for each mosquito trap observation, we assigned the proportion of each NLCD category to the 5-km grid cell where it occurred. We matched this process for each year NLCD was available because NLCD is released in multiyear increments (Appendix S1: Table S1). Values of the NLCD data were assigned to the mosquito trap data based on the year the traps were set and each year NLCD was available (Appendix S1: Table S2).

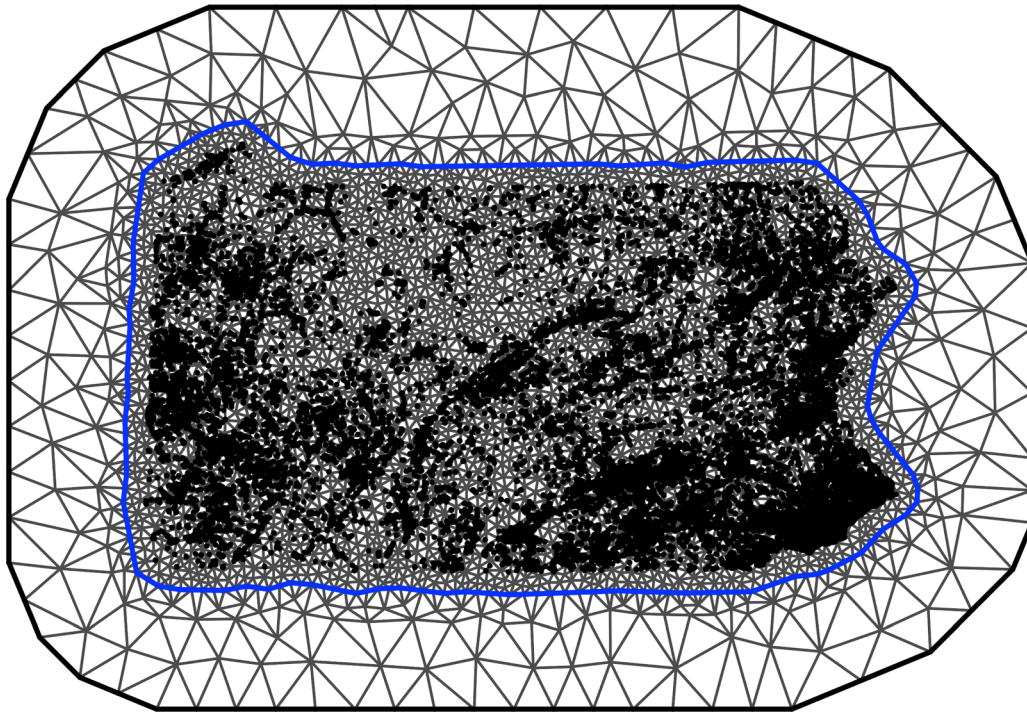
## Statistical analysis

We analyzed abundance data of *C. restuans* and *C. pipiens* using hierarchical Bayesian spatial models using stochastic partial differential equations (SPDEs) in the INLA in program R (Lindgren et al., 2011; R Core Team, 2021; R-INLA, 2021; Rue et al., 2009). The SPDE approach in R-INLA incorporates a Gaussian Markov random field, which consists of a numeric vector that links each observation to a spatial location (Krainski et al., 2019). When using SPDE in R-INLA, the spatial field for geostatistical data is described using a weighted sum of piecewise linear basis function that is usually defined across the study area, referred to as a mesh (Righetto et al., 2020). The mesh is made by a constrained

Delaunay triangulation effect and projects the spatial effect across the entire study area (Krainski et al., 2019).

To make the mesh (Figure 2), we used methods described by Krainski et al. (2019). We used the observations of the mosquito captures as an irregular boundary. For the inner triangle lengths of the mesh, which are the largest allowed triangle lengths (Krainski et al., 2019), we used the value of the prior that we used for the range of the spatial random field (Zuur et al., 2017), which we further describe below. To determine the cutoff points, which are the shortest distance allowed between the junctions of the triangle edges (Krainski et al., 2019), we divided the inner triangle lengths by five, to avoid many small triangles in clustered locations (Bakka, 2017). To avoid a boundary effect, we included an offset distance for the edge of the outer mesh, which was at least five times larger than the range (Bakka, 2017). To evaluate the mesh, we used the production of triangles that appeared regular in size and shape (Krainski et al., 2019). To avoid computational errors, increase the stability of the program, and reduce computational time when running the models, we corrected the Laplace method with variational Bayes by setting `inla.mode = "experimental"` (Gaedke-Merzhäuser et al., 2022; Van Niekerk et al., 2022; Van Niekerk & Rue, 2021).

Models were constructed a priori. To avoid collinearity between explanatory variables, the Pearson's correlation index and the variance inflation factor (VIF) were calculated prior to running the models. If pairs of variables had high correlation values (Pearson correlation  $r > 0.6$ ) or a high variance inflation (VIF  $> 5$ ), those variables were not modeled together. We made separate models for *C. restuans* and *C. pipiens* to model the response variable, which was the count of the number of mosquitoes trapped per site on a given day. The covariate Julian date was included in the model to account for seasonality. Julian date was modeled as a second-order random walk (rw2) latent model to account for a nonlinear relationship with the outcome. The variable year was included as a random effect. We initially fitted Poisson models to each dataset. If model validation indicated that this family of models could not account for the number of zeros, we used zero-inflated Poisson models. If the model needed to be corrected for under- or overdispersion, then we used negative binomial models. For each method used, we compared the deviance information criterion (DIC) values of the models and used the method with the lowest values, which is an indicator of model fit (Gelman et al., 2014). We then evaluated the models with and without the spatial effect and determined based on DIC whether accounting for spatial autocorrelation improved model fit.



**FIGURE 2** The mesh of the study area used in the integrated nested Laplace approximation (INLA) program in R to build the predictive models for *Culex restuans* and *Culex pipiens*. The black points are the trapping locations, and the blue line is the boundary of the study area as determined by the trapping locations. The mesh is extended beyond the study area to avoid a boundary effect in the calculations.

We used the default noninformative prior distributions in R-INLA for the fixed regression parameters and year hyperparameter. The default prior distribution for a fixed parameter in R-INLA is a normal distribution with mean 0 and precision 0.001, whereas the default prior for a hyperparameter has a gamma distribution and a value of 1 and 0.00001 for the shape and inverse scale parameters, respectively (Zuur et al., 2017). For Julian date and the spatial random field, we used penalized complexity priors. Penalized complexity priors have a single parameter that controls flexibility, reduces overfitting, and improves predictive performance by penalizing deviations from the base model (Moraga, 2019). These priors are specified by setting values in the following expression:

$$\text{Prob}(\sigma > u) = \alpha, \quad (1)$$

where  $u > 0$ , and  $0 < \alpha < 1$ . In the rw2 trend for Julian date, we used 0.01 for the value of  $u$  and 0.05 for the value of  $\alpha$ . For the range of the spatial random field, we used 10 km for the value of  $u$  and 0.05 for the value of  $\alpha$ . For the standard deviation (SD) of the spatial random field, we used a value of 2.0 for  $u$  and 0.05 for  $\alpha$ . We determined these values based on methods described by Zuur et al. (2017). Briefly, for Julian date, we selected a

value of  $u$  that made the trend with mosquito abundance smoother. For the range of the spatial random field, we selected a value based on the biology of the species, which included the maximum dispersal of *C. restuans* and *C. pipiens* (approximately 2.5 km) and the resolution at which the covariate data were generated (5 km). We chose a value for the SD of the spatial random field by applying a linear model to the log-transformed outcome of *C. restuans* or *C. pipiens* abundance and using the value of the residual standard error. This is the value expected if the covariates did not explain any variation in the response variable.

We computed the DIC, Watanabe–Akaike information criterion (WAIC), and conditional predictive ordinate (CPO) values and calculated the mean logarithmic CPO (LCPO) from the CPO values as described by Roos and Held (2011). The LCPO is a “leave one out” cross-validation index to assess the predictive power of the model (Gelman et al., 2014). We selected a top model for each species using the DIC and LCPO scores. Lower DIC and LCPO values suggest better model performance (Gelman et al., 2014; Gómez-Rubio, 2020). To evaluate model fit, we conducted a simulation study as described by Myer et al. (2020). For the top model of each mosquito vector species, we sampled 1000 simulated parameter sets of estimated mosquito counts from the posterior

distribution. We then plotted a histogram of the simulated results with 95% prediction intervals against the observed mosquito counts. If the observed counts were within the 95% prediction intervals of the simulated counts, we considered the model to have good prediction.

We generated predictive risk surfaces for each mosquito vector species by predicting the expected values at locations where data were not observed using the methods described by Krainski et al. (2019). Briefly, we made a prediction scenario for each species based on the corresponding top model, joined the prediction with the data in a stack, and fit the model again in R-INLA. For the prediction scenario, we extracted covariate values for each fixed effect from rasters with 5-km resolution. We made one raster for each fixed effect by averaging the daily rasters with 5-km resolution over the time lags used in the analysis for the trapping date of 15 June 2011. We selected this date because we suspected it would be representative of relatively high *C. restuans* and *C. pipiens* abundances throughout the entire study period. We then projected the summaries of the predicted posterior mean values, which we categorized into five quantiles, ranging from low to high mosquito abundance, onto a grid. All figures were generated in R.

## RESULTS

The number of *C. restuans* captured per trap was  $27.2 \pm 66.8$  (mean  $\pm$  SD) and ranged from 0 to 2246 mosquitoes. The number of *C. pipiens* captured per trap was  $12.7 \pm 40.0$  and ranged from 0 to 1460 mosquitoes caught. Zero *C. restuans* were reported in 21% of the traps, whereas zero *C. pipiens* were reported in 37% of the

traps. Forest was highly correlated with elevation and developed (Appendix S1: Table S3), so forest was not included in any models that contained elevation or developed. We used the negative binomial family to model the outcome of each mosquito species. Based on DIC and the model validation results for each mosquito species, the negative binomial models fit the data better compared to the Poisson and zero-inflated Poisson models (Appendix S1: Table S4). Inclusion of the spatial effect improved the model fit for each species based on DIC (Appendix S1: Table S4), so we included the effect in all of the models.

We found several of the independent variables to have statistically important relationships with the outcome, which is defined in Bayesian terms as having a 95% credible interval around the coefficient that does not include zero. In the most supported model for *C. restuans* (Appendix S1: Table S5), we found an important positive relationship between precipitation and *C. restuans* abundance and important negative relationships between *C. restuans* abundance and each of the temperature, developed, and elevation variables (Table 2; Appendix S1: Figure S1). The abundance of *C. restuans* in relation to Julian date showed a seasonal pattern, and abundance peaked in early June (Figure 3). In the most supported model for the abundance of *C. pipiens* (Appendix S1: Table S6), we found an important positive relationship between development and *C. pipiens* abundance and important negative relationships between *C. pipiens* abundance and each of the snow water equivalent and NDWI variables (Table 2; Appendix S1: Figure S2). The abundance of *C. pipiens* in relation to Julian date showed a seasonal pattern (Figure 3). In contrast to *C. restuans*, the abundance of *C. pipiens* peaked in mid-July

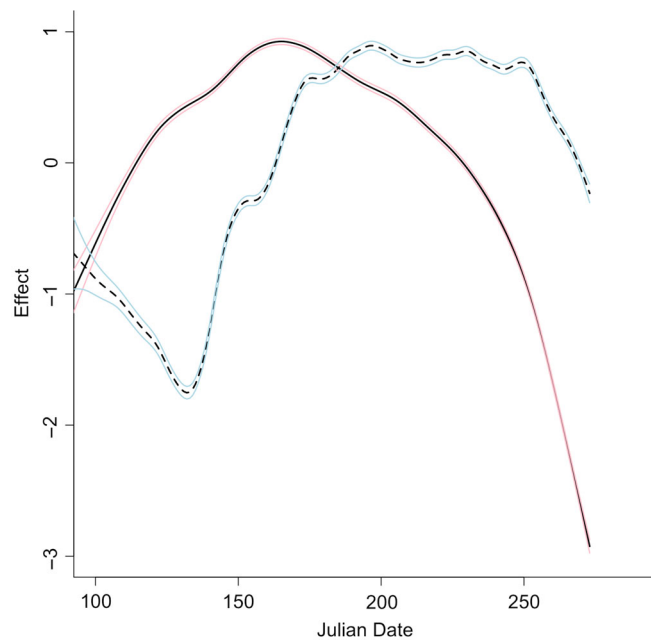
**TABLE 2** Numerical summary of the marginal posterior distribution of the fixed effects for the top R-INLA models for *Culex restuans* and *Culex pipiens*.

Species	Variable	Mean	SD	Median	Q <sub>0.025quant</sub>	Q <sub>0.975quant</sub>
<i>Culex restuans</i>	(Intercept)	2.965	0.086	2.965	2.797	3.133
	develop	−0.341	0.045	−0.341	−0.430	−0.253
	temp	−0.021	0.002	−0.021	−0.025	−0.018
	precip	0.061	0.002	0.061	0.056	0.066
	elev	−1.098	0.129	−1.098	−1.351	−0.844
<i>Culex pipiens</i>	(Intercept)	−0.538	0.128	−0.538	−0.788	−0.287
	develop	0.550	0.049	0.550	0.455	0.646
	snow	−0.004	0.000	−0.004	−0.005	−0.004
	NDWI	−1.002	0.058	−1.002	−1.115	−0.889

Note: For each variable the mean, SD, median, and 95% credible intervals ( $Q_{0.025} - Q_{0.975}$ ) are provided, containing 95% of the probability under the posterior distribution.

Abbreviations: develop, developed; elev, elevation; NDWI, normalized difference water index; precip, precipitation; quant, quantile; snow, snow water equivalent; temp, temperature.

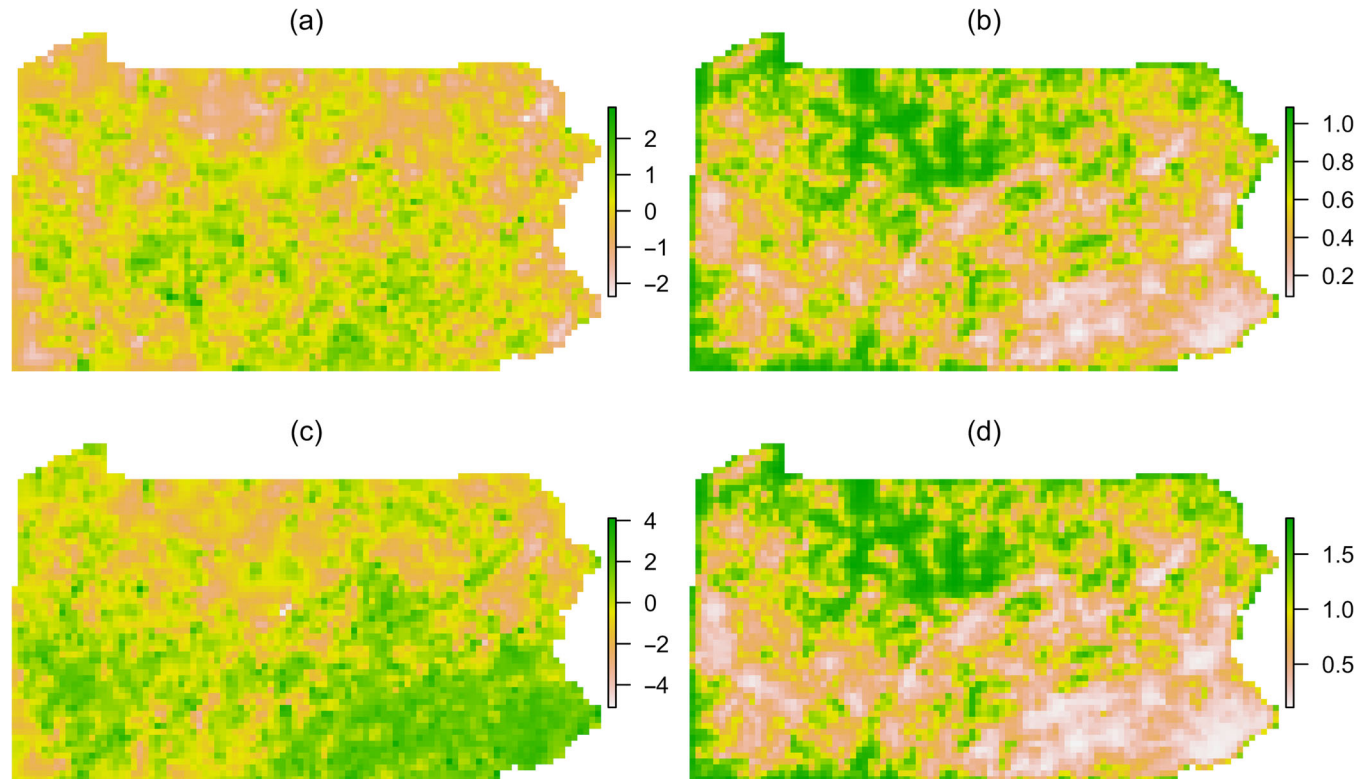




**FIGURE 3** The posterior means (solid black and dashed black lines) and 95% credibility intervals (solid pink and solid light blue lines) for the effect of Julian date on abundance of *Culex restuans* (solid black and solid pink lines) and *Culex pipiens* (dashed black and solid light blue lines) in Pennsylvania, plotted together.

(Figure 3). When plotted together, the abundance of *C. restuans* and *C. pipiens* shifted relative to one another on Julian date 185, 4 July (Figure 3). The relationship between mosquito abundance and each of the independent variables considered in the other models is included in Appendix S1: Table S7.

The posterior mean of the spatial effect represents the intrinsic spatial variability of the data after accounting for the covariates (Figure 4a,c). The positive values indicate areas where the spatial random effect causes an increase in the outcome, and negative values indicate areas where it causes a decrease (Zuur et al., 2017). If the value of the spatial random field is 0, then the spatial term has no effect (Zuur et al., 2017). The range of the spatial effect and 95% credible interval for *C. restuans* was 14.3 km (13.0–15.2) and for *C. pipiens* was 12.2 km (10.8–13.5). This indicates that for both mosquito species, traps located less than these ranges were spatially correlated. The mean and SD of the spatial random effect for both *C. restuans* and *C. pipiens* indicated that the spatial distribution of these two species was different and variable throughout the state (Figure 4a–d). Values of the SD of the spatial effect were high compared to the mean SD of the spatial effect for both *C. restuans* (mean SD of 0.6)



**FIGURE 4** For the top predictive model for the abundance of *Culex restuans* in Pennsylvania, the posterior mean of the spatial effect (a) and its SD (b). For the top predictive model for the abundance of *Culex pipiens* in Pennsylvania, the posterior mean of the spatial effect (c) and its SD (d).



and *C. pipiens* (mean SD of 1.0), which indicates a high degree of variation. The SD of the spatial effect for both *C. restuans* and *C. pipiens* was highest along the borders and in the north-central region of the state (Figure 4b,d).

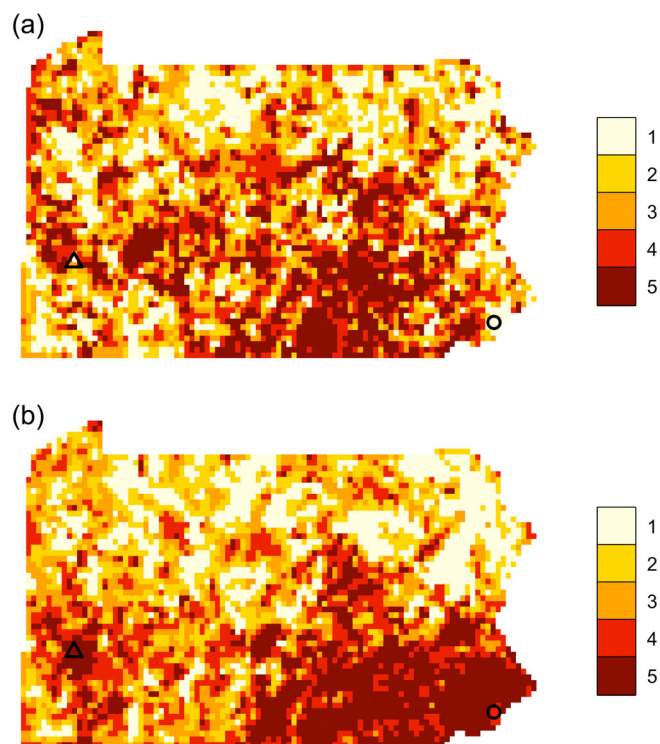
Based on the risk maps, *C. restuans* abundance was predicted to be low in Philadelphia and the surrounding area but high in only some areas around Pittsburgh (Figure 5a). In contrast, some of the highest predicted abundances of *C. pipiens* occurred in Philadelphia and Pittsburgh (Figure 5b), Pennsylvania's two largest cities. The abundance of *C. restuans* was predicted to be high in agricultural and rural areas of Pennsylvania, in contrast to the abundance of *C. pipiens*, which was predicted to be high in several urban areas with high population density and some areas with high levels of agriculture. The simulation histograms for *C. restuans* generated counts that were within the range of the observed number of mosquitoes for 0 counts adequately (Figure 6a). However, the simulated datasets overpredicted the number of mosquitoes at high counts and could not account for all the overdispersion of the original dataset. Similarly, the model for *C. pipiens* predicted the number of 0 counts adequately (Figure 6b), but overpredicted high counts of mosquito abundance and could not account for the

overdispersion in the original dataset. These results suggest that our model for *C. restuans* and *C. pipiens* likely overpredicted higher counts of mosquitoes.

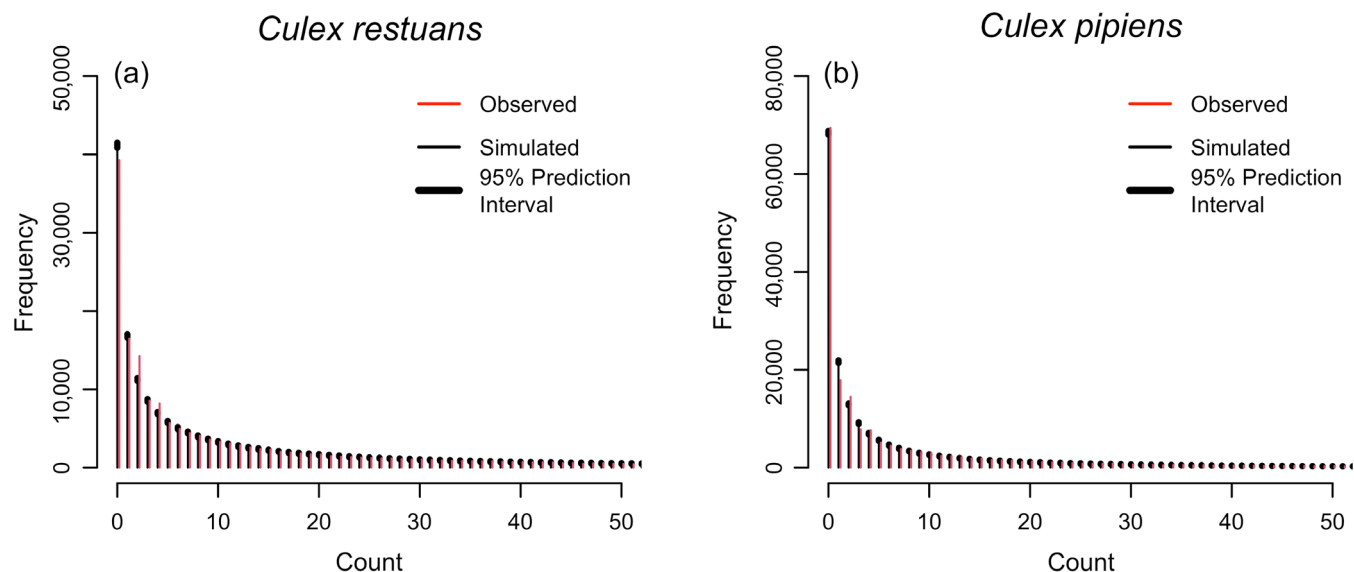
## DISCUSSION

Using recent advances in spatial statistical modeling, our results provide further understanding of the ecology and spatial distribution of abundance of *C. restuans* and *C. pipiens* in the northeastern United States. Several previous studies attempting to understand the ecology of mosquito vectors of WNV used nonspatial models at a county- or several-county extent to investigate the impact of ecological factors on mosquito occurrence or count data collected from mosquito surveillance efforts (Brown et al., 2008; Schurich et al., 2014; Tran et al., 2014). Not accounting for spatial autocorrelation violates the statistical assumption that observations are independent of one another (Bataineh et al., 2006). Inclusion of the spatial random effect improved our models based on DIC, which indicates that our data were spatially autocorrelated.

Eco-epidemiologically, the role of a mosquito species as a vector is defined by its vectorial capacity, which is measured by variables including adult female abundance, blood-feeding habits, adult survival, and intrinsic or genetic factors that influence the ability of the vector to transmit the pathogen (Rochlin et al., 2019). Transmission, surveillance, and control of vector-borne zoonoses depend on the ecology of arthropod vectors, on the environmental determinants of vector distribution, and on the ecology of reservoir hosts (Kitron, 1998). The distribution and abundance of most vectors of zoonoses are controlled by environmental determinants (Diuk-Wasser et al., 2006). Thus, the dynamics of the transmission of WNV are influenced by the abiotic and biotic processes that impact the survival and distribution of arthropod vectors (Diuk-Wasser et al., 2006). Understanding how environmental factors influence mosquito ecology and the risk of WNV is critical for the development of disease management strategies (Gardner et al., 2014). We found the abundance of *C. restuans* and *C. pipiens* to be associated with various ecological variables, including temperature, precipitation, and developed habitat, which is consistent with previous research (Ciota et al., 2014; Johnson et al., 2015; Yu et al., 2018). Our results are also consistent with population abundance models developed for these species, which indicate that mosquito population dynamics are highly dependent on temperature, but that precipitation and habitat should be considered as well (Yu et al., 2018). However, it is difficult to make direct comparisons with the results from previous studies that did not distinguish between



**FIGURE 5** Risk map of the predicted mean abundance, categorized into five quantiles (1, low; 2, low-medium; 3, medium; 4, medium-high; 5, high) of *Culex restuans* (a) and *Culex pipiens* (b) throughout Pennsylvania for 15 June 2011. The black outline of the circle shows the location of Philadelphia, and the black outline of the triangle shows the location of Pittsburgh.



**FIGURE 6** Simulation study results of the first 50 mosquito counts of 1000 simulated datasets from 1000 posterior samples for the top predictive model of *Culex restuans* (a) and *Culex pipiens* (b).

*C. restuans* and *C. pipiens* (Moua et al., 2021; Wang et al., 2011; Yu et al., 2018).

In the top predictive model for *C. restuans* and *C. pipiens*, we found abundance to be associated with different ecological variables, which supports previous suggestions that the ecology of these species is different and that these two mosquito vectors may subsequently play different roles in the epidemiology of WNV. The associations we found between the abundance of each of these vectors of WNV and land cover variables further support that *C. pipiens* is the predominant species in heavily urbanized environments in large cities (Becker et al., 2014) in contrast to *C. restuans*, which is more associated with rural, suburban sites, and less developed sites (Gardner et al., 2013; Johnson et al., 2015). The pattern of seasonal abundance we observed for *C. restuans* and *C. pipiens* was consistent with what has been reported in the literature in the northeast and north-central United States (Helbing et al., 2015; Kunkel et al., 2006). Where these species overlap, *C. restuans* were dominant in spring and early summer, whereas *C. pipiens* dominated by midsummer (Johnson et al., 2015; Kunkel et al., 2006; Lee & Rowley, 2000). This transition is termed the “*Culex* crossover” and is important in the epidemiology of WNV because large populations of *C. restuans* that reside on the interface between natural and anthropogenic environments may carry WNV between these habitats, which may lead to the virus being co-amplified by *C. pipiens* (Johnson et al., 2015). *Culex* crossovers have been found to be associated with increased WNV activity and intensity in humans (Kunkel et al., 2006; Lampman et al., 2006; Tokarz & Smith, 2020). The timing and duration of the crossovers are influenced by ambient

temperature and can vary, but typically occur in July (Lampman et al., 2006). The mean crossover day for *C. pipiens* and *C. restuans* in Ohio, which is located in the north-central United States, was on Julian day  $175 \pm 21$  (24 June; Helbing et al., 2015). This is consistent with the date of the *Culex* crossover we observed in our study (Julian day 185, 4 July) in the northeastern United States. Similar to our study, local populations of *C. restuans* in Ohio peaked in June and gradually declined through the rest of the season, whereas *C. pipiens* were most abundant in July and August (Helbing et al., 2015).

Precipitation may have been an important predictor variable for the abundance of *C. restuans* because rainfall is important in creating and maintaining surface water habitats for mosquitoes to lay their eggs and for larvae to develop (Gardner et al., 2012). In contrast, snow water equivalent and NDWI may have been the most important predictors for the abundance of *C. pipiens* due to direct negative impacts of flooding on mosquito larvae production in urban areas. For example, heavy rainfall can decrease mosquito abundance by flooding larval habitat (Epstein & Defilippo, 2001) and also prevent adult mosquitoes from laying egg rafts until the flow of the water slows (Gardner et al., 2012). The negative relationship observed between the abundance of *C. restuans* and temperature is consistent with other research in a laboratory setting where *C. restuans* were more negatively affected by temperature increases compared to other *Culex* species (Ciota et al., 2014). With each incremental temperature increase, *C. restuans* exhibited significant increases in adult and immature mortality compared to populations of *C. pipiens* (Ciota et al., 2014).

The ecological variables driving the inverse relationship between *C. restuans* abundance and elevation is unclear. Sites higher in elevation in Pennsylvania tend to have cooler temperatures, less urban habitat, and more forested habitat than sites at lower elevations. It is possible that the lower abundances at higher elevations were influenced by the lack of anthropogenic breeding habitats, including highly polluted waters with high organic concentration found at sewage treatment plants and farms (Andreadis et al., 2001) and artificial containers such as storm drains, buckets, and tires (Geery & Holub, 1989). It is also unclear if our results are indicative of *C. restuans* populations in heavily forested areas at higher elevations since these habitats were not sampled as frequently. Johnson et al. (2015) found *Culex* cross-overs of these species to only occur in urban sites sampled and to be absent in forested freshwater wetland areas, where *C. restuans* were found in high abundance. Our results indicated a seasonal *Culex* crossover. Thus, our predictions of *C. restuans* in heavily forested sites, such as in state forests, where habitat conditions for *C. pipiens* are less favorable, should be further validated.

Human risk from mosquito-borne pathogens relies primarily on mosquito surveillance data, which includes vector distribution, abundance, and the prevalence of the pathogen in infected mosquitoes (Diuk-Wasser et al., 2006). The risk of transmission of WNV to humans is strongly correlated with the density of infected vector mosquitoes in a given area (Colborn et al., 2013; Kilpatrick & Pape, 2013). Thus, determining the relationship between ecological predictors and the abundance of vectors of WNV allows for human risk of exposure to be measured on a spatial scale. The spatial risk maps we made for *C. restuans* and *C. pipiens* from the top models could be used to target areas for additional mosquito surveillance of WNV and to identify areas where additional sampling is needed. The SDs of the predictive maps appeared to be the highest in the regions that had fewer placement of traps, so these areas could be targeted for future surveillance efforts if more accurate estimates are needed in these areas.

Several statistical and mathematical models of WNV were recently reviewed for their application to local public health decision-making, and the greatest need was for planning models to be fine-grained (meters–kilometers) and short-term (days–weeks) (Keyel et al., 2021). The scope of this study was to make one risk map of each species at a fine scale that represented an average of mosquito abundance over several years that could be used to inform WNV risk at locations with no samples. However, if short-term predictions are needed for public health planning to target areas for mosquito control, it is possible to incorporate a spatial-temporal component into R-INLA

with the SPDE approach to make fine-grained and short-term models.

Bayesian software is necessary to account for spatial autocorrelation and pseudoreplication in ecological datasets because frequentist software tools are limited (Zuur et al., 2017). Traditionally, Bayesian methods of inference and prediction in spatial models used Markov Chain Monte Carlo (MCMC) algorithms (Gilks et al., 1996). Limitations of using these methods were that they were computationally demanding and unsuitable for large datasets (Blangiardo & Cameletti, 2015). As an alternative to MCMC, Rue et al. (2009) developed INLA (Krainski et al., 2019), which were more computationally efficient (Lindgren & Rue, 2015; Rue et al., 2009). To further decrease computation time, a SPDE solution was developed, which was much simpler to compute and can be used in combination with INLA to model the spatial variation (Lindgren et al., 2011; Simpson et al., 2012). INLA models with the SPDE approach have been previously used to investigate the spatiotemporal epidemiology of WNV from mosquito surveillance data at fine scales and small spatial extents in two counties in New York (Myer et al., 2017; Myer & Johnston, 2019). Our results demonstrate how this modeling approach can also be used for large statewide datasets to predict and map mosquito abundance at fine resolutions and large spatial extents. The models may have overpredicted high counts of mosquitoes for both species and may not have been able to account for overdispersion of the data due to our inability to account for other variables that may have affected population dynamics and capture rates at local scales, such as wind speed at the trap site and microhabitats used for breeding. Although bias may have been introduced from unequal sampling of sites across the state within and between years, Yoo et al. (2016) found that the abundance of *C. pipiens* predicted from mosquito surveillance data in the province of Ontario, Canada, was not always influenced by the intensity of surveillance efforts.

## CONCLUSIONS

Using mosquito surveillance data collected over nearly two decades, we developed spatial models of *C. restuans* and *C. pipiens* abundance in relation to several ecological predictors, including meteorological and landcover variables, at a statewide extent. We found that analyzing *C. restuans* and *C. pipiens* separately allowed for further understanding of the spatial distribution and ecology of these species in regions where they coexist. Eco-epidemiologically, vector abundance is related to the risk of transmission of WNV to humans and susceptible



animal populations. Developing spatial risk maps of vector abundance can help understand the ecology and epidemiology of WNV and help visualize mosquito abundance at locations that were not sampled. The risk maps can also be used to identify areas in need of additional surveillance or to help target outreach programs. Several knowledge gaps in mosquito ecology and epidemiology of vector-borne diseases could be better understood by using Bayesian hierarchical models that include spatial and/or temporal random effects. To model the spatial distribution of mosquito vectors or the epidemiology of WNV, R-INLA with the SPDE approach is a useful tool because it has fast computational speed, which is essential for large datasets, and also has capabilities of modeling data at fine scales and over large extents.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Pennsylvania Department of Environmental Protection, 2020) are available under “Mosquito Testing Data” from the Pennsylvania Department of Environmental Protection: <https://gis.dep.pa.gov/WNV/index.html>. The code used in the modeling (Bondo et al., 2022) is available from GitLab: <https://doi.org/10.5066/P9QAB3ZZ>.

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