Predicting West Nile virus transmission in North American bird communities using phylogenetic mixed effects models and eBird citizen science data

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Text S1. Methods: community resampling

Here we present the results of our simulated resampling of the best sampled bird communities in Texas, USA in the eBird database (communities with greater than 1,300 complete lists). We resampled 5-120 complete lists from the 46 most sampled communities 100 times. From these results we determined, subjectively, that with fewer than 80 complete lists, the gain in total number of communities was not worth the increased error rate and loss of species representation; at greater than 80 complete lists the loss in communities was too large for the small decrease in error and small gain in species.
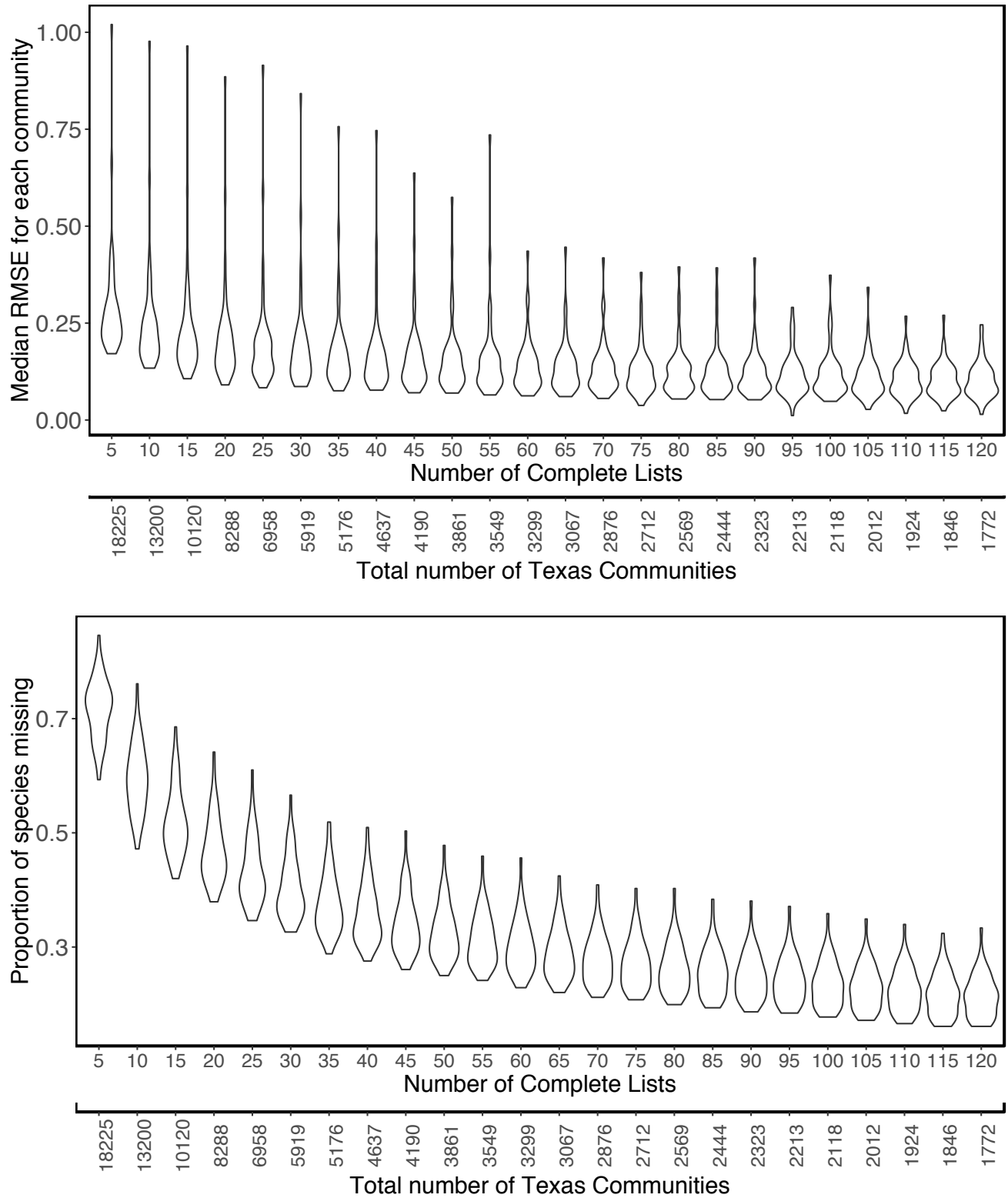
Figure S1. Result from 100 subsamples from each of the 46 communities with greater than 1,300 complete lists. Violin plots show distribution of medians across the 46 communities from the 100 resampling events. The top panel shows the RMSE between the relative proportions of all birds in the complete communities and subsampled communities as a function of the number of lists subsampled. The secondary axis shows the number of communities that would be left in the Texas dataset if the corresponding number of lists were used as a cutoff to define a well sampled community.
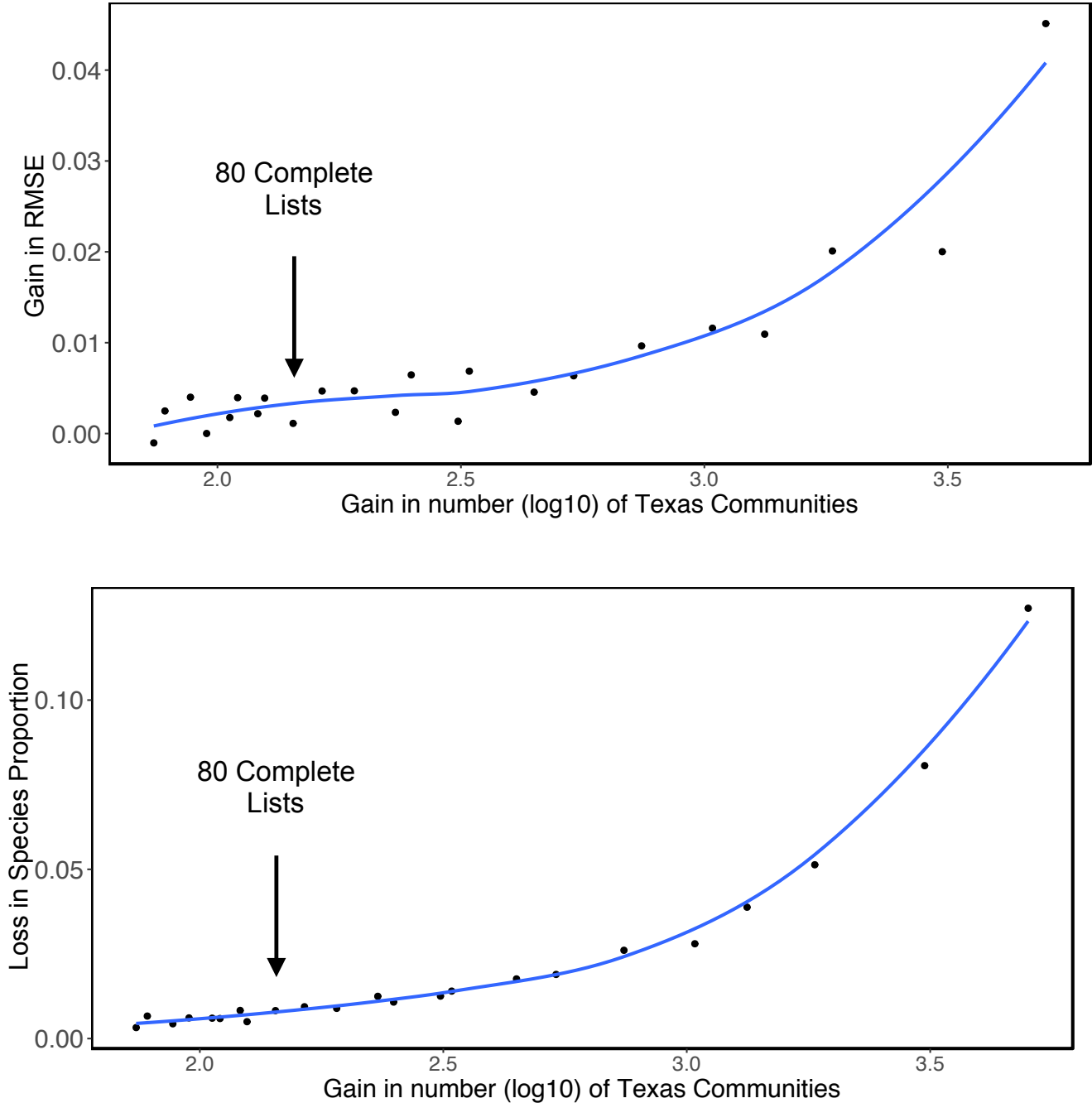
Figure S2. A second depiction of results from 100 subsamples from each of the 46 communities with greater than 1,300 complete lists. Top and bottom panels shows how much RMSE is gained, or the additional proportion of species that are lost, respectively, with an increase in retained Texas communities (which are gained when fewer complete lists are used as a cutoff to define a well sampled community, see Figure S1). Points in both panels show overall medians across all communities and 100 resampling events. Blue lines are smooths showing approximate slope. 80 complete lists resides at approximately the beginning of the accelerating portion of this curve, though our overall choice of 80 communities is fundamentally a qualitative and not quantitative decision.

Sampling region for the mosquito biting preferences model

Figure S3 shows the eBird sampling region used to inform our prior in the Bayesian component of the mosquito biting preference model.
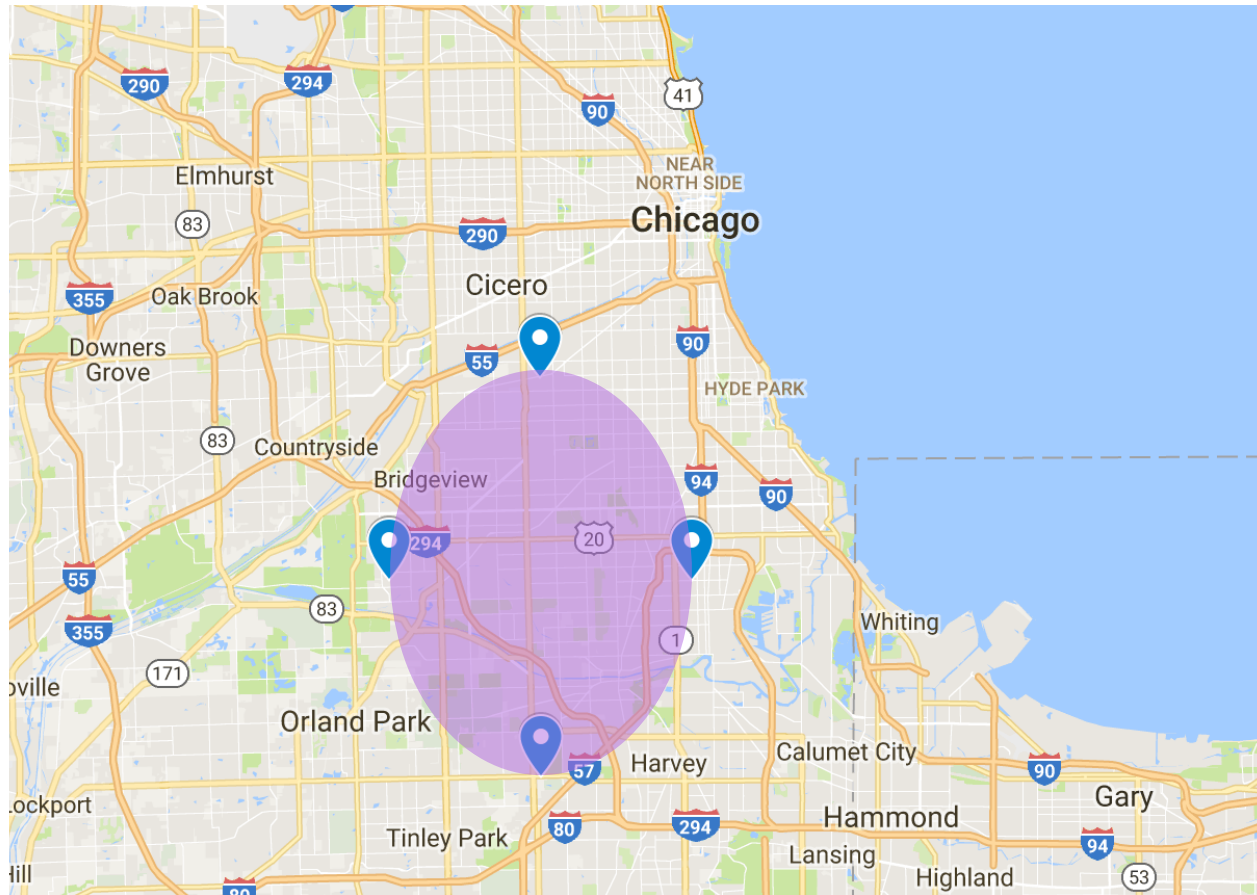

Figure S3. Delineation of the area where eBird lists were used as prior information for the bird community sampled in [1]. The center of this region was given as the location of the sampling conducted in [1]. The entire area is contained within Cook County, IL and is composed primarily of suburban Chicago, IL.

Text S2. Methods: phylogenetic mixed effects model validation

We present results for R^2 and blocked leave-one-out cross validation in Table S1. We calculated conditional R^2 (which measures the variance explained by both fixed and random factors; see [2, 3, 4]) for our phylogenetic mixed models using slightly modified code from R package MuMIn [5]). For blocked leave-one-out cross validation we left out all data for a single species at a time, refit our model with and without the species level phylogenetic random effect, and calculated goodness of fit of predicted values to the left out bird species' data for each model. For models with a normal or Poisson error distribution we use scaled root mean squared error (RMSE) between predicted values and the data with the following formula:

$$\frac{\sqrt{\frac{1}{n}\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}}{\bar{y}}. \tag{1}$$

For predicting responses using the titer model we use mean log dose across all infection experiments (which decreases fit to individual infection experiments, inflating RMSE slightly). For the binomial model (bird survival), we use area under the curve (AUC), calculated using the observed number of birds that died and did not die on each day and the estimated probabilities for each of these outcomes. Set up in this way, larger AUC values mean a better fit between the predicted values and the empirical data. AUC cannot be calculated for scenarios in which no birds died; in our calculation we ignore experiments in which no individual birds died. To calculate AUC we used the R package MESS [6]. Table S1 shows mean RMSE across all species for each method.

Despite an established method for calculating R^2 for mixed effects models [2, 3, 4], R^2 can be difficult to interpret for these models. Additionally, by convention, the biting preference model without the phylogenetic random effect (an intercept only model) has an $R^2 = 0$, which makes the ratio of R^2 values for this model difficult to interpret. The important point is that R^2 increases (in many cases greatly) for all four of our models when the species level phylogenetic random effect is included (Table S1).

The inclusion of a species level phylogenetic random effect increases the ability of three of four models to predict left-out species' responses (Table S1). For the survival model, AUC values are small overall because most bird species survive with high probability; it is difficult to predict the rare case of individual birds dying. AUC increases when a phylogenetic random effect is included in the survival model because this model is better able to predict the mortality of species that die with a higher frequency than the average species. For the biting preference model, the phylogenetic random effect marginally increases RMSE (Table S1); this may be due to minor overfitting.

Table S1. Phylogenetic mixed effects model validation. We use RMSE to quantify leave-one-out cross validation error for titer, biting preference, and detectability models, and AUC to quantify error for the survival model.

	Model							
	Titer		**Survival**		**Biting preference**		**Detectability**	
Phylogenetic random effect included?	No	Yes	No	Yes	No	Yes	No	Yes
Conditional R^2	0.65	0.93	0.805	0.898	0.00	0.97	0.51	0.92
Leave-one-out goodness of fit estimate	0.48	0.41	0.01	0.03	0.23	0.30	0.25	0.18

Text S3. Methods: Ricker function

The Ricker function:

$$y = axe^{-bx} \tag{2}$$

is a hump-shaped curve that is commonly used for modeling right-skewed patterns in ecology [7] such as density dependence (e.g. [8]). When $a = 1$ this function is a Ricker function; when $a \neq 0$ this function is a Generalized Ricker. We use a Generalized Ricker function to model patterns in titer in birds, where x is given by day. Using log(titer) as our response variable, we estimate the a and b parameters in the Generalized Ricker function using a linear model with the form log(titer) $\sim$ day + log(day).

Text S4. Results: community $\mathcal{R}_0$

Complete eBird Dataset

Estimates for WNV $\mathcal{R}_0$ using the complete eBird dataset were more variable, but had similar monthly medians to the well sampled eBird dataset in most months (Figure S4, Figure S5).

The spatio-temporal GAM model explained 97% of the variation in WNV $\mathcal{R}_0$. WNV $\mathcal{R}_0$ was once again found to be driven mostly by temperature, and vary little across human population density and years. With the full dataset, bird communities most favorable for WNV transmission were once again estimated to be in the "Llano Uplift" ecoregion, while the least competent bird communities were estimated to be in the "High Plains" and "Oak Woods & Prairies" ecoregions. Overall $\mathcal{R}_0$ was estimated to be the highest in the "Piney Woods" and "Oak Woods & Prairies" (favorable temperature in the "Oak Woods & Prairies" has a much larger effect than the unfavorable bird communities in this region), and the lowest in the "High Plains".
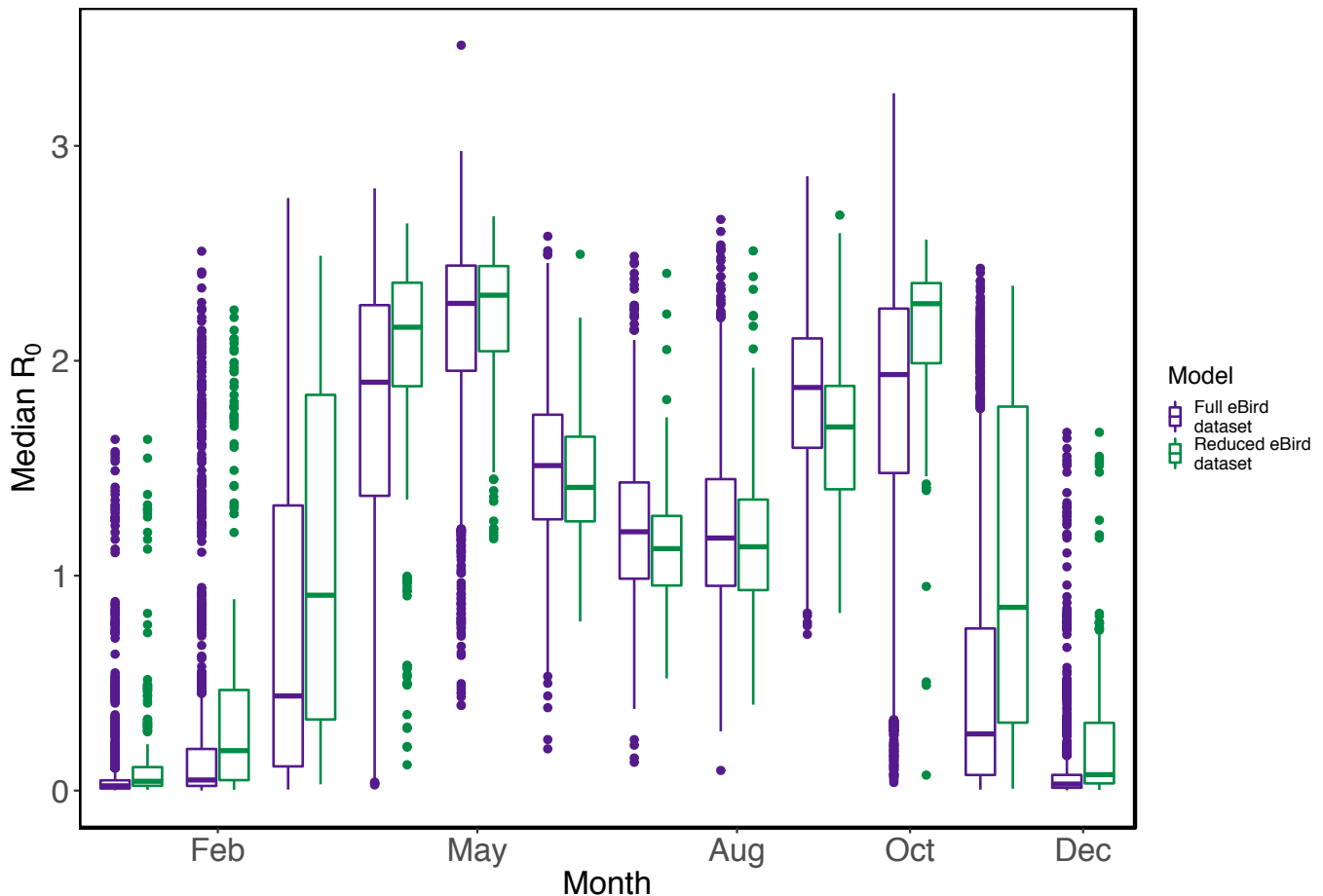

Figure S4. A comparison of $\mathcal{R}_0$ estimates. Purple and green boxplots show $\mathcal{R}_0$ estimates from models fit to the full and reduced eBird datasets respectively.
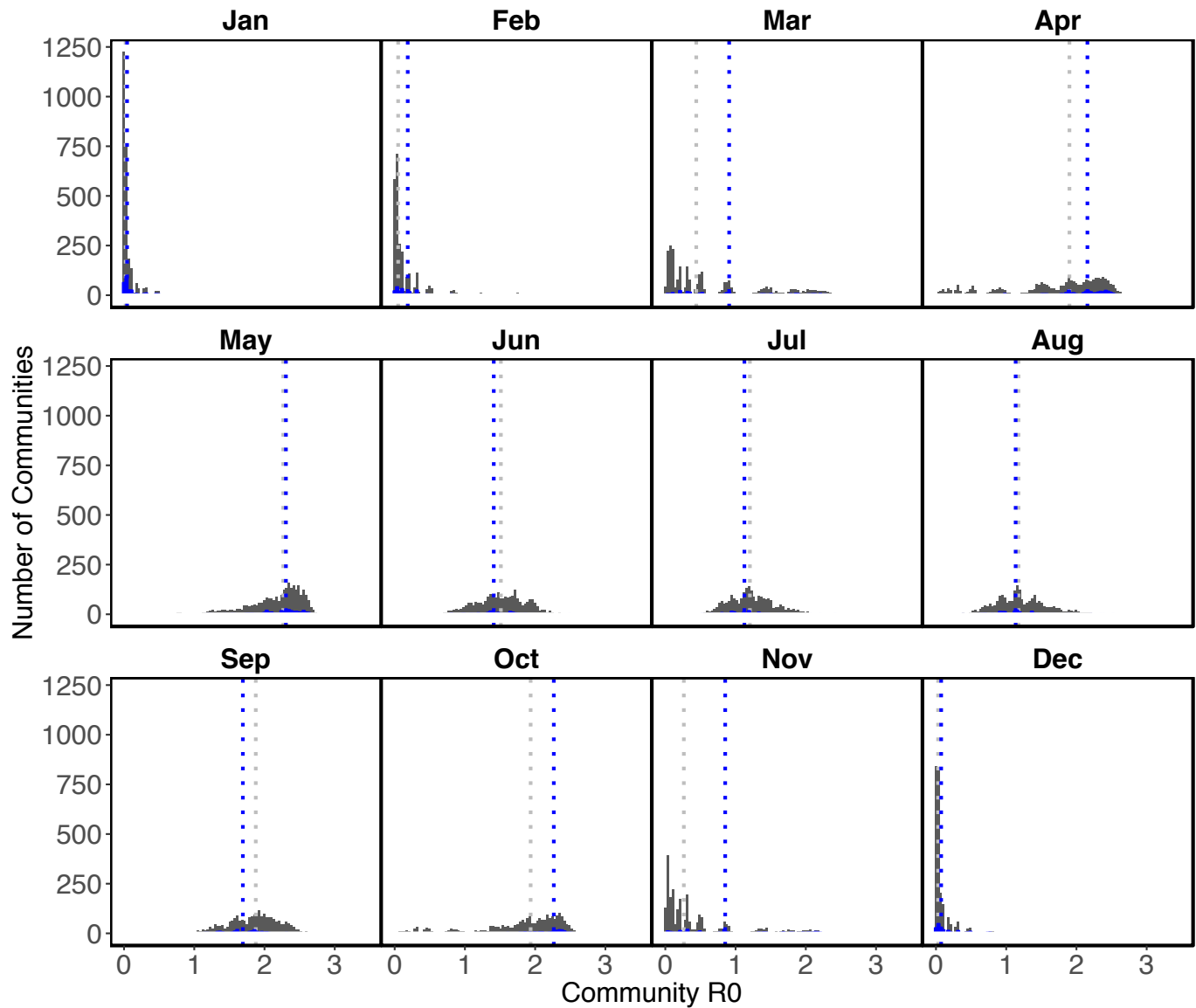
Figure S5. A comparison of $\mathcal{R}_0$ estimates. The gray histograms shows estimates for the full ebird data set and the blue histograms shows estimates for the reduced eBird data set by month. The vertical dotted gray and blue lines show the medians of the distributions.

No uncertainty propagated: reduced eBird Dataset

Estimates for WNV $\mathcal{R}_0$ when propagating no uncertainty were more variable than when all uncertainty was propagated (Figure S6 vs main text Figure 1). No uncertainty propagation increased the impact of variation in the bird community on variation in $\mathcal{R}_0$ estimates within months (Figure S6).
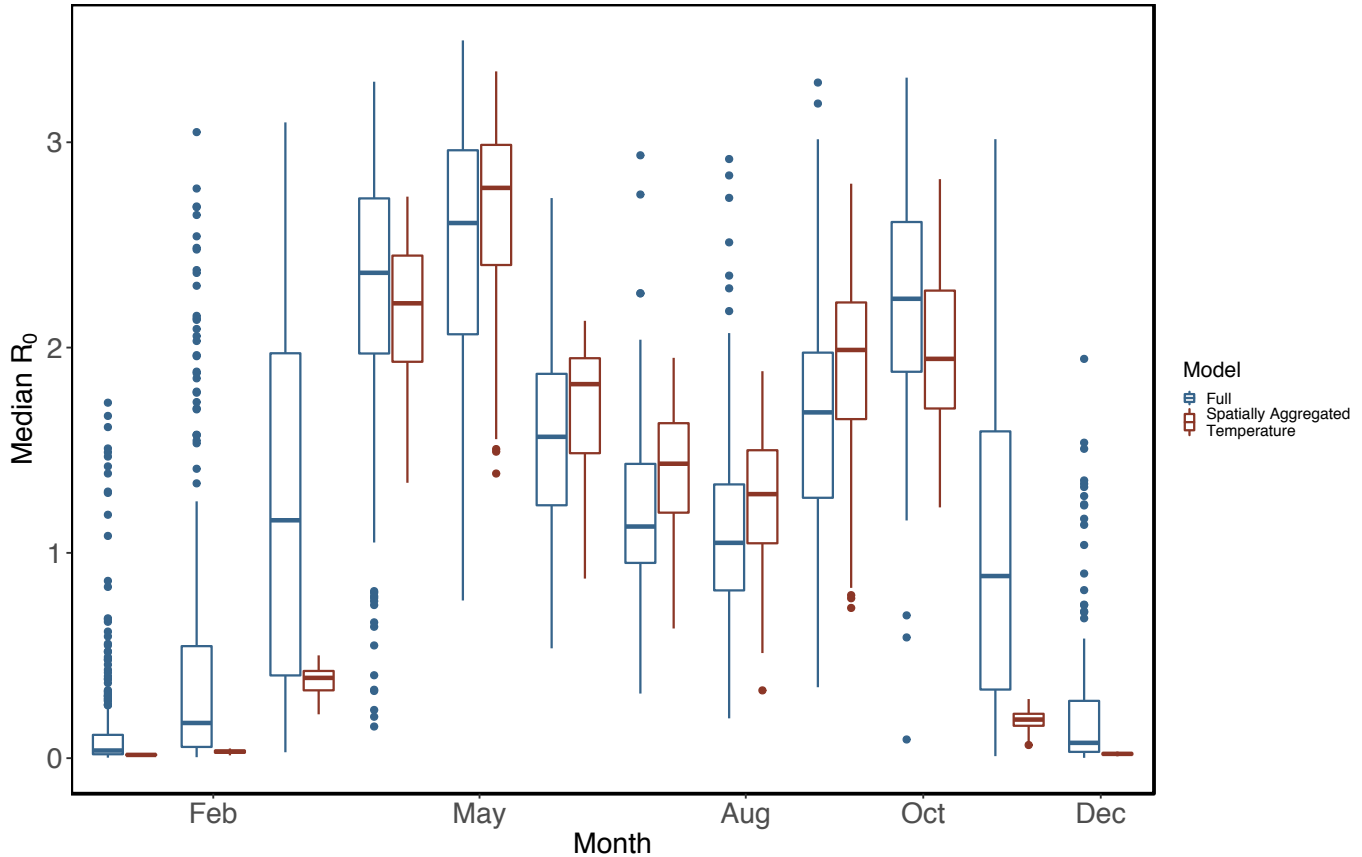

Figure S6. WNV $\mathcal{R}_0$ estimates between months and among Texas counties when no uncertainty is propagated. Blue boxplots show $\mathcal{R}_0$ estimates across Texas counties within months for a "Full" model, which used the eBird community and NOAA temperature data for each community. Red boxplots show $\mathcal{R}_0$ estimates from a model where each community retained their specific eBird community, but whose temperature was replaced with average temperature over all of Texas for that month. With no uncertainty propagated, variation in $\mathcal{R}_0$ within months attributable to variation in the bird communities (red boxplots) is much larger than when all uncertainty is propagated (see main text Figure 1). The increase in variation explained by the bird community is due to the translation of titer into bird-to-mosquito transmission probability, which has a maximum of one (see main text: Discussion for a full description of this phenomenon). Increases or decreases in medians between the models within months is due to the effects of averaging temperature prior to predicting $\mathcal{R}_0$ using the nonlinear functions for mosquito-to-bird transmission and mosquito survival across temperature.

Seasonally variable mosquito-to-bird ratio

Estimates for WNV $\mathcal{R}_0$ with seasonally vairable mosquito-to-bird ratio are shown in Figure S7. With strong seasonal variation in mosquito-to-bird ratio that follows either a sinusoidal function or a Gaussian function with peaks in July or August respectively, estimates for $\mathcal{R}_0$ are lower in the spring months, and lower overall than the estimates we obtain using our full model.
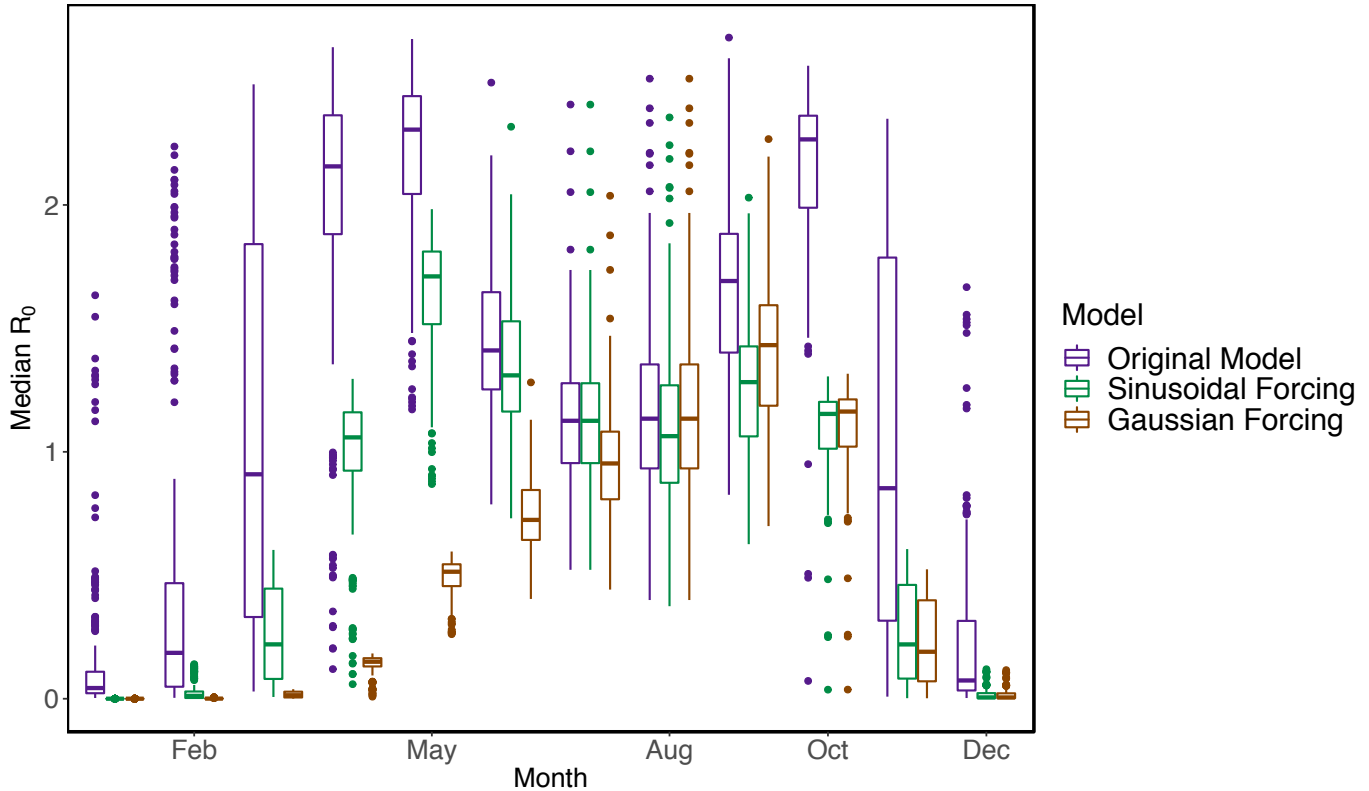

Figure S7. WNV $\mathcal{R}_0$ estimates between months and among Texas counties. Purple boxplots show $\mathcal{R}_0$ estimates across Texas counties within months for our full model, which used the eBird community and NOAA temperature data for each community, but assumes a constant mosquito-to-bird ratio across space and time. Green boxplots use the same model but assume that mosquito-to-bird ratio follows a cyclic sinusoidal function with a peak in mid July and a trough in mid February. Orange boxplots use the same model but assume that mosquito-to-bird ratio follows a Gaussian function with a peak in August. Given these hypothetical seasonal patterns in mosquito-to-bird ratio, assuming a constant mosquito-to-bird ratio (purple boxplots) results in higher $\mathcal{R}_0$ estimates in every month.

Single sources of uncertainty: reduced eBird Dataset
For each model and for most sources of uncertainty, using point estimates for a single parameter decreases the CV of $\mathcal{R}_0$ and increases the amount of variance explained in the spatio-temporal model. However, for the titer model, ignoring uncertainty in fixed effects increases the CV because of a smaller decrease in standard deviation than in the mean. In the titer model, ignoring uncertainty in the amount of evolutionary change along the most recent branch in time leading to species i results in the largest change in the CV of $\mathcal{R}_0$ for any source of uncertainty for any model, regardless of direction: a median of a 1.3 fold increase in the CV of $\mathcal{R}_0$.

Text S5. Results: species-specific contributions to $\mathcal{R}_0$

Complete eBird Dataset

Here we present which species have the largest impact on $\mathcal{R}_0$ when they are removed from each of the 30,188 communities that they occupy, which gives a distribution of effects across communities. Northern cardinals were estimated to have a median effect on $\mathcal{R}_0$ similar in magnitude to their effect in the reduced dataset, but with a larger range of effects (recorded in 68% of the bird communities in the full dataset; median: 0.91 fold decrease in $\mathcal{R}_0$, 0.76-0.99 in 95% of communities). Jay species appear as the most impactful amplifiers in the full dataset as well. As in the reduced data set, Mourning doves (*Zenaida macroura*, recorded in 78% of the bird communities in the full dataset) accounted for the largest median dilution effect, but with an increased range of effect sizes (median: 1.05 fold increase in $\mathcal{R}_0$, 1.01-1.30 in 95% of communities). Again, only 2 species (Mourning doves: *Zenaida macroura* and White-winged doves: *Zenaida asiatica*) had a median dilution effect greater than a 1.01 fold increase in $\mathcal{R}_0$.

These analyses also provide a clear example of the type of problems that arise when using undersampled bird communities. In November of 2004 in Lamb county, a single complete list was submitted with two species, Sharp-tailed sandpiper (*Calidris acuminata*) and Ring-necked pheasant (*Phasianus colchicus*). Sharp-tailed sandpipers are estimated to be moderately competent hosts, while Ring-necked pheasants are estimated to be very poor hosts. This is the only "community" in which Sharp-tailed sandpipers were recorded in all of Texas. Sharp-tailed sandpipers were estimated to have a dilution effect of 0.29, which is implausible given the magnitude of the effects we estimate for the most important amplifier and diluter species.

Text S6. data citations

Laboratory infections of birds: [9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38]

Laboratory infections of mosquitoes: bird-to-mosquito and mosquito-to-bird transmission: [35, 37, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69]

Bird detectability: [70, 71, 72, 73], and [74, 75, 76, 77, 78, 79, 80] (cited in [81])

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