

# Ecological determinants of American crow mortality due to West Nile virus during its North American sweep

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**Abstract** We examined the ecological factors influencing population declines in American crows (*Corvus brachyrhynchos*) as they were initially exposed to West Nile virus (WNV), a pathogen first detected in the US in 1999 that has since become one of North America's most prevalent vector-borne pathogens. The strongest effects were initial crow population density (denser populations were more likely to suffer declines), avian species diversity (populations in areas with high diversity were less likely to suffer a decline), human population density (populations were more likely to decline in more urban areas), and time since the pathogen's introduction to the US (populations exposed to the pathogen later in its North American sweep were less likely to suffer declines than those exposed earlier). Variables that played only a minor role included rainfall, mean maximum temperature, and total number of birds, used as a proxy for the overall reservoir competence of the community. These findings indicate that WNV declined in virulence during its rapid 5-year sweep and support the importance of the 'dilution effect' whereby a diverse host community dampens pathogen transmission and potentially slows its rate of spread. Results underscore the need for considering the entire community when trying to understand the factors shaping disease risk.

**Keywords** American crows · Dilution effect · Disease ecology · Emerging infectious diseases · West Nile virus

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## Introduction

West Nile virus (WNV) is a mosquito-vectorized pathogen whose primary vertebrate reservoir is birds. However, it infects scores of species from alligators (*Alligator mississippiensis*) to horses (*Equus caballus*) (Komar 2003) and, like many other infectious diseases, can be transmitted via its arthropod vectors to humans. This has made WNV a serious health issue, having infected over 27,000 people and caused over 1,000 human fatalities since its introduction in New York City in 1999 (CDC 2008). Because of its rapid spread and wide range of hosts, WNV has become a model system for understanding the ecological factors influencing the virulence of zoonotic diseases (Ezenwa et al. 2006; Kilpatrick et al. 2007; Allan et al. 2009; Lloyd-Smith et al. 2009).

There are at least six sets of factors that may potentially influence the degree to which WNV negatively affects populations of its hosts. First are environmental variables such as temperature and rainfall, both of which may alter the abundance of its mosquito vectors. Although the relationships between environmental factors and mosquito abundance are not necessarily simple, a priori we can expect that the effects of WNV should be more severe in warmer and wetter areas than in drier, cooler sites (Landesman et al. 2007; Soverow et al. 2009). Second is human population density or the degree of urbanization, which has been shown to positively correlate with exposure of passerine birds to WNV (Bradley et al. 2008) as well as the incidence of WNV among humans in the St. Louis region (Allan et al. 2009), most likely either because of differences in avian community composition between urban and rural areas or because of more favorable habitat for mosquitoes in urban environments.

The third factor is host density, which is expected to correlate positively with mortality rates (Begon 2008).

Although such density-dependent effects are widespread, a complication in the case of WNV is the huge range of hosts: within any one host species, it is not obvious whether to expect mortality to be related to density of the host itself or to the density of all potential hosts combined.

Fourth is the temporal pattern of pathogen spread; that is, whether mortality increased or decreased as WNV made its North American sweep. In general, a virulence/transmission rate trade-off is expected that will result in decreased virulence through time (Bull 1994; Galvani 2003). However, in the case of WNV, the wide range of potential hosts ensures substantial differences in host community composition as the pathogen enters a new area, a situation that may reduce or even eliminate the virulence/transmission rate trade-off, particularly when transmission is primarily horizontal (i.e., not from parent to offspring), as is the case for WNV (Ganusov et al. 2002). Thus, whether WNV is expected to increase or decrease in virulence through time is unclear.

Fifth is the overall reservoir competence of the avian community, defined as the probability that an infected host will transmit an infection of the pathogen to a feeding vector. This is a particularly difficult variable to estimate, since it requires not only knowledge of community composition but estimates of reservoir competence for all members of the community (Allan et al. 2009). Such data are only incompletely available, making the use of a proxy such as the total number of hosts necessary. In any case, the adverse effects of WNV are expected to increase as the overall reservoir competence of the community increases.

Last but not least, avian community diversity may either dampen pathogen spread and reduce mortality through the ‘dilution effect’ (Ostfeld and Keesing 2000a, b; Schmidt and Ostfeld 2001; LoGiudice et al. 2003; Keesing et al. 2006; Ezenwa et al. 2006; Begon 2008; Allan et al. 2009) or increase mortality through an ‘amplification effect’ (Keesing et al. 2006). Which of these opposite effects is expected in complex multi-host systems such as WNV depends on several factors, perhaps most importantly the distribution of highly disease-competent species in the avian community (Keesing et al. 2006). In systems where increased species diversity dampens pathogen spread and the dilution effect is present, the effect may occur due to any of several potential mechanisms, including reduced encounter rate between susceptible and infectious individuals, reduced probability of transmission given an encounter, decreased density of susceptible individuals, or increased recovery rate or death rate of infected individuals.

Both reservoir competence and the dilution/amplification effects imply that community composition is important to disease prevalence. However, these effects may be independent of as well as oppose each other. For example, a dilution effect mitigating the effects of a pathogen can occur

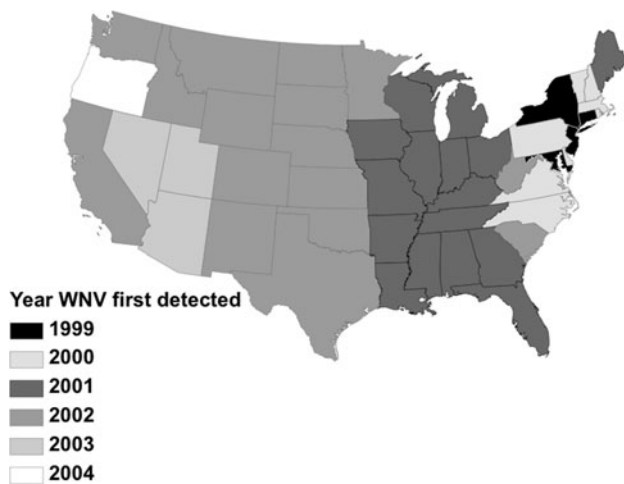
in spite of high average host competence if vectors are preferentially attracted to less competent hosts.

Our goal here is to determine which of the above ecological factors have been important in influencing the impact of WNV during its North American sweep. We focus on a single host species, the American crow (*Corvus brachyrhynchos*), for two reasons. First, it is known to be highly susceptible to WNV, with prior studies revealing severe regional declines coinciding with the spread of WNV (Hochachka et al. 2004; Yaremych et al. 2004; Koenig et al. 2007; LaDeau et al. 2007; Smallwood and Nakamoto 2009) and similarly drastic effects on individual populations (Caffrey et al. 2005; Clark et al. 2006). Second, although most other corvids (with the known exception of common ravens *Corvus corax*; Koenig et al. 2007) are also highly susceptible to WNV, American crows are the only species in this family with a distribution that encompasses nearly all of North America (Verbeek and Caffrey 2002). Thus, it offers a unique opportunity to examine the geographic patterns of mortality due to an emerging disease on a continental scale.

## Materials and methods

To determine patterns of apparently mortality due to WNV, we analyzed North American Breeding Bird Survey (BBS) data (Bystrack 1981) for the 20-year period between 1989 and 2008. To deal with the temporal spread of WNV, we divided sites into five groups depending on the year in which the pathogen was first reported in the state in which the survey was performed (CDC 2008) omitting Oregon, the last and only state in which the virus was not detected until 2004 (Fig. 1). We then standardized results for the five sets of states based on the year of first detection ( $Y_0$ ); in all cases, this was matched to the appropriate BBS data from the spring following first detection of the pathogen, since most mortality is likely to have taken place after the survey conducted during the same year WNV was first detected. Initial crow density was estimated as the mean number of crows counted over the 3 years ending with  $Y_0$ ; values were log-transformed for analysis. For each BBS route, we estimated the adverse effects of WNV as a binary variable based on whether or not the number of American crows counted in the same BBS route 4 years after  $Y_0$  was less than the initial mean crow density. This avoided bias due to different initial density of crows on different routes and gave enough time after initial detection in the state for the effects of WNV to impact the population. Data were compiled for a total of 696 routes across the continental US.

Next, for each BBS route, we calculated species richness ( $S = n$  species), species diversity ( $H = \sum p_i \ln p_i$ , where  $p_i$  is the fraction of individuals belonging to the  $i$ th species in the



**Fig. 1** Spread of West Nile virus across the US by state. Oregon, the last and only state where West Nile virus was not detected until 2004, was omitted from the analyses

community summed over all species), species evenness ( $E = H/\ln S$ ), and the total number of birds counted in the survey. All variables were averaged over the 3 years ending with  $Y_0$ .

The three measures of diversity were highly significantly correlated ( $0.16 \leq r_s \leq 0.90$ , all  $P < 0.001$ ). There were also highly significant correlations between total number of individual birds and both species richness ( $r_s = 0.36$ ,  $P < 0.001$ ) and species evenness ( $r_s = -0.22$ ,  $P < 0.001$ ), but not with species diversity ( $r_s = -0.03$ ,  $P = 0.36$ ). Thus, in order to minimize multicollinearity, we used only the species diversity measure  $H$  in the analyses.

As an index of urbanization, we calculated 1999 human population density (people  $\text{km}^{-2}$ ) for the area surrounding each BBS route using data from the US Census Bureau’s TIGER/Line census tracts (<http://www.census.gov/geo/www/tiger/tgrshp2008/tgrshp2008.html>). Values were log-transformed for analysis. Mean annual maximum temperature and mean annual rainfall over the 4 years following  $Y_0$  was determined for each site from the PRISM database (PRISM 2008). More problematical was estimation of overall community reservoir competence. Being the sum of the product of each species’ abundance and its reservoir competence index value, accurate determination of this variable requires detailed studies quantifying susceptibility, infectiousness, and duration of infectiousness for all species in a community. Such data have been painstakingly determined for a few common species but are not available for most North American birds. Particularly unfortunate is that few native nonpasserine species have been tested; although relatively few nonpasserines are reservoir competent for WNV (Komar et al. 2003; Kilpatrick et al. 2006; Loss et al. 2009), Ezenwa et al. (2006) found that nonpasserine species richness correlated with both mosquito and human

infection rates, suggesting that nonpasserines might nonetheless be important for WNV transmission.

Consequently, for the analyses presented here, we used total number of birds in the community as a proxy for total avian reservoir competence; as with the other abundance measures, values were log-transformed for analysis. Total number of birds was highly correlated ( $r_s = 0.80$ ;  $P < 0.001$ ) with an estimate of overall passerine reservoir competence obtained by extrapolating the detailed data on host competence for 20 common passerine species examined by Komar et al. (2003, 2005) and Wheeler et al. (2009) to related taxa and summing values across each community as determined from the BBS data (W. Koenig, unpublished data), suggesting that it provides at least a reasonable approximation of the desired variable (overall reservoir competence of the avian community). A summary of the covariates used in our analyses is provided in Table 1.

Analyses were conducted using general linear models with binomial error terms in R 2.10.0, library ‘nlme’ (R Development Core Team 2009). Based on evidence of spatial autocorrelation in model residuals, we included an inverse distance-weighted autocovariance term in the model to control for spatial autocorrelation and minimize prediction error (Augustin et al. 1996; Wintle and Bardos 2006; Betts et al. 2009). To test our hypotheses concerning the relationship between the probability of crow declines and the above factors, we constructed a set of 12 candidate approximating models (Table 2). Models were ranked using the Akaike information criterion corrected for sample size ( $AIC_c$ ). Using these values, we then calculated  $AIC_c$  values and model probabilities ( $w = \text{Prob}\{H|\text{data}\}$ ) (Burnham and Anderson 2002; Anderson 2008) as robust Bayesian posterior probabilities using the R library ‘bbmle’. Models with a  $\Delta AIC_c > 10$  were considered to explain no

**Table 1** Covariates included in the analyses

Variable name	Description
$Y_0$	Year WNV was first detected in the state (1999–2003)
CROWDEN	Density of American crows during the 3 years ending with $Y_0$ (log-transformed)
BIRDDIV	Species diversity of all birds ( $H = \sum p_i \ln p_i$ ) average over the 3 years ending with $Y_0$ (Shannon index)
HUMDEN	Human population density in 1999 as an index of urbanization (log-transformed)
TOTBIRDS	Total number of individual birds average over the 3 years ending with $Y_0$ (log-transformed)
RAIN	Mean annual rainfall for the 4 years following $Y_0$
XMAXTEMP	Mean maximum annual temperature for the 4 years following $Y_0$
AUTOCOV	Inverse distance-weighted autocovariance term

**Table 2** Summary of the 12 candidate models including their  $\Delta AIC_c$  values and model weights (Bayesian posterior probabilities), ranked by model weight

Variables included in the model	Model description	$\Delta AIC_c$	Model weight
CROWDEN + BIRDDIV + HUMDEN + AUTOCOV	Urbanization, crow density, and species diversity (plus AUTOCOV)	0.0	0.29
$Y_0$ + CROWDEN + BIRDDIV + HUMDEN + AUTOCOV	$Y_0$ , urbanization, crow density, and species diversity (plus AUTOCOV)	0.6	0.21
$Y_0$ + CROWDEN + BIRDDIV + HUMDEN + RAIN + XMAXTEMP + AUTOCOV	All except TOTBIRDS	1.0	0.17
$Y_0$ + CROWDEN + BIRDDIV + HUMDEN + TOTBIRDS + AUTOCOV	All but the environmental variables	1.7	0.12
$Y_0$ + CROWDEN + BIRDDIV + HUMDEN + TOTBIRDS + RAIN + XMAXTEMP + AUTOCOV	Complete model (all variables)	2.4	0.08
CROWDEN + BIRDDIV + HUMDEN + RAIN + XMAXTEMP + AUTOCOV	All except $Y_0$ and TOTBIRDS	2.8	0.07
$Y_0$ + BIRDDIV + HUMDEN + AUTOCOV	$Y_0$ , crow density, and urbanization (plus AUTOCOV)	3.3	0.06
$Y_0$ + CROWDEN + BIRDDIV + HUMDEN + TOTBIRDS + RAIN + XMAXTEMP	All except AUTOCOV	18.7	<0.001
$Y_0$ + CROWDEN + BIRDDIV + AUTOCOV	$Y_0$ , crow density, species diversity (plus AUTOCOV)	45.2	<0.001
CROWDEN + BIRDDIV + AUTOCOV	Crow density and species diversity (plus AUTOCOV)	45.4	<0.001
$Y_0$ + CROWDEN + BIRDDIV + TOTBIRDS + RAIN + XMAXTEMP + AUTOCOV	All except urbanization	46.6	<0.001
AUTOCOV	AUTOCOV only	55.3	<0.001

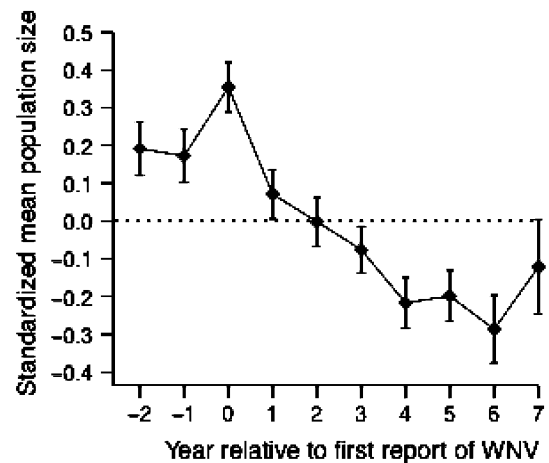
substantial variation in the data and to have essentially no support (Burnham and Anderson 2002).

Of the 12 candidate models, 7 were found to have competing support ( $\Delta AIC_c < 10$ ). These 7 were included in model averaging using the R library ‘MuMIn’. We summarized the variables included in these models by their standardized coefficients ( $\pm$  the unconditional SE) along with the overall weight of evidence supporting the hypothesis that the variable was an important predictor of crow declines based on the summed weights for the models in which the variable was included.

**Results**

Population estimates of American crows, temporally standardized relative to detection of the pathogen within each state, confirmed earlier studies indicating marked declines following the introduction of WNV. Declines were evident for 4–6 years following emergence of WNV. By year 7, populations had begun to recover in states affected early on by the pathogen (Fig. 2).

Results of the general linear models indicated that seven models received support by virtue of  $\Delta AIC_c$  values  $< 3.5$ , far less than the next best-supported model with a  $\Delta AIC_c = 18.7$  (Table 2). All seven of the supported models included avian species diversity (crows were less likely to decline in areas with high avian species diversity); human population density (crows were more likely to decline in urban areas with high human population density), and the spatial autocovariate term. In addition, crow density was included in all but the weakest of the seven models (dense crow populations were more likely to suffer a decline) while the year WNV was first detected ( $Y_0$ ) was present in five of the seven models (crows were less likely to decline



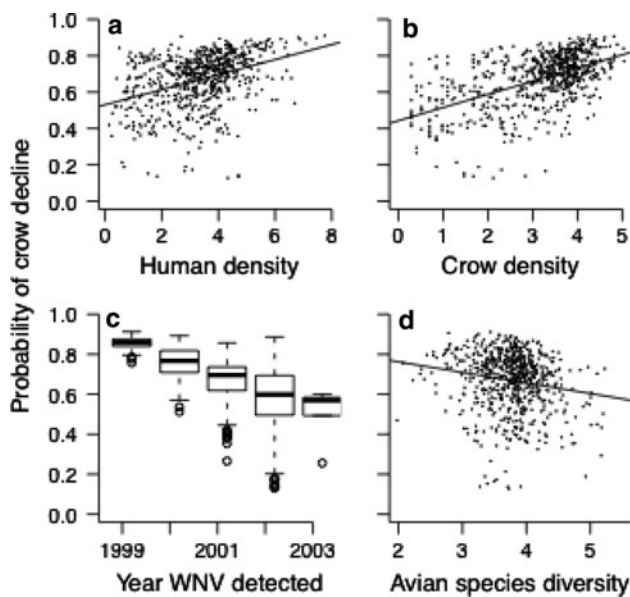
**Fig. 2** Standardized population densities ( $\pm$  SE) of American crows (*Corvus brachyrhynchos*) relative to the year when West Nile virus was first reported in the state

in areas reached later by the pathogen). There was considerably less support for the remaining three variables (RAIN, XMAXTEMP, and TOTBIRDS) being important to crow declines (Table 3). The relationships between the four variables with the strongest effects on the probability of crow declines are graphed in Fig. 3.

**Table 3** Averaged ( $\pm$  SE) model parameters

Variable	Model parameters	95% confidence intervals	Overall weight of evidence
AUTOCOV	1.08 $\pm$ 0.23	0.63; 1.52	1.00
BIRDDIV	-0.51 $\pm$ 0.20	-0.90; -0.12	1.00
HUMDEN	0.09 $\pm$ 0.26	-0.41; 0.60	1.00
CROWDEN	0.49 $\pm$ 0.25	0.01; 0.97	0.94
$Y_0$	-0.30 $\pm$ 0.33	-0.95; 0.35	0.64
RAIN	-0.14 $\pm$ 0.22	-0.58; 0.30	0.33
XMAXTEMP	0.09 $\pm$ 0.15	-0.21; 0.39	0.33
TOTBIRDS	0.04 $\pm$ 0.08	-0.12; 0.20	0.21

Parameter estimates are based on the top seven models ( $\Delta AIC_c < 3.5$ ; see Table 2) ranked in order of the overall weight of evidence for the variable being an important predictor of crow declines, based on the summed model weights in all candidate models in which the variable was included ( $n = 696$  sites)



**Fig. 3** Graphs of the probability of American crow declines versus **a** human population density (log-transformed), **b** crow density (log-transformed), **c** year West Nile virus was first detected in the state ( $Y_0$ ), and **d** avian species diversity. For graphs **a,b,d**, the individual points and the loess regressions are plotted; points are fitted from the best-performing candidate model (Table 2). Graph **c** plots the median (horizontal line) proportion of routes declining, the bottom of the 25th and top of the 75th percentiles (bottom and top of the boxes), 1.5 times the interquartile range of the data (the ‘whiskers’ of the boxes), and outliers beyond the whiskers for each year of first detection

**Discussion**

A summary of the qualitative results from the best-supported candidate models indicates at least some support for all but one of our a priori predictions, the exception being rainfall, which was negatively (albeit weakly) associated with crow declines, opposite to the expected relationship (Table 4). Two other variables had the expected positive association with declines but were only weakly supported as being important, including total number of birds (our proxy for total reservoir competence of the community) and mean maximum temperature. None of these variables was present in either of the two most highly ranked models.

The remainder of our predictions garnered moderate to strong support. The probability of crow declines was positively associated with human population density, as expected, increasing from close to 50% of populations declining in areas with few people to over 80% declining in heavily populated urban areas (Fig. 3a). An even stronger positive effect was observed with crow density, with the probability of declines increasing from around 45% in low-density populations to 80% in high-density populations (Fig. 3b). American crows are highly social cooperative breeders (Verbeek and Caffrey 2002; Caffrey et al. 2005; Clark et al. 2006) and thus extensive social contact potentially facilitating pathogen spread is not surprising. However, such density dependence was not a foregone conclusion given the complexities of multihost systems (Dobson 2004) and the fact that direct (host-to-host) transmission of the WNV pathogen is uncommon (Banet-Noach et al. 2003; Hartemink et al. 2007).

Our results also indicated that crow populations were less likely to decline as the pathogen spread across the US: over 80% of sites suffered a decline in states where the pathogen was first detected in 1999 while <60% of sites declined in states not affected until 2003 (Fig. 3c). Although there are several possible explanations for this result, the rapidity with which the pathogen spread combined with the high philopatry of American crow populations (Verbeek and Caffrey 2002) and the rarity of direct transmission of WNV renders it unlikely that this was due to changes in susceptibility of crow populations. It is also possible that there were differences in vector populations that may explain these results, but our inclusion of human population density makes it unlikely that it was solely a consequence of greater urbanization in the areas where WNV was established earlier. Rather, it suggests that at least part of this pattern is due to the virulence of WNV having declined as it made its sweep of North America, a result in keeping with other studies suggesting that WNV may have reached its peak prevalence relatively early during its expansion (Snapinn et al. 2007) and quickly began to decline in virulence, as expected theoretically from studies

**Table 4** Predictions and results of the analysis

Variable	Expected relationship with increased probability of crow decline	Result and strength of the relationship
Rainfall (RAIN)	+	– (weak)
Mean maximum temperature (XMAXTEMP)	+	+
Human population density (HUMDEN)	+	+
Crow density (CROWDEN)	+	+
Temporal pattern ( $Y_0$ )	+/-	– (moderate)
Total number of birds (TOTBIRDS)	+	+
Avian species diversity (BIRDDIV)	+/-	– (strong)

of other (usually much simpler) disease systems (Bull 1994; Galvani 2003) and as found for other disease epidemics (Fenner and Ratcliffe 1965).

Finally, our results provide strong support for avian biodiversity as a key factor reducing the mortality of American crows, with the probability of crow declines declining from over 75% in areas with low avian species diversity to <60% in areas with high diversity (Fig. 3d). This result supports the ‘dilution effect’ as being an important factor mitigating the effects of WNV, a conclusion reached by three prior studies investigating the relationship between avian biodiversity and human cases of WNV (Ezenwa et al. 2006; Swaddle and Calos 2008; Allan et al. 2009). In contrast, Loss et al. (2009) found no net effect of increased species richness on WNV transmission. Although these latter authors question the generality of a dilution effect for WNV, their study, conducted in the Chicago metropolitan area, was conceivably too limited in geographic scope to yield a sufficient range of biodiversity for a strong dilution effect to be observed. In any case, the results reported here add to the current evidence that a dilution effect plays an important role in WNV transmission in both humans and birds.

The dilution effect has also been investigated in several other systems, most thoroughly that of Lyme disease, where Ostfeld and Keesing (2000a) reported a significant negative correlation between the incidence of reported Lyme disease cases in the eastern US and species richness of terrestrial small mammals, of which only one, the white-footed mouse *Peromyscus leucopus*, is the principal natural reservoir for the disease-causing spirochete. Although our results support the presence of a dilution effect related to increased avian diversity, our analyses do not specifically address the mechanism involved other than to the extent that since host density was one of the variables included in the analyses, the effect is unlikely to be due to a decrease in the density of susceptible individuals. It remains possible that the effect is due to any of the other mechanisms discussed by Keesing et al. (2006), including a reduction in the encounter rate between susceptible and infectious individuals, a reduction in the probability of transmission given

an encounter, or an increase in either the recovery rate or the death rate of infected individuals. Additional study will be necessary to establish which of these mechanisms is responsible for the observed pattern.

Determining the ecological factors affecting disease risk of infectious zoonoses transmitted by vectors has obvious implications for mitigating the potential human health impacts of such pathogens. Our analyses demonstrate that the effects of WNV on a highly susceptible host, the American crow, during its North American sweep was influenced by a series of variables including host density, timing, urbanization, and the diversity of the avian community. The latter provides compelling evidence for a ‘dilution effect’ related to avian species diversity independent of host density and the potential for increased number of hosts to enhance pathogenic effects via increased community reservoir competence.

In the case of WNV and several other vector-borne zoonotic pathogens such as Lyme disease-causing *Borrelia*, many of the most competent reservoir species, including white-footed mice, deer (*Odocoileus* spp.), jays (*Aphelocoma* spp. and *Cyanocitta* spp.), crows (*Corvus* spp.), grackles (*Quiscalus* spp.), house finches (*Carpodacus mexicanus*), and house sparrows (*Passer domesticus*), are particularly abundant in fragmented and other heavily populated habitats. Thus, the risk of human exposure to these pathogens is likely to increase with urbanization due to increased abundance of competent pathogen vectors in conjunction with lower overall biodiversity (Ostfeld and Keesing 2000b; Allan et al. 2003). Increased attention should be devoted to understanding the role of biodiversity in buffering disease prevalence as a key ecosystem function, particularly in urban areas where high human population density and low species richness potentially exacerbate disease risk.

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