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Land Cover Variation and West Nile Virus Prevalence: Patterns, Processes, and Implications for Disease Control

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ABSTRACT

Identifying links between environmental variables and infectious disease risk is essential to understanding how human-induced environmental changes will effect the dynamics of human and wildlife diseases. Although land cover change has often been tied to spatial variation in disease occurrence, the underlying factors driving the correlations are often unknown, limiting the applicability of these results for disease prevention and control. In this study, we described associations between land cover composition and West Nile virus (WNV) infection prevalence, and investigated three potential processes accounting for observed patterns: (1) variation in vector density; (2) variation in amplification host abundance; and (3) variation in host community composition. Interestingly, we found that WNV infection rates among *Culex* mosquitoes declined with increasing wetland cover, but wetland area was not significantly associated with either vector density or amplification host abundance. By contrast, wetland area was strongly correlated with host community composition, and model comparisons suggested that this factor accounted, at least partially, for the observed effect of wetland area on WNV infection risk. Our results suggest that preserving large wetland areas, and by extension, intact wetland bird communities, may represent a valuable ecosystem-based approach for controlling WNV outbreaks.

Key Words: West Nile virus—Emerging infectious disease—Vector-borne disease—*Culex*—Passeriformes—Wetlands—Land cover. Vector-Borne Zoonotic Dis. 7, 173–180.

INTRODUCTION

THE EFFECT OF LAND USE change on infectious disease emergence has garnered widespread attention in recent years (Foley et al. 2005, Patz et al. 2000, 2004), stimulating an increase in research aimed at understanding associations between land use/land cover and infectious disease risk. One common approach used by such studies involves quantifying landscape characteristics and exploring patterns of association between land cover and indices of infectious disease risk (Curran et al. 2000, Ostfeld et al. 2005). In many cases, the ultimate goal of these analyses is to predict future distributions of disease based on environmental characteristics, however, there remain several important complications with this approach. Foremost among these is that often, where correlations between land use/land cover and disease prevalence have been established, the underlying processes accounting for observed patterns remain unknown (Boone et al. 2000, Engenhalter et al. 1999, Gibbs et al. 2006). As a consequence, significant gaps remain in our understanding of how human-induced landscape changes influence infectious disease dynamics, severely limiting efforts to prevent and control emerging and reemerging diseases.

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West Nile virus (WNV) is a recently emerged vector-borne disease in the United States, and land cover variation may play an important role in shaping distributions of this disease (Brownstein et al. 2002, Gibbs et al. 2006, Ruiz et al. 2004). One mechanism by which land cover could influence disease prevalence is through direct effects on the abundance of hosts or vectors in the environment (Beck et al. 1994, Dister et al. 1997, Olsson et al. 2005). Alternatively, effects of land use/land cover on disease risk could be mediated by variation in interactions among species occurring in different habitat types, or by differences in the relative composition of hosts or vectors across environments (LoGiuidice et al. 2003). Distinguishing between these processes is critical for understanding how to predict and control future WNV outbreaks.

In this study, we examined associations between land cover composition and WNV prevalence, and investigated three potential mechanisms accounting for observed patterns: (1) variation in vector density; (2) variation in amplification host abundance; and (3) variation in host community composition. Because mosquitoes in the genus *Culex* are the primary vectors of WNV (Turell et al. 2001, 2005), we used the number of *Culex* mosquitoes captured per trap night as a measure of vector density across habitats, and measured WNV prevalence as the rate of infection in these mosquitoes. We used total passerine bird (order: Passeriformes) abundance as an estimate of host abundance based on laboratory and field evidence implicating multiple species of passerines as key virus amplification hosts (Komar et al. 2003, 2005, Reisen et al. 2005a, 2006). Last, based on results from a related study linking high nonpasserine bird diversity and abundance to reduced WNV prevalence, and implicating nonpasserine birds as important WNV dilution hosts (Ezenwa et al. 2006), we used a novel index, the passerine to nonpasserine abundance ratio, to estimate the relative composition of competent versus noncompetent WNV hosts in the environment.

MATERIALS AND METHODS

Study sites and land cover composition

We established six study sites in St. Tammany Parish, Louisiana, located in areas varying in land use/land cover. To quantify land cover composition across sites we used the 2001 National Land Cover Database, a classified land cover dataset derived from 30-m resolution Landsat-7 Enhanced Thematic Mapper (ETM) imagery collected circa 2000 (Homer et al. 2004). Using ArcGIS 9.0 (ESRI, Redlands, CA), we calculated the percent area of eight land cover types within a 1-km radius of each study site (total area = 3.14 km^2): water, developed land, barren land, forested upland, shrub land, herbaceous upland, cultivated land, and wetland (Fig. 1; see www.epa.gov/mrlc/nlcd.html for class definitions). Since only four cover types accounted for over 90% of the land area across sites, forested upland (39%), wetland (32%), developed land (10%) and shrub land (10%), these cover classes were used to explore associations with WNV prevalence.

Mosquito density and WNV prevalence

Between June 3 and October 28, 2003, we collected adult mosquitoes once per week at a fixed location within each study site. On each trapping night, two CO$_2$ light traps and one gravid trap were set per site and run from dusk until dawn. Traps were retrieved the morning after each session and mosquito specimens were transported to the laboratory where species identification and virus testing were performed as described in Ezenwa et al. (2006). Vector density was calculated as the total number of all *Culex* mosquitoes captured divided by the total number of trap nights. Mosquito infection prevalence was calculated using the maximum likelihood (MLE) method (Chiang and Reeves 1962, Walter et al. 1980), implemented in the Microsoft Excel Add-In PooledInfRate 2.0 (Biggerstaff 2004). Twenty *Culex* mosquito pools were found to be WNV positive, and infection prevalence (MLE per 1000 mosquitoes) ranged from 0 to 3.34 (Ezenwa et al. 2006). We combined all *Culex* species in our estimate of WNV infection prevalence because all of these species were potential WNV vectors. However, since 85% of WNV isolations came from a single species, *Culex nigripalpus*, we also calculated infection prevalence for *Culex nigripalpus* only. Because our results were qualitatively similar for analyses using either

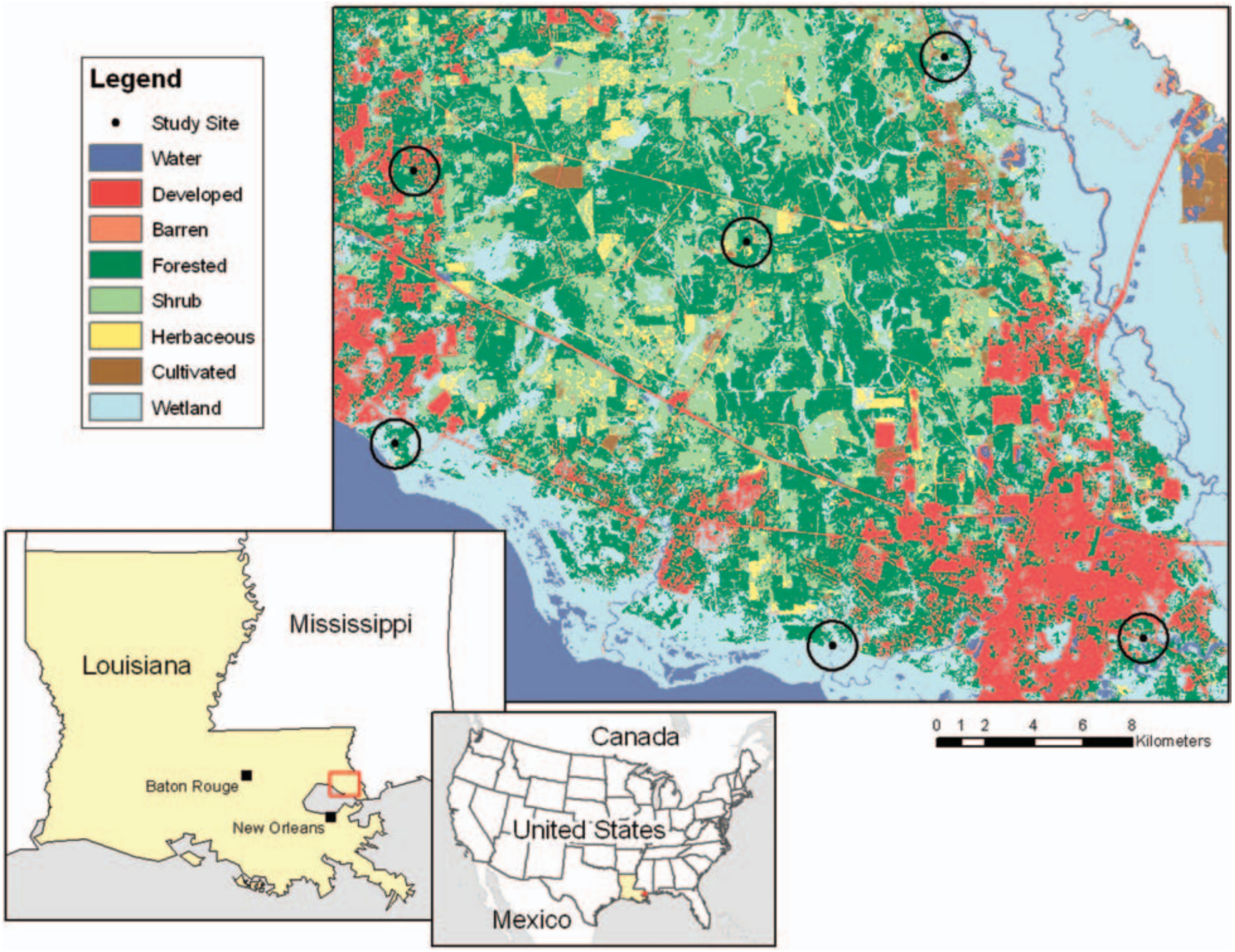

FIG. 1. Location and land cover composition of six study sites in southeastern Louisiana. Buffers of 1-km radius around each site show the area used for quantifying land cover variation across sites. Land cover classes are based on the 2001 National Land Cover Database.

all *Culex* MLE or *Culex nigripalpus* MLE, we only report results from the all *Culex* analyses.

Avian abundance and species composition

We estimated bird abundance using the point transect method as detailed in Ezenwa et al. (2006). Briefly, 10 transect points spaced ≥ 200 m apart were established within a 1-km radius of each study site, with one point set at the mosquito trap in every case. All 60 transect points were surveyed once by a single observer between June 24 and 7 July 2003. Surveys began at dawn and were completed by 11:30 AM. Point counts lasted for 10 minutes during which all bird species seen and heard were recorded. The horizontal distances between all birds and the transect point were recorded in 10 m intervals up to 100 m. A total of 56 species were identified across all sites including 35 passerine and 21 nonpasserine species (Ezenwa et al. 2006). We used the computer program DISTANCE (Thomas et al. 2005) to estimate the total abundance of all passerines and all nonpasserines at each site. Relative host community composition was calculated as the ratio of passerine to nonpasserine abundance.

Statistical analyses

First, we tested associations between land cover composition, WNV prevalence, host, and vector characteristics using simple linear regression analyses. Next, we examined whether host or vector variables accounted for correlations between WNV prevalence and land cover using an information theoretic approach (Burnham and Anderson 2002) to compare the fit of a series of candidate models (including either land cover variables only, host/vector variables only, or a combination of land cover and host/vector variables) to observed WNV prevalence data. For each candidate model, we calculated the Akiake information criterion corrected for small sample size (AICc), the difference in AICc between each candidate model and the best fitting model (Δ AICc), and the Akaike weight (ω_i) which provides information on the relative support, or likelihood, for each model. We used the ratio of Akaike weights (ω_1/ω_j) to assess the evidence in support of the best fitting model over other candidate models (Burnham and Anderson 2002). We also compared basic regression statistics (F, adjusted r^2, p) for each model. AIC calculations were performed in the software program R (R Core Development Team). All variables were log transformed to normalize data distributions prior to analysis.

RESULTS

Vector and host abundance patterns

Across all sites, we collected 42,666 *Culex* mosquitoes including 5 potential WNV vectors: *Cx. erraticus, Cx. quinquefasciatus, Cx. nigripalpus, Cx. restuans,* and *Cx. salinarius*. *Cx. salinarius* was the most abundant species collected, comprising approximately 45% of collections, followed by *Cx. nigripalpus* with 31%, *Cx. erraticus* with 17%, *Cx. quinquefasciatus* with 2%, and *Cx. restuans* with less than 1%. Approximately 5% of *Culex* specimens were unidentifiable to species level. In terms of potential WNV hosts, of the 56 bird species identified across all sites, nine of the top ten most abundant species were passerines (Table 1); and the top three species, northern cardinal (*Cardinalis cardinalis*), American crow (*Corvus brachyrhynchos*), and blue jay (*Cyanocitta cristata*) have all been implicated as important WNV amplification hosts in St. Tammany Parish (Komar et al. 2005).

Land cover associations

Only one of four land cover types was significantly correlated with *Culex* infection prevalence. Percent wetland cover was significantly negatively correlated with WNV prevalence ($F = 21.1$, $r^2 = 0.84$, $p = 0.01$), but there was no association between prevalence and either percent forested upland ($F = 6.29$, $r^2 = 0.61$, $p = 0.07$), developed land ($F = 2.41$, $r^2 = 0.38$, $p = 0.2$), or shrub land ($F = 1.66$, $r^2 = 0.36$, $p = 0.29$). Focusing on wetland area, we then examined correlations between percent wetland cover and *Culex* density, passerine abundance, and the passerine to nonpasserine ratio. Wetland area was a significant predictor of host composition, with the proportion of passerines to non-passerines declining with an increase in wetland cover ($F = 29.1$, $r^2 = 0.88$, $p = 0.006$; Fig. 2A). In contrast, there was no significant association between wetland area and either passerine abundance ($F = 0.008$, $r^2 = 0.002$, $p = 0.93$; Fig. 2B) or *Culex* density ($F = 1.0$, $r^2 = 0.2$, $p = 0.37$; Fig. 2C).

TABLE 1. TEN MOST ABUNDANT BIRD SPECIES ACROSS STUDY SITES AND PERCENT OF THE TOTAL COMMUNITY REPRESENTED BY EACH SPECIES

Species	*Passerine (P), Nonpasserine (NP)*	*Abundance estimate*	*Percent of total community (%)*
Northern cardinal (*Cardinalis cardinalis*)	P	4299	14.1
American crow (*Corvus brachyrhynchos*)	P	227	8.6
Blue jay (*Cyanocitta cristata*)	P	2567	8.4
Red-winged blackbird (*Agelaius phoeniceus*)	P	1791	5.9
Tufted titmouse (*Baeolophus bicolor*)	P	1791	5.9
Carolina wren (*Thryothorus ludovicianus*)	P	1612	5.3
Red-bellied woodpecker (*Melanerpes carolinus*)	NP	1433	4.7
Carolina chickadee (*Poecile carolinnsis*)	P	955	3.1
Eastern towhee (*Pipilo erythrophthalmus*)	P	896	2.9
Northern mockingbird (*Mimus polyglottos*)	P	717	2.3

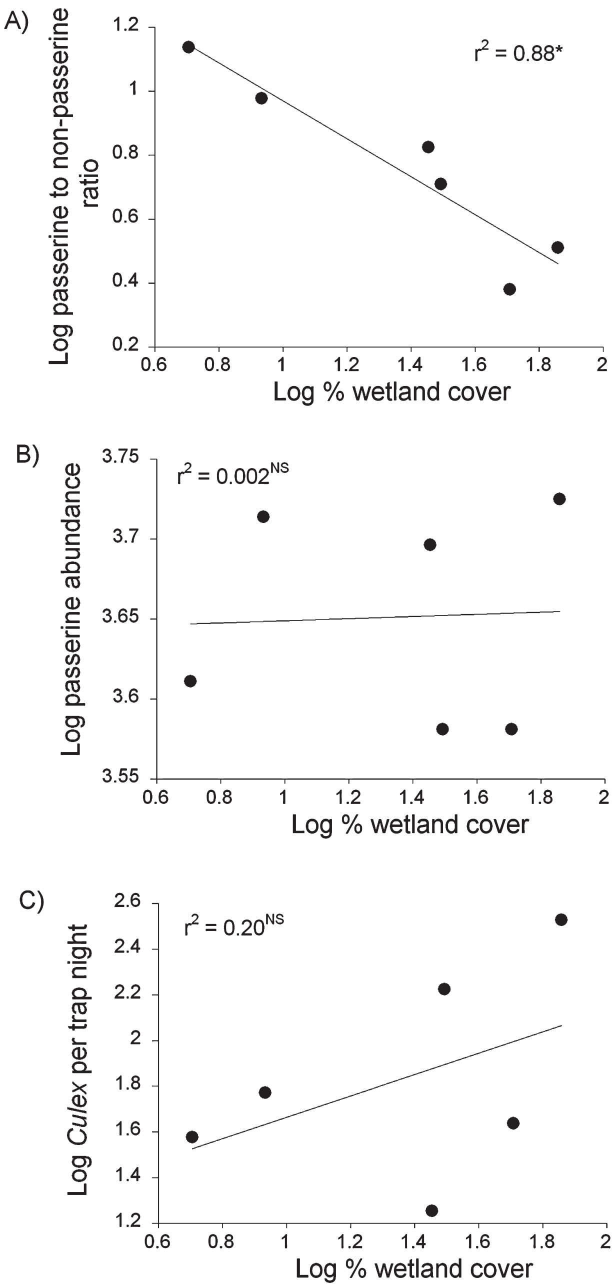

FIG. 2. Associations between percent wetland cover and (**A**) host community composition (passerine to nonpasserine ratio); (**B**) host abundance (passerine abundance); and (**C**) vector density (*Culex* per trap night). *$p <$ 0.01; NS = not significant.

Model comparisons

Given the strong association between wetland area and passerine to nonpasserine ratio, we tested whether host composition could partially account for the observed association between wetland cover and WNV prevalence. Comparing models including either percent wetland cover, passerine to nonpasserine ratio, or both, we found that the model with passerine to nonpasserine ratio as the sole predictor of WNV prevalence had the most support based on Akaike weights, while the model including both wetland cover and passerine to nonpasserine ratio had the least support (Table 2). The weight of evidence (Akaike weight ratio) supporting the highest ranked model (model 1: passerine to non-passerine ratio) over the other candidate models was 1.79 for model 2 (percent wetland cover) and 22.6×10^5 for model 3 (percent wetland cover + nonpasserine to passerine ratio). The passerine to nonpasserine ratio model was also the best fitting model based on r^2 values (Table 2).

DISCUSSION

Of four landscape variables investigated in this study, wetland area was the only significant predictor of WNV prevalence. Interestingly, an increase in wetland area was associated with a decline in virus prevalence, suggesting that wetlands had a dampening effect on WNV amplification. This result directly contradicts the commonly cited idea that wetlands pose an increased risk for many mosquito-borne diseases by increasing vector densities and disease transmission (Reisen et al. 2000, Schafer et al. 2004, Willott 2004). We found no significant correlation between wetland area and *Culex* density, although there was a trend toward increasing mosquito density with increasing wetland area (Fig. 1C). However, given that mosquito infection rates declined with increasing wetland area despite this positive trend between wetland area and mosquito density, it is highly unlikely that variation in mosquito density can account for the observed negative relationship between wetland area and WNV prevalence.

Wetlands are well-known to support both a high density and diversity of bird species (Inman et al. 2002, Sallabanks et al. 2000), thus associations between wetlands and bird abundance or community composition could also be important factors driving the correlation between wetland area and WNV prevalence. Previous work in this study system has shown that

TABLE 2. COMPARISON OF MODELS PREDICTING WEST NILE VIRUS PREVALENCE ACROSS STUDY SITES

Model	*AICc*	*ΔAICc*	*Akaike weight*	*F*	*Adj.* r^2	*p*
1) log passerine to nonpasserine ratio	25.3	0	0.641	26.5	0.84	0.04
2) log % wetland area	26.46	1.16	0.359`	21.1	0.80	0.01
3) log passerine to nonpasserine ratio + log % wetland area	54.56	29.26	0.00000000284	11.4	0.81	0.007

AICc, Akiake information criterion corrected.

bird diversity and abundance are key predictors of vector infection rates (Ezenwa et al. 2006). As such, we explored the degree to which differences in the bird community across sites could account for the observed wetland pattern. When we looked at associations between wetland area and passerine abundance, we found no significant correlation between the two variables indicating that wetland area had little effect on the absolute abundance of potential WNV amplification hosts. Thus, a decline in the number amplification hosts in larger wetlands is unlikely to explain the negative association between wetland area and WNV prevalence. In fact, shrubland area was a significant positive predictor of passerine abundance ($r^2 = 0.85$; $p = 0.03$; unpublished data), yet variation in this landscape feature had no effect on virus infection rates, reinforcing the fact that land cover effects on WNV prevalence are not mediated by absolute changes in amplification host abundance in this system.

In terms of host community composition, we found that the ratio of passerine to nonpasserine abundance was significantly and negatively correlated with wetland area. Our use of the passerine to nonpasserine ratio as an estimate of the relative composition of competent and non-competent hosts in a habitat is an extension of prior work linking bird diversity, abundance and WNV prevalence in this study system (Ezenwa et al. 2006). Since nonpasserine birds potentially disrupt efficient WNV transmission by acting as dilution hosts (Ezenwa et al. 2006), whereas many passerine species, including the most abundant species identified at our study sites, act as efficient virus amplification hosts (Komar et al. 2003, 2005), a difference in the relative composition of passerine and nonpasserine birds should have a strong effect on the number of virus transmission events occurring in a community. Given the strong association between the passerine to nonpasserine ratio and wetland area, it is plausible that variation in host community composition accounts for the observed WNV prevalence-wetland area pattern. In support of this idea, our comparison of three candidate models explaining variation in WNV prevalence suggested that the effects of percent wetland cover and passerine to nonpasserine ratio were nonindependent. The model with both variables included as predictors had almost no support ($< 1\%$) while the two models with each variable as a sole predictor had the majority of support ($> 99\%$). Of the two single predictor models, the passerine to nonpasserine ratio model had more support according to both Akaike weight and adjusted r^2 comparisons, suggesting that this variable can account, at least partially, for the association between WNV prevalence and wetland area. Given the relatively low evidence ratio (approximately 2:1) supporting the passerine to nonpasserine model over the wetland area model, however, additional work comparing similar models and using a larger dataset will be needed to better tease apart the links between land cover, host community structure, and WNV prevalence.

Even though the present study focused on only a small number of sites, our results are nevertheless intriguing. While previous work demonstrated that bird diversity and abundance are strongly linked to WNV prevalence in both vectors and people (Ezenwa et al. 2006), results of the current study extend these findings by suggesting that changes in land cover composition that influence bird community structure can contribute to variation in WNV disease risk. Specifically, our results suggest that variation in wetland cover is strongly associated with mosquito infection rates, due in part to the effects of wetland area on bird community composition. Implications of these findings are that preserving large wetland areas may help moderate WNV disease risk by protecting wetland bird communities that act as natural buffers to WNV amplification. Supporting this conclusion are results from a recent WNV study in California that, contrary to initial predictions, showed no significant difference in *Culex tarsalis* infection rates in a wetland site with a dense wading bird (order: Aredidae) colony compared to a similar site without a colony. In fact, the mosquito infection rate at the colony site was lower than the non-colony site (2.13 versus 3.06), despite an almost 2 to 1 difference in mosquito density (Reisen et al. 2005b), suggesting that wetland birds can act to dampen WNV amplification.

More broadly, our results indicate that land cover effects on WNV disease distribution can be mediated by complex community level processes that go beyond simple changes in single host or vector abundances. This is exemplified by the lack of any direct association between wetland area and either *Culex* density or passerine abundance, contrasted with the strong association between wetland area and the measure of relative host composition. Based on these new insights, priorities for future research should include developing a better understanding of how land cover changes influence WNV host and vector communities and their interactions. This type of information will make us better equipped to predict and control future WNV outbreaks, and will be key to advancing a more ecosystem-based approach to combating infectious diseases.

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