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Climatic variability and landscape heterogeneity impact urban mosquito diversity and vector abundance and infection

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Abstract. Urban habitat heterogeneity can modify interactions across species and lead to spatially fine grained differences in β-diversity patterns and their associated ecosystem services. Here, we study the impacts of landscape heterogeneity and climatic variability on: (1) the richness and diversity patterns of mosquitoes (Diptera: Culicidae) and (2) the abundance and West Nile virus infection rate of the house mosquito, *Culex pipiens*, in Chicago, USA. We conducted a four year long study (2005–2008) in 8 sites that captured a gradient of urban heterogeneities. We found a total of 19 mosquito species, a representative sample of mosquito species richness in the area, according to both model estimation (Chao2 ± S.E. = 20.50 ± 2.29) and faunal records for Chicago. We found that heterogeneity in the landscape was the best predictor of both mosquito species richness and diversity, with the most heterogeneous landscapes harboring the largest number of species. In general there were no changes in species richness over the years that could be associated with weather patterns and climatic variability (WPCV). In contrast, changes in diversity were associated with WPCV. Our results also showed that WPCV had major impacts on house mosquito abundance and West Nile virus mosquito infection rate (MIR) patterns. Although MIR was independent of mosquito diversity, it was associated with overall mosquito abundance, which had a convex association with species richness (i.e., abundance increases to a point after which it decreases as function of species richness). Finally, our results highlight the importance of considering dominant vector species as part of a community of vectors, whose biodiversity patterns can directly or indirectly impact the risk of infectious disease transmission.

Key words: Chicago; entomological risk; Filariasis; habitat gradient; metacommunity; nuisance; richness; Rift Valley fever; Schmalhausen's law; West Nile virus.

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Introduction

Environmental change has led to species loss over ecological and evolutionary time scales (McKinney and Lockwood 1999, Gould 2002). The impact of human activities on the environment is currently driving a loss of species that, over a range of spatial scales, can be compared with major shifts observed through the history of life on earth, where the number of species has been dramatically reduced over relatively short periods of time (Myers et al. 2000, Gould 2002). This pattern of biodiversity loss is of special concern given the poor ecological knowledge about most species on earth. For example, it is difficult to "a priori" assert which species could play stabilizing roles in ecosystems, or more generally, what is the role of species on ecosystem functioning (Loreau et al. 2001, Hooper et al. 2005). Also, it has been increasingly recognized that sustainable exploitation of several natural resources essential for the persistence of human life on earth, ecosystem services, rely on management practices that are internally related to the conservation of species diversity (Tallis et al. 2009). Emphasis has been placed primarily on ecosystem services associated with the biodiversity of "natural ecosystems" (Nelson et al. 2009, Tallis et al. 2009). However, little attention has been devoted to the ecosystem services associated with diversity in places where abundant interactions between humans and other species take place, such as cities, where most humans already live, and where trends indicate a rapid increase over the coming years (Storper and Scott 2009). In this sense, cities are of special interest because of the potential for vast disease transmission and pathogen exposure (Bradley and Altizer 2007), including vector-borne diseases that affect humans in both developing and wealthy nations (Utzinger and Keiser 2006, Ruiz et al. 2007).

Cities are novel ecosystems that have emerged with human population growth and occupy between 1 to 6% of the global land-cover (Meyer and Turner II 1992). The landscape of urban settlements is fragmented and patchy as product of the historical impact of human activities (Kinzig et al. 2005). Patches embedded within the urban landscape can be diverse: from natural parks to residential neighborhoods; and from open areas to those with a large amount of canopy cover (Dreistadt et al. 1990, Rebele 1994). Landscape heterogeneity can be defined as the presence of different and diverse features in the landscape (Berling-Wolff and Wu 2004). Several studies have demonstrated that landscape heterogeneity can impact the diversity of organisms such as insects (Frankie and Ehler 1978, McIntyre 2000), birds (Blair 1996, Loss et al. 2009*b*) and more generally whole communities of plants and animals (Tait et al. 2005, Croci et al. 2008). Thus, landscape heterogeneity of cities offers unique opportunities to study processes driving biodiversity patterns.

Cities also allow to test whether β-diversity differences, in this case understood as changes in species composition across the different habitats encompassing the urban landscape (Denys and Schmidt 1998, Zanette et al. 2005), are driven by any of the main processes shaping diversity patterns: selection, drift, speciation and dispersal (Vellend 2010). A predominant role for drift can be revealed by habitat homogeneization leading to nested patterns, i.e., where differences in species richness are due to species loss (McKinney and Lockwood 1999, Baselga 2010), the turnover of species can highlight the presence of selection/speciation processes, while dispersal limitation can be tested by comparing associations of β-diversity differences with the geographical distance between sites sampled (Baselga 2010, Vellend 2010).

The fundamental processes shaping diversity patterns also occur in a dynamically changing environment (Levins 1968). Species can become more or less abundant by the influence of the changing environment, primarily through habitat disturbance (Grime 1973, Connell 1978). However, this aspect has been poorly studied in cities, which are of special interest because the lack of information to assess their vulnerability to climate change impacts on the dynamics of disease transmission (Keiser et al. 2004, Utzinger and Keiser 2006).

In a similar fashion, cities are attractive settings to study the impacts of biodiversity on other ecological patterns. In this sense the "dilution-effect", i.e., the decrease in disease risk as function of increased diversity (Celli 1908, Keesing et al. 2010) can be studied in relation to the diversity of vector communities. While "dilution-

effect" patterns have been primarily described as a function of vertebrate host diversity (Schmidt and Ostfeld 2001) and its best mechanistic articulation, zooprophylaxis [the diversion of bites from a focal host species by the presence of alternative host species (Sota and Mogi 1989)] was proposed more than a century ago (Celli 1908, Hackett and Missiroli 1931) little to no attention has been given to the impacts that vector diversity could have on shaping the risk of vector-borne disease transmission (Graham et al. 2009, Chaves et al. 2010).

Here, we study the impacts of landscape heterogeneity and climatic variability on: (1) the richness and diversity patterns of mosquitoes (Diptera: Culicidae) and (2) house mosquito, *Culex pipiens*, abundance and West Nile virus infection rate in Chicago, USA. We use data collected in 8 sites from 2005 to 2008. We use a multidisciplinary approach where we look at diversity patterns statically and dynamically. With the static approach we use tools from geographic information systems to ask: which landscape characteristics promote the diversity of mosquitoes in urban environments? We complement the insights of the static approach with a dynamic approach where we explore how mosquito diversity patterns are shaped by the different elements of climatic variability, i.e., the variability of meteorological forces at time scales shorter than those used to define climate but longer than those used in weather descriptions. We then move forward and test hypotheses regarding the role of the above outlined fundamental diversity processes in shaping β-diversity across patches. With our data we also ask whether increased mosquito diversity is associated with a decrease in the abundance and West Nile virus (WNv) infection rate of *Culex pipiens*, the house mosquito. We ask this last question because vectorial capacity, i.e., the number of new infections a mosquito can generate per unit time (Garrett-Jones 1964), is a linear function of mosquito abundance and any factor that reduces mosquito abundance is expected to reduce the entomological risk of disease transmission. Our results show that landscape heterogeneity, weather patterns and climatic variability are associated with the diversity patterns of mosquito communities, the abundance of *Culex pipiens* and its WNv mosquito infection rate. Although *Cx. pipiens* infection rate was not significantly associated with diversity, it was impacted by mosquito abundance (of all species collected), which itself had a convex relationship with mosquito species richness. Finally, our results highlight the need to consider the diversity of the communities associated with dominant vector species to fully understand the impacts of biodiversity on disease risk.

Methods

Data

Study location.—We studied mosquito diversity in a total of eight sites in southwest Chicago, Illinois, USA (Fig. 1). Sites were selected to be representative of key aspects of the region, and selection was based on characteristics that included housing age, vegetation, land use, socioeconomics, human population density and topography. For each site we derived variables that measured: vegetation (canopy cover), landcover (impervious and open urban land surfaces) and topography (elevation and slope). Vegetation and landcover data were obtained from the National Land Cover Database 2001, with a resolution of 30 m, available at ⟨http://www.mrlc.gov/nlcd.php⟩. Topography data came from the USGS National Elevation Database at 30 m resolution. Elevation data were used to calculate slope using ArcGIS 9.3 (ESRI, Redland, CA). For further details see Ruiz et al. (2007) and Loss et al. (2009*a*). Of the eight sites, five can be considered residential areas (S1, S5, S7, S10, S11) and three were "natural areas" (WW, SC, EC). The 8 sites ranged in size from 2.09 km^2 to 7.64 km^2.

Rainfall and temperature data.—Temperature and precipitation were estimated at each site for the mosquito season, which spans from mid May to mid October, i.e., weeks 21 to 41. Estimates were based on spatial interpolation of records from archived weather data. A total of 20 stations were within 15 km of the study areas. For additional details on the procedures see Ruiz et al. (2010).

Mosquito collection.—Mosquitoes were collected from field sites once every 2–3 weeks from mid-May to mid-October, 2005–2008. A mosquito trapping session at each site in 2005 consisted of up to four CO_2-baited CDC miniature light traps with traps distributed at ground and tree canopy

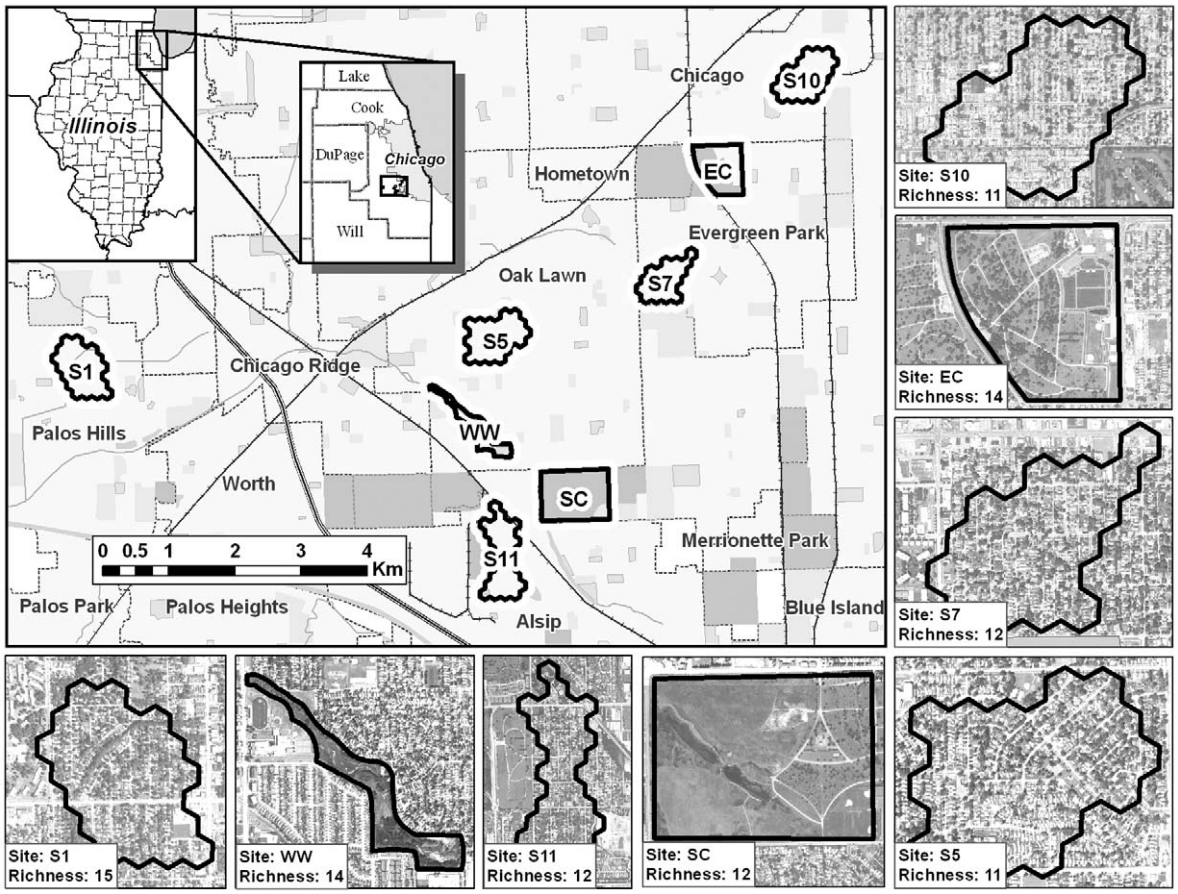


Fig. 1. Map of the study sites. The insert in the upper left corner shows the location of Chicago (spanning across Dupage and Cook Counties) in the state of Illinois, Mid-Central USA. The main panel shows the location of the 8 sites in this study. The bottom and right side of the figure show expanded views of aerial photographs of the studied sites. The code of the sites is as follows: Palos Hills North (S1); Wolfe Wildlife Refuge (WW), Alsip (S11); St Casimir Cemetery (SC); Oak Lawn Central (S5); Evergreen Park–West (S7); Evergreen Cemetery (EC); Chicago–Ashburn East (S10).

level. In 2005 elevated light traps captured more mosquitoes than ground level traps (more than 97% of the mosquitoes were captured in canopy traps, with mosquito species in the ground traps being a subset of the canopy traps, see supplement for original data), so from 2006 to 2008 sampling was restricted to elevated light traps. Each light trap was set up for 15 hours, between 1700 and 0800 h, we'll refer to this sampling effort as trap-night. Individual mosquitoes were identified to species using morphological characters (Andreadis et al. 2005). Because morphological traits are often not reliable to separate *Culex pipiens* from *Culex restuans* in the field (Harrington and Poulson 2008) individual mosquitoes that could not be identified into any of these two species were first grouped as *Culex* spp. Then, we used a PCR-based technique (Crabtree et al. 1995) to identify a representative subsample, at least 20 individuals for each trapping session, of all *Culex* spp. mosquitoes captured. The resulting ratio from this molecular identification was employed to assign the remaining of the *Culex* spp individuals, from each site and sampling session, as *Cx. pipiens* or *Cx. restuans*.

West Nile virus infection.—Blood free *Cx. pipiens* mosquitoes were pooled and tested for WNV

Table 1. Total mosquito species abundance per site (2005–2008). The two bottom rows show the total number of individuals sampled and the total number of trap-nights in the sampling effort.

Mosquito species	Site							
	WW	SC	EC	S11	S10	S7	S5	S1
Aedes vexans (Meigen)	1743	1815	662	1579	140	625	444	628
Anopheles perplexens Ludlow	1	0	0	0	0	0	0	1
Anopheles punctipennis (Say)	16	19	19	30	3	8	14	33
Anopheles quadrimaculatus Say	14	50	4	24	3	2	3	30
Anopheles walkeri Theobald	0	0	0	0	0	0	0	5
Coquillettidia perturbans (Walker)	16	25	6	10	3	5	1	45
Culiseta inornata (Williston)	13	1	15	3	2	2	8	16
Culex erraticus (Dyar and Knab)	1	89	0	7	0	0	0	0
Culex pipiens Linnaeus	3655	2435	3126	3165	1220	3494	2679	3997
Culex restuans Theobald	171	139	177	24	20	134	141	327
Culex tarsalis Coquillett	12	7	11	7	1	27	8	3
Aedes (Ochlerotatus) canadensis (Theobald)	0	0	1	0	0	0	0	1
Aedes (Ochlerotatus) japonicus (Theobald)	1	0	3	2	0	2	0	2
Aedes (Ochlerotatus) triseriatus (Say)	34	118	1305	101	2	3	10	61
Aedes (Ochlerotatus) trivittatus (Coquillet)	786	286	243	1025	87	30	62	152
Orthopodomia signifera (Coquillett)	1	0	1	0	0	6	2	0
Psorophora ciliata (Fabricius)	0	0	0	0	1	0	0	0
Psorophora ferox (von Humboldt)	0	0	0	0	0	0	0	1
Uranotaenia sapphirina (Osten Sacken)	0	2	1	0	0	0	0	0
Total number of individuals	6464	4986	5574	5977	1482	4338	3372	5302
Total number of trap-nights	178	133	149	159	142	177	165	162

RNA using reverse transcription, real time polymerase chain reaction (Hamer et al. 2008). Maximum likelihood estimates for infection rates were calculated using the pooled infection rate method (Ebert et al. 2010).

Statistical analysis

Landscape composition.—To quantitatively describe the composition of the sites we performed a principal component analysis (PCA) on the above described vegetation, landcover and topography variables. Briefly, PCA is a dimension reduction technique based on the eigen-decomposition of a variance-covariance matrix of variables, followed by the reconstruction of components by the projection of the original data matrix on eigenvectors associated to the different eigenvalues (Venables and Ripley 2002). Since there is no reason to "a priori" assume that the best way to measure landscape composition with these variables is to compute the PCA on the means, we also computed the PCA on the variables range and standard deviation for the study sites. We computed the area for each site using ArcGIS 9.3 to test for effects of area on the abundance of species (MacArthur and Wilson 1963). To test for possible effects of the context, i.e., the immediate landscape matrix surrounding the study sites (Wiens et al. 1993), we also computed a PCA on the same variables for the buffer strip of 100 m around each site perimeter. The perimeter/area ratio was also computed in order to account for a possible effect of patch shape (Wiens et al. 1993).

Richness estimation.—To determine if our sampling was representative of the mosquito community of Chicago, we estimated the richness (total number of species) for the eight sites using the Chao2 estimator (Chao et al. 2005) on the incidence matrix (Table 1). We chose Chao2 because our sampling was based exclusively on the use of light traps. We also estimated a species accumulation curve using the rarefaction method (Colwell and Coddington 1994), where the expected species richness and its standard deviation are obtained by sampling individuals based on their abundance per trap-night. For the analysis we used the package vegan for R.

Richness and diversity association with landscape and climatic variability patterns.—To study patterns of mosquito species richness and diversity (a.k.a., species evenness) we, respectively, counted the number of species and estimated the Shannon index (Krebs 1998) for each site, both for the whole study period and for each year. We studied the association between richness and diversity with measurements of landscape composition and annual climatic patterns. We used a

twofold strategy to understand the spatial/temporal scale at which landscape and climatic variability are associated with patterns of mosquito diversity. First, we focused on the spatial patterns of richness and diversity for the whole study period. We studied the correlation between the measurements of landscape composition described previously and the richness and diversity of each site for the whole study period. Then we performed a linear regression of richness and diversity on the predictors with the highest correlation. For richness we also regressed its logarithm as function of the site area logarithm to test for the presence of a species area relationship as predicted by the theory of island biogeography (MacArthur and Wilson 1963).

We then moved one step forward and tested alternative hypotheses regarding the importance of β-diversity drivers across the sites. If species dissimilarity across sites was driven by dispersal limitation we expect richness dissimilarities to be positively associated with increasing geographic distance. We also expect to see more species turnover than nestedness across sites, i.e., with the difference in richness due to the presence of different species across sites. If the dissimilarity was driven by habitat suitability we will expect the pattern to be positively associated with increasing dissimilarities on landscape conformation; we also expect to see a low species turnover relative to the species nestedness across sites, i.e., with the difference in richness due primarily to the loss of species in the less species rich sites. To test these alternative hypotheses we computed the multi-site Sorensen index, β_{SOR}, which allowed us to partition the dissimilarity between sites as driven by species turnover (i.e., richness differences due to species being different) using the multi-site Simpson index, β_{SIM}, and by species nestedness (where the richness across sites is different because species are subsets of the most species rich site) using the nestedness index, β_{NES} (Baselga 2010). We computed the dissimilarity between each two sites for the three previously described β-diversity indices. To visualize the similitude between species composition, geographical distance and landscape conformation we performed an agglomerative cluster analysis (Venables and Ripley 2002). We also estimated the Pearson correlation between the dissimilarities and the geographical and landscape conformation distance, testing its significance with a Mantel permutation test to account for the lack of independence in the observations (Sokal and Rohlf 1994).

Second, we focused on the spatio-temporal patterns by studying the annual per site data. We analyzed annual totals because the sampling of the sites was not synchronous, which restricted the possibility of analysis at a more finely grained temporal scale. We employed linear mixed effects regression models (Faraway 2006) to study the association of species richness and diversity evenness in the sites across years with different aspects of climate. As a first approximation, we considered site and year as random factors. This was done in order to account for the lack of independence in our data as a product of the repeated sampling at the same sites (Chaves 2010). We also weighted the regression with the number of traps-nights per year and site to correct for the heteroscedasticity, i.e., unequal variance, due to the unequal sampling effort across years and sites (Faraway 2004). Following the selection of the random factors, we fitted a full mixed effects regression that included as fixed predictors, i.e., independent variables, the average, standard deviation and kurtosis of temperature and rainfall for each year estimated with data from mid May to mid August. We selected random and fixed factors by a process of backward elimination, based on the minimization of the small sample size bias corrected Akaike information criterion, AICc, and Bayes information criterion, BIC, in order to ensure a robust process of model selection (Faraway 2006). For the models selected as best we verified the normality, homoscedasticity (i.e., equal variance) and independence assumptions of the error. We inspected residuals vs fitted values plots, normal quantile plots, and performed the Shapiro-Wilk test for residual normality (Faraway 2006).

Mosquito abundance patterns.—To study the relationship of mosquito abundance with climatic variability, species richness and diversity evenness we fitted mixed effects multiple regressions (Chaves 2010) for the annual average number of total mosquitoes/trap-night and for *Cx pipiens*/trap-night per site as a function of the number of species (richness), Shannon index

(diversity evenness), and average, standard deviation and kurtosis of temperature and rainfall, weighting the regression to account for the unequal annual sampling effort per site (Faraway 2004), and with site and year as random factors. We selected models and verified model assumptions following the same procedures described in the section describing the statistical analysis for *Richness and Diversity Association with Landscape and Climatic Variability Patterns*. To further inquire on possible non-linear impacts of the covariates we also fitted regression trees of the annual average number of mosquitoes/trap-night and *Cx pipiens*/trap-night as function of richness, diversity and climatic and landscape covariates. Briefly, a regression tree is a set of rules developed from the independent (or predictor) variables that can best recreate the observed pattern in the response variable (Olden et al. 2008), mosquito abundance in our analysis. We employed this technique given its power to capture non-linear relationships between variables, and the lack of assumptions about spatial or temporal autocorrelations (Chaves 2010). Regression trees also allowed to model the impacts of climatic variability (dynamic factors) and landscape composition (static factors) together, an unfeasible analysis within the framework of linear models.

Mosquito infection patterns.—We used regression trees to model the estimated annual infection rates from *Culex pipiens* mosquito pools per site as function of landscape and climatic variability co-variates, species diversity and richness, total mosquito (all species) and *Culex pipiens* abundance per trap-night. We chose this technique for its ability to capture the non-linear relationships between variables and by allowing the simultaneous analysis of dynamical and static factors. For this analysis we did not consider the estimates for sites S5 (mean, [95% CL]: 30.74, [17.02–52.85]) and WW (40.21, [12.97–110.58]) in 2007, which were unusually high and likely an artifact of the small number of pools employed for the estimation (Ebert et al. 2010).

Results

We collected a total of 37,495 individual mosquitoes over 1,265 trap-nights at the 8 sites during 2005–2008. Table 1 summarizes the species and cumulative abundance of mosquitoes and night-trap sampling effort for each site. The number of mosquitoes captured in the ground traps in 2005 was 176 (out of 6697, i.e., less than 3% of the total captures, raw data available in the Supplement). Since this number was so low, diversity and richness estimates were almost identical when these traps were included or excluded. Thus, to increase the power of each analysis, we decided to include the 2005 ground traps in all our analyses. Most mosquito species were native, with the exception of *Aedes japonicus*, a recent invasive species of North America (Peyton et al. 1999). The mosquito species we collected exploit a very diverse array of habitats and also present several strategies for seasonal overwintering (see Appendix: Table A1 for a detailed account). Model estimation of species richness robustly support that mosquito species sampling was comprehensive and representative of the meta-community present in the area. We collected 19 species, which is within the range of the Chao2 species richness estimate (Fig. 2A). Also, the species accumulation curve levels off (Fig. 2A) as expected with a comprehensive sampling of diversity. Finally, the thoroughness of our sampling is further supported by the incidental sampling of the area where only 4 additional rare species have been found (Loss et al. 2009*a*). Fig. 2B shows the results of the PCA analysis used to measure landscape composition. The PCA on the standard deviation of the landscape components explained the most variability (89%) when compared with a PCA on the range (88%) or average (83%) of the landscape components. Since the PCA on standard deviation of the landscape components measures the sites landscape variability, the resulting components can be interpreted as a measure of landscape heterogeneity. The first component (LAND) is a contrast between high variability values for elevation, slope and canopy (positive values), impervious surfaces and open land cover (negative values). The second component (LAND2) is a weighted average of all variables but elevation, where more positive values indicate more habitat heterogeneity (for details on the loadings of these two components see Appendix: Table A2). A paired t-test showed no significant differences between the context (the 100 m strip area buffer around each site

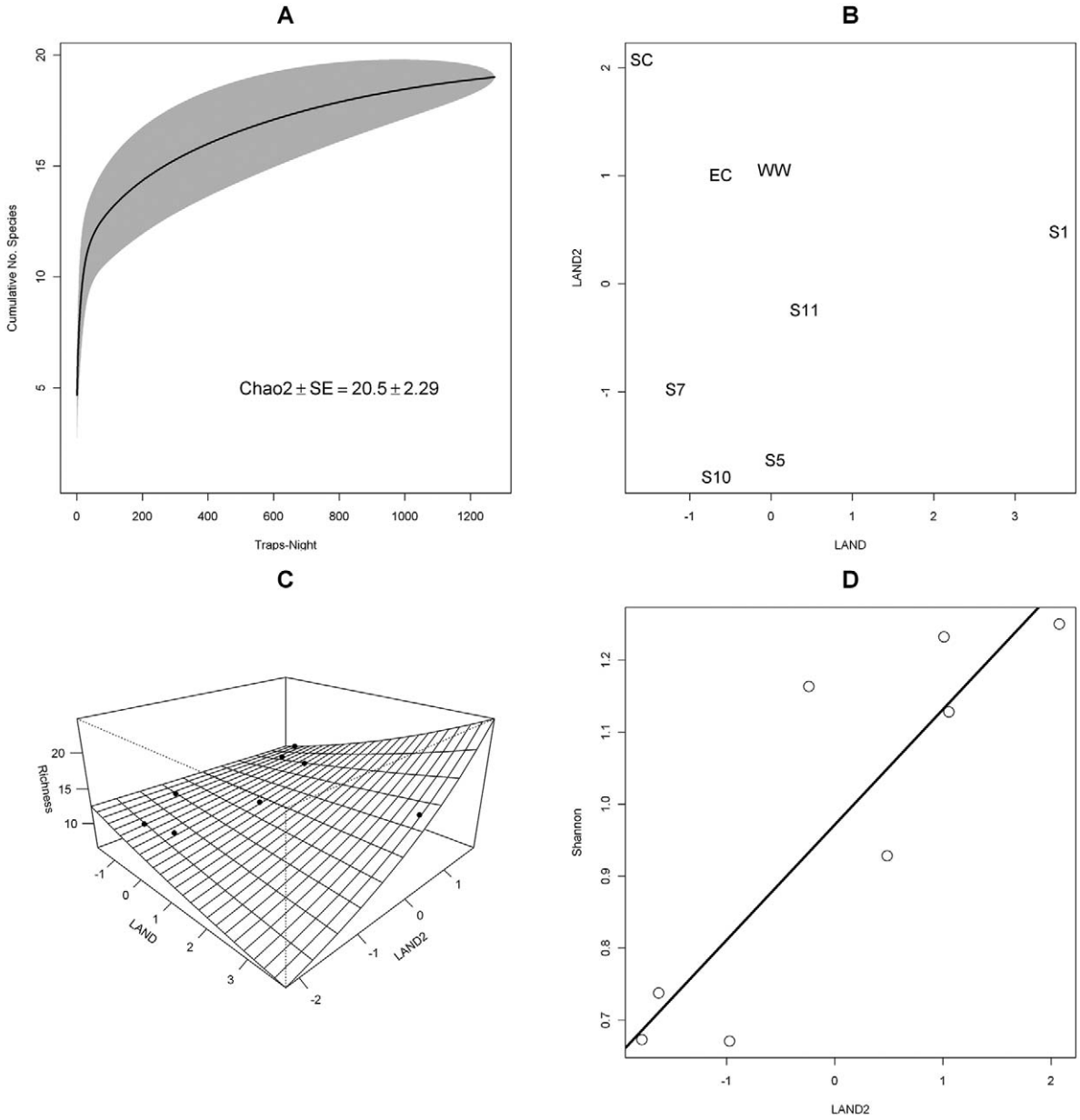


Fig. 2. Mosquito species richness and diversity in the City of Chicago. (A) species accumulation curve. As shown by the plot the mosquito community was extensively sampled. (B) First two components of a principal component analysis on the standard deviation of elevation, slope, canopy, impervious surfaces and percent of open land cover. (C) Surface of the best model fitted to explain mosquito species richness. The model shows a non-linear relationship between landscape heterogeneity and species richness, where mosquito species richness is maximized by habitat heterogeneity. (D) Linear regression between community evenness and landscape heterogeneity.

perimeter) and sites conformation (see Appendix: Table A2). Fig. 2B also shows that sites presented a gradient of landscape heterogeneity**.** When temporal dynamics were ignored, and the analysis was only focused on spatial patterns, log-transformed Richness was best explained by the

interaction between LAND and LAND2 (Fig. 2C). This model ($F_{3,4} = 21.02$, $P < 0.007$, $R^2 = 0.94$) outperformed simpler models, which considered: LAND ($F_{1,6} = 3.12$, $P < 0.13$, $R^2 = 0.34$); LAND2 ($F_{1,6} = 5.07$, $P < 0.06$, $R^2 = 0.45$), log area of the sites ($F_{1,6} = 0.87$, $P < 0.39$, $R^2 = 0.13$) and patch shape, i.e., ratio area/perimeter ($F_{1,6} = 0.28$, $P < 0.61$, $R^2 = 0.04$) as unique explanatory variables. Diversity evenness (Fig. 2D) was best explained by LAND2 ($F_{1,6} = 21.25$, $P < 0.0036$; $R^2 = 0.78$). Here, the positive slope (estimate ± SE: 0.1599 ± 0.0346, $t_6 = -4.61$, $P < 0.0036$) indicates that more homogeneous habitats were less diverse. In all the best linear regressions the assumptions of an identical and independent normal distributed error were fulfilled.

β-diversity measurements indicated a moderate degree of difference in species composition across sites ($\beta_{SOR} = 0.39$), with most of the differences explained by species turnover ($\beta_{SIM} = 0.25$) than by species nestedness ($\beta_{NES} = 0.14$). Fig. 3 Shows that in general patterns of clustering by the differences in β-diversity according to the β_{SOR} index do not match those of geographical and landscape distance. In fact, the correlations between β_{SOR} and its components (β_{SIM} and β_{NES}) were low and not statistically significant (Fig. 3).

Analysis of spatio-temporal patterns of richness and diversity evenness revealed that climatic variability is an important factor in explaining evenness in mosquito communities (Appendix: Table A3). However, for richness no simple climatic factor was of importance to explain differences across years, since, as shown by the process of model selection (Appendix: Table A3), the best model only considered site as random factor. For richness most of the variability was at the level of individual observations (Table 2). By contrast, for diversity evenness most of the variability was temporal (Table 2), and the most important predictor was rainfall (Table 3). Also, both the average and kurtosis of temperature were statistically significant in explaining the observed diversity evenness patterns.

Regarding mosquito abundance of all species and of *Culex pipiens* specifically, with the linear regression approach (Table 4) the use of random effects was unnecessary (Appendix: Table A4) and abundance was related to species richness in a non-monotonic fashion (represented by a convex second degree polynomial), where mosquito density is maximized at intermediate species richness, and the lowest mosquito abundance was associated with the highest mosquito species richness. For all mosquito species we found that increases in the average annual rainfall and temperature, and the kurtosis of temperature diminished the average number of mosquitoes per night-trap. This model was statistically significant ($F_{5,26} = 9.465$, $P < 3.115e-05$). For *Cx pipiens* abundance (Table 4) we found that average temperature and diversity (Shannon index) and richness were significant factors ($F_{4,27} = 7.452$, $P < 0.000352$). The relationship with richness was similar to that observed for all mosquito species. Although the squared term for richness was not significant, the AICc of this model was more than 3 units below a model without it. Increased temperature and more diverse communities were associated with fewer *Cx pipiens* individuals. In all the best linear models assumptions of identical and independent normal distributed error were fulfilled.

To visualize the results from the regression trees (Fig. 4) it is necessary to know that inequalities at each tree node are followed to the left branch. For example, for all mosquito species more variability in Rainfall (SDR > 1.392) predicted the highest mosquito abundance per trap-night (67.55). When SDR ≤ 1.392, abundance was determined by landcover heterogeneity (LAND2). When LAND2 < 0.6071, abundance was between 18 and 54 mosquitoes trap-night, with the value depending on rainfall variability (SDR) and area of the sampled site (Area_Km2). When LAND2 ≥ 0.6071 abundance was between 12 and 22 mosquitoes per trap-night, with less mosquitoes associated with less species richness. Here, it is worth highlighting how this regression tree ($R^2 = 0.69$, Fig. 4) was more successful than the multiple regression ($R^2 = 0.65$, Table 4) at capturing the relationship between diversity and overall mosquito abundance. The *Cx. pipiens* tree showed that abundance of this mosquito species was not sensitive to landscape features, with the greatest abundance, 30 mosquitoes/trap-night, associated with high variability in temperature (SDT > 7.747). When SDT ≤ 7.747 the tree showed that increased kurtosis in the rainfall (KR ≥ 8.389) was associated with increased mosquito abun-

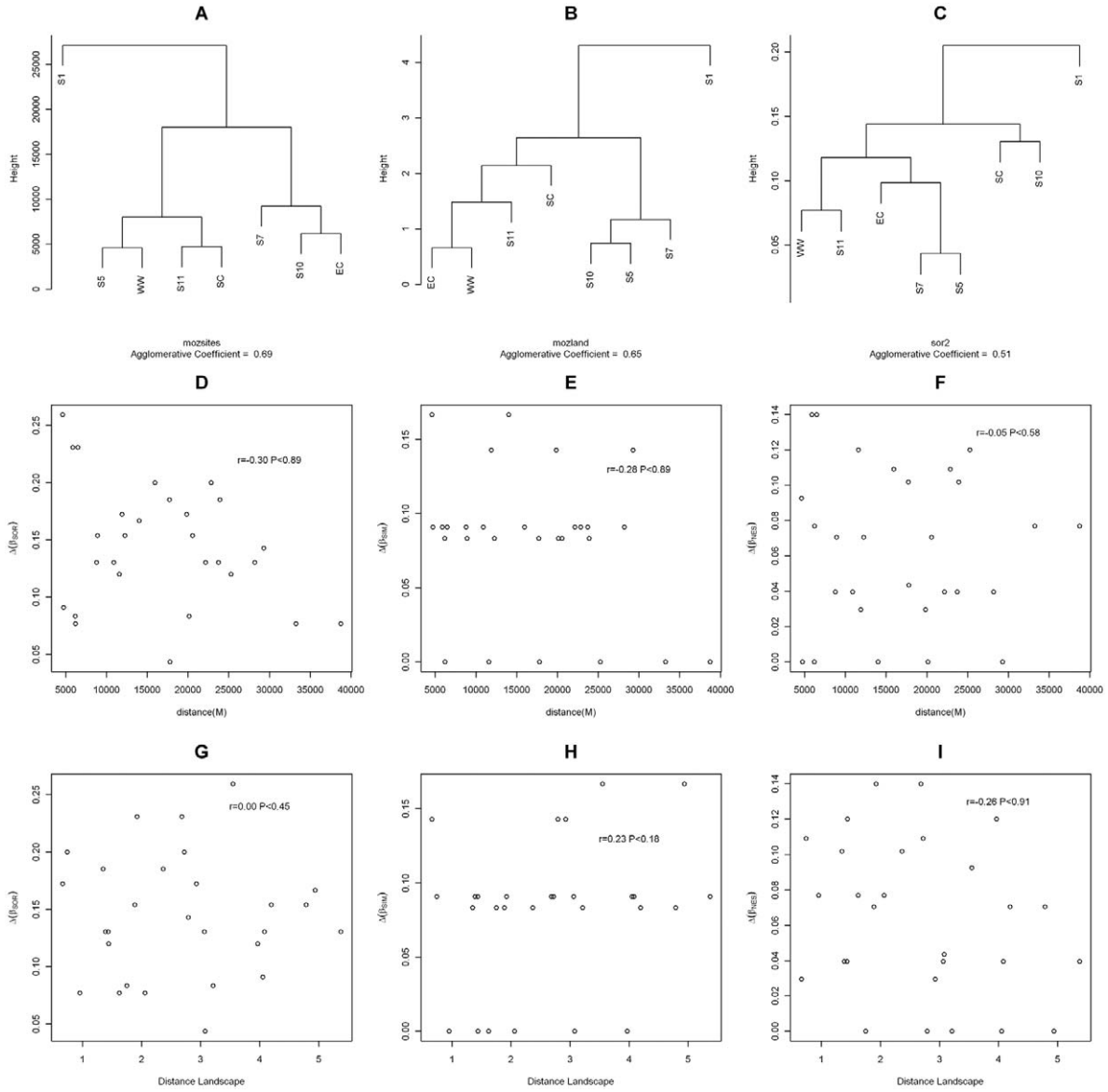


Fig. 3. β-diversity relationships with geographic and landscape distance. (A) Cluster analysis of the euclidean distance between sites. (B) Landscape, measured with LAND and LAND2, see Fig. 2 for details. (C) The β-diversity measured with the multi-site Sorensen dissimilarity index. β-diversity dissimilarity (Δ), SOR = Sorensen, SIM = simpson and NES = Nestedness, association with Euclidean distance between sites (in meters, Panels D, E, F) and landscape (measured with LAND and LAND2, Panels G, H, I, see Methods and Fig. 2 for details). In panels D–I the significance (P) of Pearson's correlation (r) was obtained with a Mantel test.

dance (between 17–27 per trap-night). Here, more even communities (Shannon $\geq$ 0.774) had a reduced abundance of mosquitoes (17 per trap-night). When KR $<$ 8.389 mosquito abundance was between 10 and 19 individuals per trap-night.

The mosquito infection rate tree (Fig. 5) showed that rainfall variability was the most important factor explaining the variability in West Nile virus mosquito infection rates (MIR). More leptokurtic rainfall patterns (i.e., those where the variability is concentrated around the

Table 2. Parameter estimates for the random factors of the best spatio-temporal mixed effects models explaining mosquito species richness and diversity.

Random factor (variance)	Richness	Diversity
Site	0.0005	0.00046
Year	—	0.1670
Error	0.0144	0.0346

Table 3. Parameter estimates for the fixed factors of the best spatio-temporal mixed effects model explaining mosquito species diversity.

Fixed factor	Estimate	95% CI	P
Rainfall (average)	6.95	4.23–9.41	<0.001†
Temperature (average)	0.77	0.06–1.38	0.004†
Temperature (kurtosis)	6.05	4.06–7.70	<0.001†

†Statistically significant ($P < 0.05$).

median rainfall, KR $<$ 5.38) with low rainfall (MR$<$ 0.33 mm/week) predicted the maximum observed MIR, which was about 20. Besides rainfall, landscape and total mosquito (all species) density also explained differences in MIR. When KR $<$ 5.38 and MR$\geq$ 0.33 mm/week, mosquito densities above ~22 mosquitoes per trap-night reduced the infection rate from 15 to 10. Flat landscapes with high coverage of impervious surface (LAND $\geq$ 0.23) also increased the infection rate, from 8 to 11.

Discussion

Cities provide unique opportunities to test hypothesis regarding the drivers of biodiversity patterns and to measure their associated "ecosystem services" (McIntyre 2000, Grimm et al. 2008). The importance of understanding mosquito biodiversity in cities is two-fold: as a model to study general questions on the processes driving biodiversity patterns across ecosystems (Eisen et al. 2008, Gleiser and Zalazar 2010, Julião et al. 2010), and because little if any attention has been given to the potential role of mosquito biodiversity as associated with reductions in the entomological risk of disease transmission (Schäfer et al. 2004, Yasuoka and Levins 2007, Ferguson et al. 2010). Our study shows that mosquito species richness and diversity are a function of landscape heterogeneity. This is noteworthy because the fitting of a species area curve to our data was not significant, unlike the results from other urban ecology studies (Helden and Leather 2004, Zanette et al. 2005, Matteson et al. 2008). This may be related to the fact that habitat heterogeneity was not related to habitat size, unlike studies that reported significant associations (Helden and Leather 2004, Matteson et al. 2008). In fact, MacArthur and Wilson (1963), were well aware that one of the possible reasons behind the species area curve relationships was the increase of different habitats with area. In our study habitat heterogeneity did not increase with area. This is likely a feature common to several cities where more diverse habitats for living organisms are in parks and other natural areas, which are not necessarily the largest contiguous landscape units. We think the importance of habitat heterogeneity to explain mosquito diversity patterns is related to the presence of different mosquito larval habitats. To further articulate this point we need to consider the natural history of mosquitoes, which undergo a major niche transformation during their ontogenetic development: adults are terrestrial, while larvae are aquatic

Table 4. Parameter for the best model explaining overall mosquito and *Culex pipiens* abundance per trap-night.

	All mosquitoes ($R^2 = 0.65$)				*Culex pipiens* ($R^2 = 0.52$)			
Parameter	Estimate	SE	t	P	Estimate	SE	t	P
Intercept	32.18	2.27	14.16	<0.0001†	19.09	1.33	14.33	<0.0001†
Richness	40.88	12.09	3.38	0.00229†	29.98	7.89	3.80	0.000750†
$(\text{Richness})^2$	−26.36	13.62	−1.94	0.06393‡	−10.54	7.56	−1.39	0.174641 ‡
Temperature (average)	−45.52	14.36	−3.17	0.00387†	−5.46	1.51	−3.60	0.001249†
Rainfall (average)	−35.60	14.24	−2.50	0.01903†	—	—	—	—
Temperature (kurtosis)	−13.31	5.23	−2.54	0.01720†	—	—	—	—
Diversity (Shannon index)	–	–	–	–	−7.33	1.65	−4.44	0.000137†

†Statistically significant ($P < 0.05$).
‡Comparison of this model to a simpler one resulted in a statistically significant difference ($P < 0.05$) for that reason the quadratic term is included.

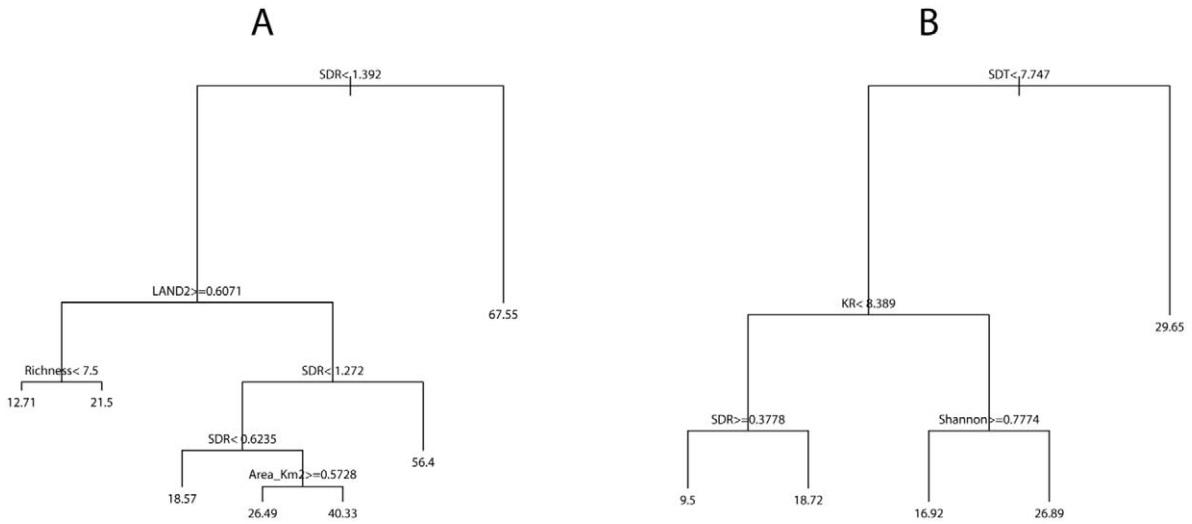


Fig. 4. Mosquito abundance regression trees. (A) All species, $R^2 = 0.69$ and (B) *Culex pipiens*, $R^2 = 0.59$. Shannon = Shannon index, Richness = number of species, K = Kurtosis, SD = Standard Deviation, R = rainfall, T = temperature. LAND2 is a measurement of landscape heterogeneity and Area_Km2 is the area of the sampled site in squared Km. Values in the terminal nodes are for average mosquito abundance per trap-night. For each tree all predictions were cross-validated and the minimum split size, i.e., minimum number of observations per node, was eight.

(Silver 2008). Although adult blood foraging at the community level does not appear to be segregated nor specialized (Chaves et al. 2010), specialization in larval habitat exploitation does appear to be the rule (Mogi 1978, Schäfer and Lundström 2001, Barker et al. 2003, Juliano 2009). In fact, the anatomy of mosquito larvae mouth parts present a degree of morphological adaptations across species not observed in adults (Merritt et al. 1992). Thus, habitat filtering, or selection/speciation (Vellend 2010), where presence of mosquito species is linked to the presence of habitats across heterogeneous landscapes, seems to be a major determinant of mosquito biodiversity patterns in Chicago.

Further support for habitat filtering as the most important process driving urban mosquito biodiversity patterns comes from the lack of support for alternative processes. We tested whether differences in species composition across sites could be explained by geographic distance, and found no significant support to the role of distance, thus discounting a major role for dispersal as a process driving mosquito diversity in Chicago. This could be related to the fact that the urban landscape at large is a landscape matrix that does not limit the dispersal (Perfecto and Vandermeer 2008) of the various mosquito species. Indeed, we found no significant differences between the landscape composition of our sites and their context, i.e., the buffering area surrounding our study sites. Also, biodiversity differences across sites were more related to a species turnover than to the lack of species from the more species-rich sites, a result that does not support an important role for drift (Hubbell 2001, Vellend 2010) as a major driver of urban mosquito biodiversity patterns.

The understanding of the relative role of selection and speciation as drivers of mosquito biodiversity will require further study, beyond the scope of the current study. As shown by our analysis most of the differences in species composition across sites is due to the turnover of species, which can reveal the conjunction of both ecological and evolutionary processes. To solve whether differences are purely ecological or have an evolutionary imprint, a comparative analysis of community phylogenetic structure is necessary. Non-random patterns of phylogenetic clustering may reveal the relative importance of competition and evolutionary conservatism on

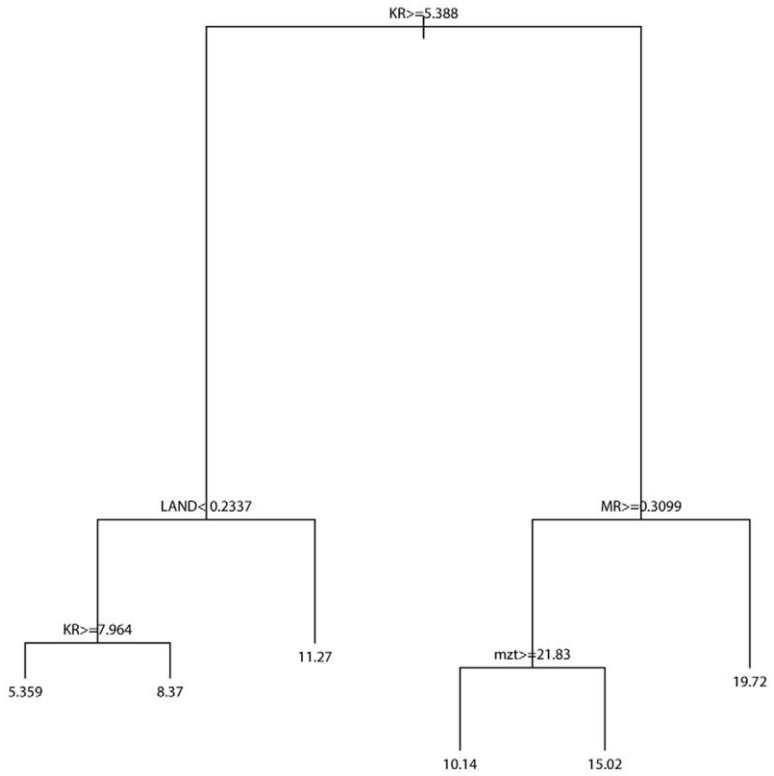


Fig. 5. Mosquito infection rate regression tree $R^2 = 0.85$. K = Kurtosis, M = mean, R = Rainfall, LAND = Land topography index (positive values indicate flats areas with open and impervious surfaces), mzt = total mosquito (all species) density per trap-night. Values in the terminal nodes are estimated pooled mosquito infection rate. For this tree all predictions were cross-validated and the minimum split size, i.e., minimum number of observations per node, was eight.

community composition (Vamosi et al. 2009). Also beyond our study is the assessment of possible bias in mosquito species detection related to our sampling method (Huffaker and Back 1943, Brown et al. 2008). Although it has been shown that modern mosquito traps such as the mosquito magnet outperform mosquito light traps in terms of mosquito abundance and diversity in trap comparisons (Brown et al. 2008), we feel confident about our exhaustive sampling of the mosquito meta-community, as confirmed by model estimation, by the species accumulation curve and by faunal descriptions of mosquitoes of North America.

Our study also points to the need to fully account for the dynamics of the changing environment when testing the importance of the different processes shaping diversity patterns. All the fundamental processes proposed by Vellend (2010) are internally related to dynamic changes in the environment, and our results clearly illustrate this point. Although species richness was unaffected by the changing environment, spatio-temporal patterns of diversity were associated with climatic variability in a fashion where more rainfall and extreme variability in temperature, as measured by kurtosis, increased the evenness of the mosquito communities sampled in our sites. This result is of particular interest because it reveals that mosquito communities are sensitive not only to average environments, but also to their patterns of variability (Levins 1968). This pattern of sensitivity to climatic variability has also been observed in communities of tropical mosquitoes (Franklin and Whelan 2009), where mosquito assemblages present consistent temporal patterns of assembly linked to rainfall seasonality. In fact,

the abundance of mosquitoes per trap-night in our study was most sensitive to the variability in rainfall as measured by the standard deviation of rainfall. Similarly different components of climatic variability were of importance to explain the abundance per trap-night of *Cx pipiens*. This pattern of increased sensitivity to the variability of meteorological conditions as opposed to their average values is an expression of Schmalhausen's law, whereby organisms are more sensitive to small changes in environmental conditions when pushed beyond their limits of tolerance for any single environmental variable (Chaves and Koenraadt 2010). For mosquitoes, the sensitivity to rainfall reinforces the idea that climatic variability impacts mosquito diversity through disturbances to larval habitats that could promote the co-existence of species (Chesson and Huntly 1997).

Beyond the major role of climatic variability in determining the patterns of abundance of all mosquito species, and especially *Cx pipiens*, a pattern described in other settings (Yasuoka and Levins 2007, Yang et al. 2008, Barker et al. 2010), our results show that increases in biodiversity reduce the abundance of mosquitoes. For all mosquitoes the linear regression showed a convex relationship with species richness, meaning that the most species rich communities harbor fewer mosquitoes. Increases in diversity evenness were associated, both in the linear model and regression tree, with reduced abundance of *Cx pipiens*. These results support the idea that mosquito diversity is associated with the ecosystem service of mosquito nuisance species reduction in urban areas. The latter is illustrated by both the reduction of overall mosquito density and especially that of *Cx pipiens*, a major vector of filarial worms and several viruses causing encephalitides. Whether the pattern of reduced mosquito abundance is related to interactions between mosquito species or between mosquitoes and other species, and how variable these interactions can be because of rainfall variability, is an open question. Previous studies have shown that *Cx pipiens* can be regulated by the interaction with other species, especially predators (Mogi and Okazawa 1990) and that its abundance is related with habitat degradation (Britton 1914), probably mediated by oviposition habitat selection (Chaves et al. 2009) which is sensitive to meteorological variability (Chaves and Kitron 2011), release from predators (Calhoun et al. 2007), and a faster and environmentally autonomous development (Chaves et al. 2011). In this sense, we can affirm that habitat homogenization in cities has positive impacts on the house mosquito, a trend common to other "pest" species (McKinney and Lockwood 1999).

Mosquito infection rates (MIR) in Chicago followed patterns previously described for West Nile virus, where highly variable rainfall regimes and relatively dry years can increase the entomological risk of disease transmission (Shaman et al. 2002, 2005, Ruiz et al. 2010). Although there was no direct association between mosquito diversity and the entomological risk of disease transmission, our study shows that infection is associated with total mosquito density (i.e., the number of mosquitoes from all species/trap-night), which itself is associated with mosquito species richness. According to our models, the relationship between mosquito abundance and species richness is non-monotonic, with the abundance of mosquito being maximized at low richness levels, yet not at the lowest species richness. Thus, in principle, more species rich mosquito communities could be a predictor for a decreased entomological risk of disease transmission. However, other reasons could explain the patterns we observed. Other plausible explanations for the patterns we observed range from the presence/absence of reservoirs (Hamer et al. 2008), to differences in the environmental conditions for pathogen development (Edman 1988), and mosquito control (Gubler 2007). Nevertheless, several studies have shown that nuisance produced by mosquitoes is unequivocally increased with the density of mosquitoes (Edman and Kale 1971, Fujito et al. 1971, Sota et al. 1991). Thus, the decrease of nuisance species abundance with diversity is a major result that illustrates the ecosystem services associated with increased species diversity. Finally, our study highlights the need to consider the communities associated with dominant vector species in order to fully understand the relationship between biodiversity and disease transmission patterns.

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APPENDIX

Table A1. Mosquito species, native/exotic status, larval habitats and overwintering strategies.

Mosquito species	Native/ exotic	Larval habitat	Overwintering strategy[1]
Aedes vexans (Meigen)	N/E¶	Flood water†	Diapausing eggs
Anopheles perplexens Ludlow	N	Clear calcareous springs and associated run-off habitats‡	Adult females
Anopheles punctipennis (Say)	N	Slow moving streams and permanent pools†	Adult females
Anopheles quadrimaculatus Say	N	Marshes and ponds†	Adult females
Anopheles walkeri Theobald	N	Marshes and ponds edges with abundant emergent vegetation†	Diapausing eggs
Coquillettidia perturbans (Walker)	N	Permanent bodies of water with muddy substrates and abundant emergent vegetation (e.g., cattails)†	Larvae
Culiseta inornata (Williston)	N	Temporary and semi-permanent woodland pools†	Adult females
Culex erraticus (Dyar and Knab)	N	Lakes, ponds, and slow moving sections of streams†	Adult females
Culex pipiens Linnaeus	N/E¶	Artificial containers (e.g., catch basins, barrels, flower pots, discarded tires) and stagnant, temporary pools with a high organic content; highly tolerant of polluted waters†	Adult females
Culex restuans Theobald	N	Natural and artificial containers (e.g., catch basins) §	Adult females
Culex tarsalis Coquillett	N	Newly-created sunlit surface water pools that are frequently surrounded by grasses and annual vegetation†	Adult females
Aedes (Ochlerotatus) canadensis (Theobald)	N	Temporary (vernal) leaf-lined woodland pools†	Egg
Aedes (Ochlerotatus) japonicus (Theobald)	E	Natural and artificial containers including rock holes along stream beds, tree holes, catch basins, bird baths, and discarded tire casings†	Egg
Aedes (Ochlerotatus) triseriatus (Say)	N	Natural tree holes†	Egg
Aedes (Ochlerotatus) trivittatus (Coquillet)	N	Temporary woodland pools and floodwater depressions†	Egg
Orthopodomia signifera (Coquillett)	N	Tree holes†	Egg/larvae
Psorophora ciliata (Fabricius)	N	Temporary grassy pools and roadside ditches in sunlit areas†	Egg
Psorophora ferox (von Humboldt)	N	Temporary woodland pools and depressions in shaded floodplains†	Egg
Uranotaenia sapphirina (Osten Sacken)	N	Permanent swamps and ponds†	Adult females

† From Andreadis et al. (2005), ‡ Bellamy (1956), § Reisen et al. (1989).
¶ These are likely ancient invasive species of the New World, but have been established long enough in the Chicago area to be considered native.

Table A2. Loadings of the first two components from a principal component analysis (PCA) on the standard deviation (SD) of several landscape components for each study site. The PCA on the standard deviation (89 %) outperformed the PCA on mean (83%) and range (88%) values in terms of the variability explained by the first two components. The first component from the PCA on the SD of landscape components was not statistically different to the estimate for the buffer area of 100 m around each site perimeter ($t_7 = 0$, $p < 1$, Paired *t*-test).

Variable	LAND (PC1)	LAND2 (PC2)
Elevation	−0.612	NA†
Slope	−0.600	0.150
Canopy	−0.412	0.403
Impervious surfaces	+0.216	0.656
Open surface	+0.221	0.619

† NA = value very close to zero.

Table A3. Selection of spatio-temporal models for richness (number of species) and diversity (Shannon Index), as function of average and variability measurements of climatic variables. AICc stands for Akaike information criterion corrected for size bias and BIC for Bayes information criterion. Best models are bolded.

	Richness		Diversity	
Model covariate	AICc	BIC	AICc	BIC
Null: No covariates; site and year as random factors	110.4	116.3	142.0	**146.6**†
Null: No covariates; site as random factor	**96.7**	**101.1**	147.5	151.9
Null: No covariates; time as random factor	108.4	112.8	145.2	149.6
Rainfall (mean, S.D.) + temperature (mean, S.D.); site and year as random factors	114.9	131.5	147.5	159.2
Rainfall (mean, kurtosis) + temperature (mean, kurtosis); site and year as random factors	116.8	132.8	145.4	157.1
Rainfall (mean) + temperature (mean, kurtosis); site and year as random factors	—	—	**139.8**	**150.1**†
Rainfall (mean) + temperature (kurtosis); site and year as random factors	—	—	140.3	150.2

†Although BIC is minimized in a model explaining diversity without fixed factors in the main text we chose to discuss the results of the best model with fixed factors. We did this because it is known that BIC can be biased to select simpler models (Faraway 2006). We also want to highlight that if null models are ignored, the best models explaining diversity according to AICc and BIC match.

Table A4. Selection of spatio-temporal models for mosquito abundance per trap-night of all species and *Culex pipiens* as function of diversity, measured with the Shannon index, and richness, number of species, as function of average and variability measurements of climatic variables. AICc stands for Akaike Information Criterion corrected for size bias and BIC for Bayes Information criterion. Best models are bolded.

	Mosquito abundance		*Culex pipiens* abundance	
Model covariate	AICc	BIC	AICc	BIC
Null: No covariates; site and year as random factors	391.3	396.2	358.2	363.1
Null: No covariates; site as random factor	399.0	403.0	358.4	362.4
Null: No covariates; year as random factor	390.3	394.3	355.6	359.6
Full: richness, diversity (Shannon index), rainfall (mean, S.D., kurtosis) + temperature (mean, S.D., Kurtosis); year as random factor	329.2	337.8	307.1	315.8
Full: Richness, diversity (Shannon index), rainfall (mean, S.D., kurtosis) + temperature (mean, S.D., Kurtosis)	272.0	283.4	239.7	251.1
Richness (second degree polynomial), mean and kurtosis temperature, mean rainfall	**263.9**	**271.8**	—	—
Richness (second degree polynomial), diversity (Shannon index), mean temperature	—	—	**228.4**	**234.3**