

# Rodent assemblage structure reflects socioecological mosaics of counter-urbanization across post-Hurricane Katrina New Orleans

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## ABSTRACT

Often overshadowed by global trends in urbanization, counter-urbanization is also on the rise worldwide. Left unaddressed, counter-urbanization can result in conditions that imperil human well-being. For example, counter-urbanization is hypothesized to increase the prevalence of ecological hazards like synanthropic pest and pathogen host species by shifting habitat and resource availability. In this study, we addressed this hypothesis by examining whether the abundance or diversity of rodent hosts varies according to the prevalence of abandoned, unmaintained properties across a mosaic of counter-urbanization in post-Hurricane Katrina New Orleans (Louisiana, USA). We also sought to determine whether management of vacant lots can influence the abundance or diversity of rodents across counter-urbanizing landscapes. Analysis of capture data from multi-year trapping efforts across the greater New Orleans area showed that total rodent abundance was highest in residential areas with high levels of vacancy and unmaintained vegetation as well as low household income and low residency. Greater rodent abundance and richness also occurred in areas with features related to infrastructure loss, such as trash and debris, especially in winter. While these results highlight that property abandonment can augment populations of pest and pathogen host species, our findings also indicate that management of abandoned areas can potentially mitigate public health concerns in counter-urbanizing landscapes.

## 1. Introduction

Global demographic shifts are giving rise to two seemingly contradictory outcomes; an increasing proportion of the world's population resides in cities, and an increasing number of cities are experiencing population loss. For example, in 2012, the global population surpassed the threshold at which more people live in urban centers than elsewhere, and over 66% of the world's population is expected to reside in cities by the year 2050 (United Nations, Department of Economic and Social Affairs, Population Division, 2015). Yet urban population growth is globally and regionally heterogeneous. Often overshadowed by trends like the growth of mega-cities, counter-urbanization is also on the rise worldwide. In Europe, for instance, > 40% of cities with > 200,000 inhabitants have recently declined in population size (Mykhnenko & Turok, 2008). In the United States, 13% of cities with ≥100,000 inhabitants have been experiencing population loss (Großmann et al., 2013; Wiechmann et al. 2012).

Counter-urbanization can result from a range of concurrent and successive factors including economic decline, disasters, and shifting

demography, that determine the pace and magnitude of population loss. While counter-urbanization can be a slow progression – for example, decreasing population growth rates underlie steady declines that are unfolding in cities across a number of European countries (Haase, Rink, Grossmann, Bernt, & Mykhnenko, 2014; Nassauer & Raskin, 2014) – chronic population loss can be punctuated by acute disruptions. For instance, a decadal progression of population loss in Detroit (Michigan, USA) has recently been exacerbated by a severe economic recession (Ryznar and Wagner 2007). Similarly, chronic population loss in New Orleans (Louisiana, USA) spiked in 2005, when levee failures and flooding triggered by Hurricane Katrina resulted in a mass exodus (Wang, Tang, & Wang, 2014).

Landscapes can be transformed by counter-urbanization. Often considered to be synonymous with idled and derelict infrastructure, counter-urbanization also can lead to higher rates of land abandonment (Gulachenski, Gherzi, Lesen, & Blum, 2016; Nassauer & Raskin, 2014). Land abandonment can result in ecological shifts, including biotic changes like increased vegetation growth (i.e., greening). In Detroit, for example, vegetation has increased in areas with greater abandonment

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<https://doi.org/10.1016/j.landurbplan.2019.103710>

Received 27 November 2018; Received in revised form 29 September 2019; Accepted 11 November 2019

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and vacancy rates (Ryznar and Wagner, 2007). Similarly, the composition of plant communities in post-Hurricane Katrina New Orleans (hereafter 'post-Katrina New Orleans') reflects socioeconomically stratified patterns of abandonment (Lewis et al., 2017). Unmanaged greening, which is sometimes referred to as green blight (Lewis et al., 2017), can lead to conditions that could be considered beneficial, such as greater shading and elevated biological diversity (Kattwinkel, Biedermann, & Kleyer, 2011; Riley, Herms, & Gardiner, 2018), but it can also generate ecological disservices, including conditions that are of concern to human well-being (Branas et al., 2018; Eskew & Olival, 2018; Gulachenski et al., 2016; Katz, Connor Barrie, & Carey, 2014; Rael, Peterson, Ghersi, Childs, & Blum, 2016; Troy, Morgan Grove, & O'Neil-Dunne, 2012; Troy, Nunery, & Grove, 2016). Disservices associated with unmanaged greening are receiving greater attention by those charged with safe-guarding public health in cities (Branas et al., 2018; Bogar & Beyer, 2015; Garvin, Branas, Keddem, Sellman, & Cannuscio, 2013; Troy et al., 2016), with the aim of mitigating risks and improving the well-being of affected communities (Lewis et al., 2017).

Counter-urbanization can imperil human health by creating conditions that favor pests and pathogen vectors (Eskew & Olival, 2018; Gulachenski et al., 2016; Rael et al., 2016), which can potentially elevate zoonotic disease risk. Especially across novel human-environment interfaces where residents and wildlife may come into contact (Despommier, Ellis, & Wilcox, 2006). Idled or degraded infrastructure can, for example, increase the availability of habitat supporting pathogen vectors like mosquitos. As has been demonstrated in Baltimore (Maryland, USA), where disinvestment in housing and associated infrastructure has allowed mosquitos to become hyper-abundant, increasing the risk of mosquito-borne pathogen transmission to local residents (LaDeau, Leisnham, Biehler, & Bodner, 2013). Similarly, areas of New Orleans that have experienced greater levels of abandonment since Hurricane Katrina appear to harbor larger commensal rodent populations (Rael et al., 2016). Like mosquitos, commensal rodents in New Orleans are known to carry zoonotic pathogens of concern such as *Bartonella* sp., *Angiostrongylus* sp., and Hantaviruses (Cross et al., 2014; Peterson et al., 2017; Rael et al., 2018). Evidence that abandonment can lead to hyper-abundance of zoonotic pathogen hosts (Rael et al., 2016) highlights the possibility that commensal rodents may drive zoonotic disease outbreaks in areas experiencing counter-urbanization. It is unclear, however, whether the factors driving rodent-associated pathogen transmission risk in urbanizing landscapes (Bordes, Blasdel, & Morand, 2015; Han, Schmidt, Bowden, & Drake, 2015) also determine transmission risk in counter-urbanizing landscapes. Determining the factors that shape rodent diversity and abundance in counter-urbanizing environments thus represents a key step towards preventing zoonotic disease outbreaks worldwide.

Because rodents generally exhibit strong site fidelity, assemblage structure typically corresponds to local habitat characteristics (Meerburg, Singleton, & Kijlstra, 2009). In rural and natural areas, rodent species richness is positively associated with habitat heterogeneity (Horvath et al. 2001). Similar trends have been found in urbanizing landscapes (Cavia, Cueto, & Suárez, 2009). For example, rodent assemblage structure in Buenos Aires (Argentina) varies across a gradient of urbanization, where greater diversity occurs in less urbanized areas (Cavia et al., 2009). Rodent presence and abundance in cities also reflects socioeconomic conditions and factors like accessibility to structures and human-derived food resources (Himsworth, Parsons, Jardine, & Patrick, 2013; Feng & Himsworth, 2014). This is well illustrated by rodent control efforts that aim to limit access to public trash receptacles, which can reduce rodent abundance (Lambropoulos et al., 1999). Some evidence also suggests habitat and resource heterogeneity (i.e., the location and connectivity of parks and other green space) elevate local abundance across urban environments (Combs, Puckett, Richardson, Mims, & Munshi-South, 2018). It is not known, however, whether and how rodent assemblages vary across habitat mosaics in counter-urbanizing landscapes, which can exhibit starkly different

configurations than those that occur in urban and suburban landscapes (reviewed in Gulachenski et al., 2016). For instance, counter-urbanizing landscapes frequently exhibit reduced management or infrastructure inputs due to declining tax bases related to population loss (Gulachenski et al., 2016), which can shift the composition ecological communities (Lewis et al., 2017), potentially resulting in localized areas of greater habitat heterogeneity and resource availability (Kattwinkel et al., 2011; Lewis et al., 2017).

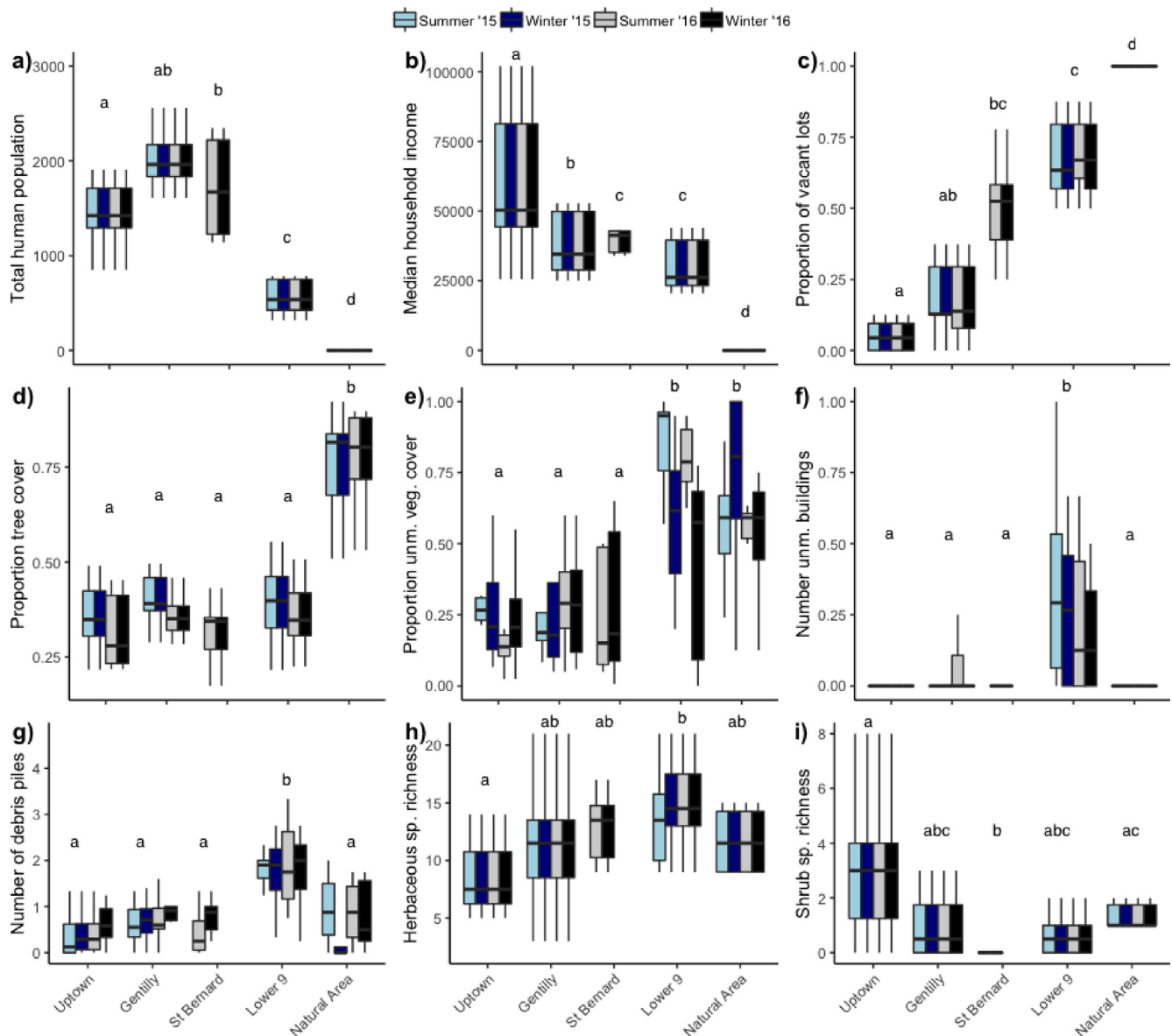
In this study, we examined how rodent assemblage structure varies across post-Katrina New Orleans. Our aim was to elucidate how rodent abundance, richness and diversity vary across mosaics of counter-urbanization. We also aimed to assess whether rodent assemblage structure differs across areas with contrasting municipal policies on post-Katrina vacant lot management in order to shed light on how interventions can shape health risks in counter-urbanizing cities. We hypothesized that rodent abundance and richness vary in relation to land cover, vegetation, as well as human sociodemography (Cavia et al., 2009; Feng & Himsworth, 2014; Walsh, 2014). We predicted that rodents are more abundant in areas exhibiting greater abandonment (measured as vacancy) as well as features indicative of infrastructure decline, such as unmaintained vegetation and debris, as has been observed with other pests and vectors elsewhere (LaDeau et al., 2013). We also predicted that rodent diversity is higher in areas with greater plant or land cover diversity (i.e., 'diversity begets diversity') (Horvath et al. 2001; Stevens & Tello, 2011). We met our study objectives and evaluated our predictions by comparing rodent abundance, richness and diversity among study areas exhibiting varying levels of abandonment, areas that have been subject to contrasting land management strategies, and a natural area adjacent to the city that is devoid of human residency.

## 2. Methods

### 2.1. Study area and study design

Hurricane Katrina, considered to be one of the deadliest and most destructive hurricanes in U.S. history, transformed the sociocultural, built, and ecological features of the New Orleans metropolitan area. Storm surge and the failure of levees flooded over 80% of the urbanized East Bank of New Orleans, displacing approximately 86% of the population. While the population of the city has rebounded since the storm, population recovery has been heterogeneous, with some areas remaining well below pre-Katrina levels (Fussell, Curtis, & DeWaard, 2014; Lewis et al., 2017). The storm also reconfigured ecological communities in New Orleans. For example, pre- and post-Katrina surveys indicate that flooding reduced the abundance of birds and mammals across the city (Yukey, 2012). Comparisons of land cover (Gotham, Blum, & Campanella, 2014) also indicate that Katrina-related flooding reduced landscape diversity across the city. Plot-based plant surveys indicate, however, that post-Katrina vegetation communities reflect post-disaster landscape management as much or more than Katrina-related flooding (Lewis et al., 2017). Post-Katrina management also has resulted in mosaics of abandonment that have reinforced legacies of sociodemographic disparities (Gulachenski et al., 2016; Lewis et al., 2017; Rael et al., 2016).

To meet our study objectives, we assessed rodent abundance and richness in five focal study areas across the greater New Orleans metropolitan region. Study area boundaries were set based on US Census data and historical neighborhood boundaries as described in Lewis et al. (2017). The study areas capture variation in household income, post-Katrina population recovery, and land management (Supplemental Table 1, Fig. 1) that has given rise to differences in vegetation characteristics (Lewis et al., 2017). We trapped rodents in three Orleans Parish neighborhoods: Uptown, Gentilly, and the Lower 9th Ward. The Uptown neighborhood largely escaped Katrina-related flooding, and consistent with this, the predominantly higher income neighborhood

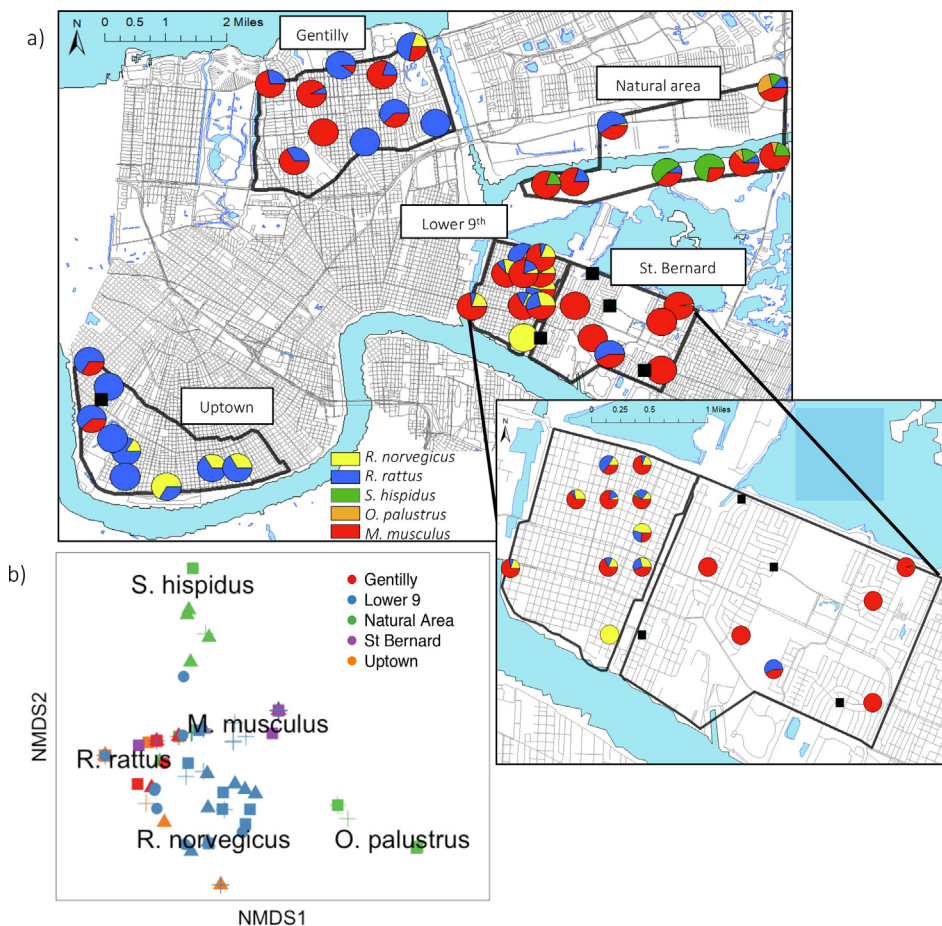


**Fig. 1.** Temporal and spatial variation in socio-environmental characteristics across post-Katrina New Orleans. All variables differed significantly across the city. Letters indicate significant differences among the study areas. Some variables exhibited significant inter-annual variation; for example, unmaintained vegetation (e) was significantly lower in 2016 relative to 2015; while the amount of debris (g) was higher in 2016 relative to 2015. (a,b) Variables developed from 2010 US Census data, (c) variables based on satellite imagery, (d) variables based on GIS derived land-cover classification, (e-g), variables utilizing data generated from on-the-ground estimates from within-block trapping areas, and (h, i) data collected from vegetation plots randomly places within focal trapping blocks.

exhibits the lowest level of vacancy relative to all other study areas (Fig. 1c). Both Gentilly and the Lower 9th Ward experienced extensive flooding, though population recovery has been greater in Gentilly, where median household income is higher and vacancy is lower relative to the Lower 9th Ward (Fig. 1b & c). Comparisons across the three neighborhoods thus offer perspectives on whether rodent communities differ according to human sociodemography and vacancy. We also trapped in the Arabi and Chalmette neighborhoods of St. Bernard Parish (Fig. 2), which are adjacent to the Lower 9th Ward neighborhood. While both the Lower 9th neighborhood and the areas within St. Bernard Parish experienced similar levels of flooding and vacancy (Fig. 1c), the patchwork of managed and unmaintained vegetation in the Lower 9th Ward stand in stark contrast to homogeneously managed vegetation in the adjacent St. Bernard Parish neighborhoods (Lewis et al., 2017; Fig. 1e). Institutional programs intended to foster population recovery created striking mosaics of abandonment across public and privately owned vacant properties in Orleans Parish (Lewis et al., 2017). This is

particularly evident in the Lower 9th Ward, where the New Orleans Redevelopment Agency owns ~600 lots, and these publicly owned lots have been mowed and maintained, while ruderal vegetation growth has been left relatively unchecked on many privately-owned vacant lots (Lewis et al., 2017; Gulachenski et al., 2016). Nearly all vacant properties in the adjacent St. Bernard Parish neighborhoods, on the other hand, have been subject to strict management practices regardless of ownership, including regular mowing of > 1000 lots under the jurisdiction of St. Bernard Parish (Lewis et al., 2017; Gulachenski et al., 2016). Comparisons across the municipal boundary thus offer perspectives on whether rodent communities differ according to municipal land management policies. Lastly, we collected rodents in a non-residential natural area located to the north of the Lower 9th Ward and Chalmette, adjacent to East New Orleans, which enabled us to compare rodent assemblage structure across a full spectrum of land use. The natural area sites are all located along a corridor that was, prior to the 1950s, a mixture of tidal swamp forest, freshwater marsh, and brackish





**Fig. 2.** Distribution of rodent species across post-Katrina New Orleans. (a) Aggregate estimate of occurrence from summer 2015 to winter 2016/2017, with relative abundance of each species from each study site presented in pie charts, alongside a blow-up of the Lower 9th Ward and St. Bernard Parish study areas. Black squares represent study sites where we conducted trapping but did not capture rodents. Black outlines correspond to focal study area boundaries. (b) Non-metric dimensional scaling plot of rodent assemblage structure, colored by study area, with symbols representing season of trapping, summer and winter 2015 (15S, 15W), and summer and winter 2016/2017 (16S, 16W).

marsh. Between 1940 and 1970, the area received dredged sediments from an adjacent navigation canal, which eliminated tidal influence. Since that time, the area has been minimally disturbed by human influence (e.g., development), though it has been subject to storm surge as a result of catastrophic events like Hurricane Katrina in 2005.

## 2.2. Rodent trapping

We estimated rodent abundance and diversity across 48 study sites between May 2015 and February 2017. As described in Lewis et al. (2017), we selected ten study sites within each of the four residential focal study areas by overlaying a 500 m × 500 m grid generated in ArcGIS over the metropolitan area of New Orleans and surrounding areas. We then selected a random subset of 10 sites within each focal residential area that fell at the intersection of the grid-lines for inclusion in our study. Study sites within each residential area corresponded to a city block. We similarly selected eight equally-sized study sites in the non-residential natural area. With the exception of the sites in St. Bernard Parish, we trapped at all sites in the summer (May–August) of 2015, winter (November–February) of 2015/2016, summer of 2016, and winter of 2016/2017. We only trapped at sites in St. Bernard Parish during the summer of 2016 and winter of 2016/2017.

During each trapping bout, we placed 30 live Tomahawk traps (Tomahawk Live-trap Co., WI, USA) to target larger bodied rodents (i.e., rats) and 30 live Sherman traps (H.B. Sherman Traps, Tallahassee, FL, USA) to target smaller bodied rodents (i.e., mice) within each study site. Pairs of Sherman and Tomahawk traps were placed within 1 m of each other. We placed all traps outside in areas of observed or potential rodent activity (e.g., near visible runways, trash bins, compost, debris piles, etc.) in yards, alleys and in vacant lots whenever present. The placement of traps within each study site was dependent on property

access. In residential areas, all trapping occurred within the boundaries of each study site (i.e., block), unless we were not able to obtain access to a sufficient number of properties to place all traps. When access was limited, we placed traps on properties that directly faced the focal study site. This was only done at one study site within the Gentilly study area during all trapping bouts, and at two different study sites during different seasons in the Uptown neighborhood. We set all Tomahawk traps for a minimum of three continuous nights. Tomahawk trapping was sustained at each site until the total capture count reached an asymptote (i.e., we “trapped out” a block). For Sherman traps, we completed trapping for a minimum of 3 continuous nights, but limited trapping to 4 nights total. To ensure estimates of rodent abundance from the Sherman and Tomahawk trapping are equivalent across all sites, we have limited our analyses to data collected within the first four nights of Tomahawk trapping. Abundance estimates from Tomahawk traps as measured in the first 4 nights of trapping are reflective of the full asymptotic trapping estimates (Pearson’s correlation:  $r = 0.94$ ,  $p < 0.001$ ). For both Sherman and Tomahawk traps, we set and baited traps with a mixture of peanut butter and bacon bits each afternoon and checked and closed all traps the following morning. Each morning we counted the number of traps that were positive for rodents, positive for non-target (i.e., non-rodent) species, and sprung but empty traps. We released non-target animals in the area of capture, whereas all rats and mice were euthanized and necropsied at the City of New Orleans Mosquito, Termite, Rodent Control Board facilities in accordance with Tulane-approved IACUC protocols 0451 and 0460.

## 2.3. Socio-environmental habitat and vegetation assessments

We used four methods to assess habitat, vegetation cover and sociodemographic variables at each study site: 1) on-the-ground estimates

of percent cover in specific within-site trapping areas; 2) on-the-ground plant diversity data from vegetation plots within each study site; 3) land cover categories from sub-metric satellite imagery of our study sites; and 4) sociodemographic variables from the 2010 US Census. On-the-ground estimates of percent cover were obtained for each trapping bout at each study site. We first demarcated the trapping area boundaries within a study site, which typically aligned with property boundaries. We then visually estimated the proportion of coverage within each trap area that corresponded to the following attributes: unmaintained vegetation (grass taller than 15 cm and bushes with branches less than 15 cm from the ground), bare dirt (including unpaved areas underneath raised homes), and impervious surfaces (concrete and asphalt). We also counted the total number of unmaintained buildings (identified as buildings that were missing major structural features such as the roof or windows), and the number of debris piles (food waste, compost, and miscellaneous trash such as tires and construction debris). Following Lewis et al. (2017), measures of plant diversity-including shrub, tree and herbaceous species- at each study site were estimated by surveying a 400 m<sup>2</sup> circular vegetation plot in accordance with US Forest Service protocols (Nowak et al., 2008; USDA-FS 2016). We completed vegetation surveys at all study sites in the Gentilly, Lower 9th and Uptown neighborhoods during the summer of 2015, whereas surveys in St. Bernard and the natural area were completed in the summer of 2016. Differences in prevailing conditions likely did not influence vegetation characteristics across the study period; there were no anomalous temperature or precipitation events and the number of days during which rain occurred, annual rainfall totals, and days with extreme cold or heat were all consistent from 2014 to 2016.

We characterized land cover according to high-resolution satellite imagery for each year of the study. To do this, we acquired two Pleiades satellite images of the greater New Orleans metropolitan area, each with four multispectral bands and 0.5-meter spatial resolution, captured on 17 March 2015 and 28 March 2016. Using ESRI ArcGIS 10.3.1, we completed a supervised classification of five land cover categories: mature trees, open grass, urban surfaces (impervious surfaces and bare soil), buildings, and open water. We validated and improved classifications through visual inspection as well as the inclusion of rasterized GIS layers of building footprints and GIS layers of open water bodies such as canals. This reduced uncertainties that can arise when features are obscured by trees and other similar aspects of the landscape. We implemented the same process for characterizing the natural area sites, but rather than using block boundaries, we instead bounded land cover data within a 250 m × 250 m polygon, which corresponds to the average size of the study sites corresponding to residential city blocks. We intersected the study sites with US Census block boundaries to derive sociodemographic attributes according to the 2010 US Census (Gotham et al., 2014).

Finally, we created a categorical variable to characterize the level of vacancy and abandonment on a block, as this allowed us to differentiate between locations where there was little to no human influence (the natural areas) and residential areas with high and low levels of vacancy. To do this, we obtained spatial layers of parcel boundaries for both Orleans and St. Bernard Parishes (<https://www.gis.nola.gov>; <https://gis-stbernard.opendata.arcgis.com>, respectively), which we overlaid onto Google Earth satellite imagery to count the total number of lots and number of vacant lots within each study site. We considered a lot to be vacant if a home, shed or other man-made structure (e.g., swimming pool) did not fall within its boundaries. We categorized study sites where < 50% of the lots were vacant as low vacancy sites. We categorized study sites where 50% – 99% of lots were vacant as high vacancy sites. We characterized locations where 100% of the area was vacant lots (e.g., in the natural areas, one location within a city park, and one area fully located in a roadside) as natural sites. The availability of true-color historical imagery available at multiple time points through Google Earth enabled us to estimate annual variation in vacancy over the course of the study period.

## 2.4. Statistical analyses

### 2.4.1. Study area characterization

To understand how socio-environmental features of interest varied among the five focal study areas, we calculated the mean and standard deviation of all variables across all study sites located within a given area (Supplemental Table 1). The sociodemographic factors of interest included: the proportion of vacant lots at each study site and US Census-based estimates of median household income and total human population. The environmental features of interest included remotely sensed measures of proportional coverage of mature trees, grass, urban surfaces, and buildings. Additional environmental features of interest also included on-the-ground measures of proportional coverage of bare dirt, impervious surfaces, and unmaintained vegetation, as well as the number of unmaintained buildings and debris piles within each study site. For the variables that were normally distributed, we used repeated-measures ANOVA followed by pairwise comparisons of least-square means (Tukey HSD) to determine if socio-environmental features differed temporally and spatially among the study areas (Fig. 1). For the variables that were measured as proportions (e.g., the satellite-derived land cover estimates), we used beta regression to determine how each varied across the study areas (Eskelson, Madsen, Hagar, & Temesgen, 2011) using the *betareg* package in R (R development core team, 2008). In preparation for further analysis, we then checked all of the variables for collinearity. Several of the socio-environmental variables were highly correlated, and thus we selected only a subset for use in subsequent analyses (see section 2.4.3).

### 2.4.2. Spatiotemporal characterization of rodent assemblage structure

We first assessed how the composition of rodent assemblages varies among the study areas through non-metric multi-dimensional scaling (NMDS) based on Bray-Curtis dissimilarity index values using the *vegan* package in R (Oksanen et al., 2017). The NMDS plot displays the rank-order position of communities within non-dimensional space (Fig. 2). To determine if spatially proximate assemblages were more similar than spatially disparate assemblages, we calculated a Mantel correlogram and Mantel's *r* values across a progression of spatial lags (Mantel, 1967) by comparing the community dissimilarity matrix to a matrix of pairwise distances between study sites in the R package *ade4* (Bougeard & Dray, 2018; Chessel et al., 2004; Dray and Dufour, 2007) (Supplemental Fig. 1). We utilized a probabilistic model of species co-occurrence (Veech, 2013) to identify if some rodent species were more or less likely to co-occur with one another than would be expected by chance. These analyses were completed using the presence-absence matrix from all study sites where we trapped rodents and all years, using the '*cooccur*' package in R (Griffith, Veech, & Marsh, 2016).

To assess how rodent assemblages varied over time and across gradients of urbanization and vacancy, we constructed three generalized linear mixed models (glmm) to determine whether: 1) overall rodent abundance; 2) rodent species richness; and 3) rodent Shannon diversity differed among the study areas and across seasons (Zuur, Leno, Walker, Saveliev, & Smith, 2009). We calculated rodent abundance by summing all individuals of all species collected from each study site in a given trapping bout; and we calculated rodent species richness by summing the number of species collected at each study site in a given trapping bout. We calculated Shannon diversity using the *vegan* package in R. For the models predicting rodent abundance and richness, we used glmm with a Poisson error distribution, as the data are discrete counts, while we used a Gamma distribution for the Shannon diversity model (Zuur et al., 2009). For all of these models, we included study area and season as fixed effects, and year as a random effect (Zuur et al., 2009). Following each analysis, we performed pairwise comparisons of least-square means (Tukey HSD) to determine how abundance, richness, and diversity varied among study areas, using the *lsmeans* package in R (Lenth, 2016). For all analyses, we set  $\alpha = 0.05$ .

#### 2.4.3. Socio-environmental predictors of total rodent abundance and individual species abundance

We utilized a multi-level modeling approach as outlined in Jackson, Turner, Pearson, and Ives (2012), which involved using generalized linear mixed models (glmm) to determine the relative strength of socio-environmental variables (Supplemental Table 1) as predictors of total rodent abundance and individual species abundance. Such approaches can be more informative than more traditional methods of assessing variation in assemblage structure (e.g., RDA, CCA, NMDS) by offering greater power and lower sensitivity to collinearity of variance (Jackson et al., 2012). This approach also allows for the simultaneous exploration of drivers of assemblage-level and species-level attributes within a single model (Jackson et al., 2012). Prior to completing the glmm analysis, we checked all potential predictor variables for co-linearity using correlation analysis (Jackson et al., 2012). We removed the remotely sensed estimates of grass cover and building cover as they were highly correlated with the measure of vacant lots on a block ( $r = 0.80$ , and  $-0.83$ , respectively). We also removed the remotely sensed measure of impervious surface cover, as it was highly correlated with the remotely sensed measure of tree cover ( $r = -0.71$ ). After down-selecting the suite of socio-environmental variables for inclusion in the glmm model, we standardized all predictor variables to a mean of 0 and a variance of 1. Standardizing variables allows for the direct comparison of coefficients, which are then representative of effect sizes (Jackson et al., 2012). As our dependent variable was a count of total rodent abundance, we compiled a global glmm with a negative binomial distribution, which fit the data better than other probability curves for count data (e.g., Poisson). The global model included the suite of socio-environmental predictor variables hypothesized to relate to rodent abundance as fixed effects: the categorical measure of vacancy, median household income, total human population, remotely sensed based estimates of tree cover, as well as on-the ground estimates of bare dirt, impervious surfaces, unmaintained buildings, debris, and unmaintained vegetation. We also included the interaction term of vacancy  $\times$  debris, vacancy  $\times$  unmaintained vegetation and vacancy  $\times$  unmaintained buildings to represent hypothesized interactions between vacancy and other features of infrastructure loss. We additionally included an interaction between season  $\times$  and debris and season  $\times$  unmaintained vegetation. We included species as a random effect in the global model, and we included a term in which each fixed effect was included as a random intercept within species in a hierarchical fashion, as outlined in Jackson et al. (2012) (e.g.,  $\text{Abundance} \sim \text{Vacancy Category} + (1|\text{Species}) + (\text{Vacancy Category}|\text{Species})$ ). Lastly, we included the variable year as a random effect to account for the repeated measurements of rodent abundance at each site. We determined the top-selected model by comparing all combinations of variables, including all single-variable models and a null model. When comparing among models, we always included the fixed effect if the random slope|species variable was included in the model (Jackson et al., 2012). We then ranked each model according to AIC (Jackson et al., 2012), and considered the model with the lowest AIC as the top-selected model. Though there were two top models that differed by a single nested variable (Supplemental Table 2), we presented the results from the model with the fewest predictor variables. We also did not perform model averaging of coefficients (Burnham and Anderson, 2002). All analyses were conducted in R using the glmmTMB packages (Bates, Maechler, Bolker, & Walker, 2015; Brooks et al., 2017).

To determine that we had properly specified the model and did not have residual kurtosis or spatial autocorrelation, we performed diagnostic tests on randomized quantile residuals that we generated by comparing observed values to simulated observations from 250 runs of the best-fit model (Dunn & Smyth, 1996; Hartig, 2018). We then checked these models for over/under dispersion using qqplots, and spatial autocorrelation using Moran's I with the R packages DHARMA and ape (Hartig, 2018; Paradis, Claude, & Strimmer, 2004).

#### 2.4.4. Socio-environmental predictors of total rodent diversity

We focused on identifying the features that best predict rodent richness, as measures of Shannon diversity did not differ much among our study areas. To do so, we utilized a glmm analysis with a Poisson error distribution. As with the aforementioned analysis, we first constructed a global glmm model that included the full suite of socio-environmental variables as fixed effects, and we included year as a random effect. We also included measures of tree species richness, shrub richness, herbaceous richness, and land cover diversity as measured from satellite imagery. We selected among the models using AIC. Because we identified several top models, we used model averaging to calculate the model-averaged weights and model-averaged coefficients of variables.

### 3. Results

#### 3.1. Study area characterization

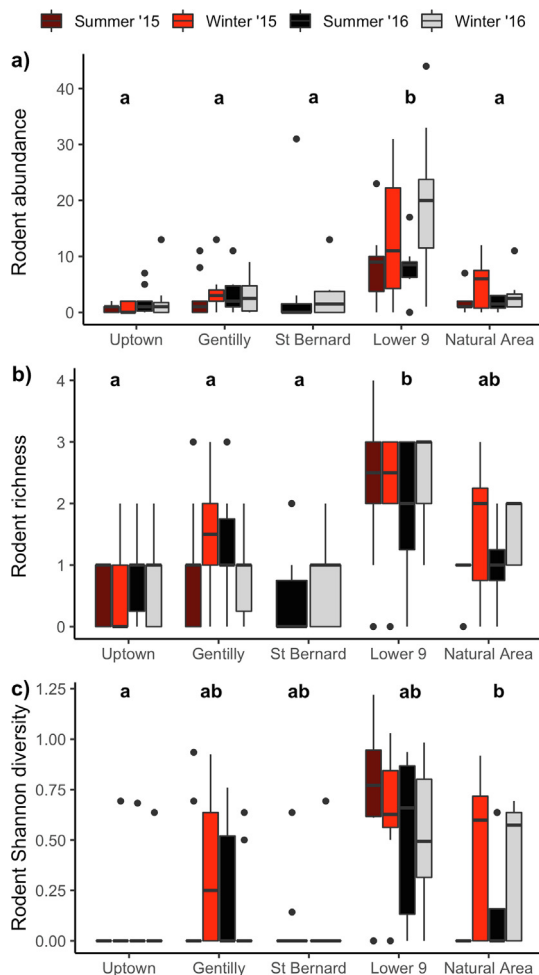
We found evidence of among-year, but not within-year, temporal variability in site characteristics. On-the-ground estimates that were collected across seasons (e.g., amount of debris, unmaintained houses, unmaintained vegetation, etc.) did not vary within a given year (repeated measures ANOVA,  $p > 0.05$  for all models). However, of the variables that were collected on a yearly basis, the remotely sensed estimate of urban cover was significantly higher in 2016 relative to 2015 ( $p = 0.04$ ,  $\text{coef.} = 0.19$ ). Consistent with this, we also found that the on-the-ground estimate of unmaintained vegetation (averaged across season) was lower in 2016 relative to 2015 ( $p = 0.003$ ,  $\text{coef.} = -0.06$ ). We additionally found that the on-the-ground estimate of debris ( $p = 0.02$ ,  $\text{coef.} = 0.20$ ) was higher in 2016 relative to 2015 (Fig. 1).

After accounting for temporal variation, all of the socio-environmental features collected in our study also significantly differed among the focal study areas (Fig. 1a&b). The Lower 9th Ward neighborhood harbored a significantly lower human population than all of the other study areas, excluding the natural area ( $p < 0.05$ , Tukey HSD), while median household income (US Census data) was significantly higher in the Uptown study area relative to all other study locations ( $p < 0.05$ , Tukey HSD). The full range of vacancy observed across New Orleans, is presented in Fig. 1 as a continuous measure, which not surprisingly indicates that the unoccupied natural area had significantly higher 'vacancy' relative to all other study areas (Fig. 1c). Excluding the natural areas, the focal study blocks in the St. Bernard Parish and Lower 9th Ward study areas had a significantly higher proportion of vacant lots relative to all other residential study areas ( $p < 0.05$ , Tukey HSD). Additionally, study sites within the Lower 9th Ward had significantly more unmaintained building and debris piles relative to sites in all other study areas ( $p < 0.05$ , Tukey HSD, Fig. 1f&g). Unmaintained vegetation was similar in both Lower 9th Ward and natural area sites, though unmaintained vegetation within the two study areas was significantly higher relative to all other study areas ( $p < 0.05$ , Tukey HSD, Fig. 1e). Tree species richness was significantly higher in the natural area sites relative to sites in all other study areas ( $p < 0.05$ , Tukey HSD, Appendix A). Shrub species richness was significantly higher in the Uptown study area (mean = 3.0 species) in comparison to the St. Bernard study area (mean = 0.4 species) ( $p < 0.05$ , Tukey HSD, Fig. 1i), while herbaceous species richness was lower in the Uptown study area (mean = 8.5 species) in relation to the Lower 9th Ward, which registered greater herbaceous richness than any other study area (mean = 14.5 species) ( $p < 0.05$ , Tukey HSD, Fig. 1h).

#### 3.2. Spatiotemporal characterization of rodent assemblage structure

We captured 818 rodents from the 48 study sites, including individuals of three non-native commensal species (*Rattus rattus* ( $n = 213$ ), *Rattus norvegicus* ( $n = 119$ ) and *Mus musculus* ( $n = 461$ )) as





**Fig. 3.** Rodent abundance and diversity over time across post-Katrina New Orleans. (a) Total rodent abundance differed significantly across focal study areas (letters indicate significant differences among the study areas). No statistically significant relationship was detected between total rodent abundance and season or year. (b) Total rodent richness also differed significantly across study neighborhood, but did not differ significantly across season or year. (c) Shannon diversity differed significantly among study areas, but there was no significant intra- or inter- annual variation in diversity.

well as two species native to Louisiana (*Sigmodon hispidus* ( $n = 21$ ) and *Oryzomys palustris* ( $n = 5$ )) during 2015, 2016, and 2017 (Fig. 2). We collected both of the native species in the natural area, and one of the native species (*S. hispidus*) in the Lower 9th Ward. We captured all of the non-native species in every study area, though not at every study site (Fig. 2). Consistent with this, we found that rodent assemblage composition varied across the study areas (Fig. 2). We rejected the null hypothesis that there was no spatial relationship in rodent assemblage structure (Mantel's  $r = 0.26$ , two-tailed  $p$ -value  $< 0.001$ ), as more spatially proximate rodent assemblages were more similar than spatially distant assemblages (Supplemental Fig. 1).

The probability of occurrence of some species was significantly related to that of other species. We found a positive association between *R. norvegicus* and *M. musculus* individuals ( $p = 0.04$ ), while we found a negative association between *R. rattus* and the two native rodent species (*R. rattus* – *S. hispidus*:  $p = 0.01$ ; *R. rattus* – *O. palustris*:  $p < 0.01$ ), as well as between *R. rattus* and *M. musculus*,  $p < 0.01$  (Supplemental Fig. 2).

We found greater variation in total rodent abundance, richness and diversity among the study areas than over time (Fig. 3). We captured significantly more rodents in the Lower 9th Ward relative to all other areas ( $p < 0.05$  for all pairwise comparisons: Lower 9th – Gentilly,

coef. = 1.46971; Lower 9th – natural area, coef. = 1.41; Lower 9th – St. Bernard, coef. = 2.08; Lower 9th – Uptown, coef. = 2.38; Fig. 3a). Additionally, we found a statistically significant positive association between rodent abundance and winter season ( $p < 0.01$ , coef. = 0.53), whereas no association was found with abundance and year (Fig. 3a). Rodent richness also differed among neighborhoods, with the Lower 9th Ward harboring more richness compared to all other study areas ( $p < 0.001$  for all pairwise comparisons: Lower 9 – Gentilly, coef. = 0.68; Lower 9th – natural area, coef. = 0.55; Lower 9th – St. Bernard, coef. = 1.31; Lower 9th – Uptown, coef. = 1.23) (Fig. 3b). Additionally, the natural area harbored a significantly higher rodent richness relative to the Uptown study area (coef. = 0.68,  $p < 0.05$ ). We did not find a significant relationship between rodent richness and season or year (Fig. 3b). Lastly, Shannon diversity was significantly higher in the Lower 9th Ward study area relative to only the Uptown study area (coef. = 2.44,  $p = 0.02$ ). Shannon diversity did not differ significantly among seasons or years (Fig. 3c).

### 3.3. Socio-environmental predictors of total rodent abundance and individual species abundance

The top selected glmm for rodent abundance was  $< 2 \Delta AIC$  than the next best model. As these two top-selected models include the same suite of variables, with the exception of a single additional random slope term, we present the results of the model with the fewest parameter values (Fig. 1A). We found no evidence of kurtosis or spatial autocorrelation with this model (one-sample Kolmogorov-Smirnov test,  $p > 0.05$ ,  $D = 0.04$ ; Moran's  $I$ ,  $p > 0.05$ ).

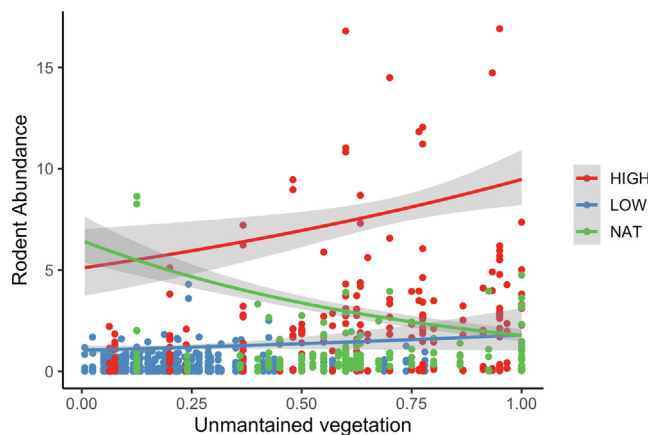
The fixed effects variables included in the top selected model were: unmaintained vegetation cover, total human population, season, median household income, remotely sensed estimates of tree cover, vacancy, as well as the number of unmaintained buildings (Table 1). The top selected model also included the fixed-effects interaction terms: unmaintained vegetation  $\times$  vacancy and debris  $\times$  season (Table 1). Of the fixed-effects variables, vacancy had the strongest influence on rodent abundance, with low vacancy areas (estimate =  $-1.02$ , SE = 0.26) and natural areas (estimate =  $-0.70$ , SE = 0.31) harboring fewer rodents compared to high vacancy areas. Vacancy also interacted with unmaintained vegetation, which was positively associated with rodent abundance. This relationship was much stronger in high vacancy areas (Fig. 4). Unmaintained vegetation alone also was a strong predictor of rodent abundance (estimate = 0.55, SE = 0.19,  $p < 0.001$ ), followed by the debris  $\times$  season interaction term (estimate = 0.45, SE = 0.13,  $p < 0.001$ , Fig. 5).

Different socio-environmental variables predicted individual species abundances (Table 2). Season explained the largest amount of among-

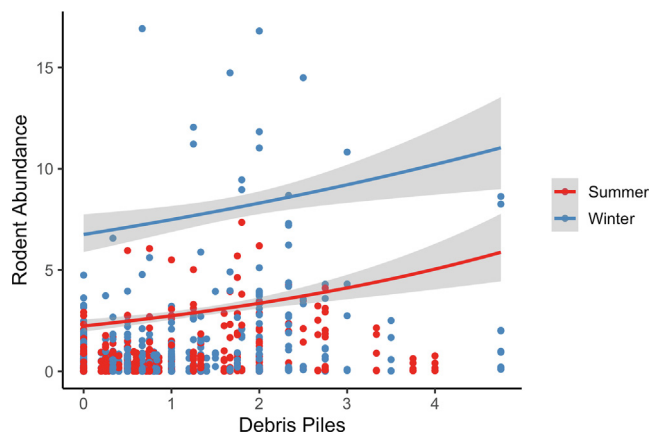
**Table 1**

Coefficients and significance of socio-environmental variables included in the best-supported model predicting rodent community abundance. The magnitude of fixed effects variables indicate the influence of a given variable on overall rodent community abundance.

Variable	Estimate	Std. Error	P – value
Intercept	–1.38	0.88	0.12
Vacancy (low)	–1.02	0.26	< 0.001
Vacancy (natural)	–0.70	0.31	0.03
Unmaintained veg.	0.55	0.19	< 0.001
Debris $\times$ Season	0.45	0.13	< 0.001
Vacancy (low) $\times$ Unmaintained veg.	–0.36	0.26	0.17
Vacancy (natural) $\times$ Unmaintained veg.	–0.11	0.21	0.60
Median household income	–0.28	0.32	0.38
Season (winter)	0.25	0.33	0.44
Tree cover	0.23	0.36	0.53
Unmaintained buildings	0.05	0.05	0.32
Debris	–0.12	0.11	0.30
Total population	–0.15	0.12	0.20



**Fig. 4.** The total abundance of rodents was positively related to the proportion of area covered in unmaintained vegetation at a study site; the effect was most pronounced on residential blocks where > 50–99% of lots were vacant (red line). Lines represent values from the top-selected glmm model predicting rodent abundance. Grey shading represents standard error. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** The total abundance of rodents was positively related to the amount of debris (i.e., the number of debris piles) at a study site, though only during winter. Lines represent values from top-selected glmm model predicting rodent abundance. Grey shading represents standard error.

**Table 2**

Total variance, standard deviation and coefficients of random effects included in the best-supported model predicting rodent abundance. The magnitude of the random effect variables indicates the influence of a given variable on among-species variation. The top two coefficients with the largest effect on the abundance of each rodent species are in bold.

	Tree cover	Med. Income	Unmaint. Veg	Season (winter)
Variance	0.45	0.21	0.08	1.84
SD	0.67	0.46	0.27	1.36
Species				
<i>S. hispidus</i>	<b>0.93</b>	−0.53	<b>0.74</b>	−0.04
<i>M. musculus</i>	−0.40	−0.51	<b>0.58</b>	<b>2.07</b>
<i>R. norvegicus</i>	−0.43	−0.26	<b>0.78</b>	<b>0.62</b>
<i>O. palustris</i>	<b>0.92</b>	−0.46	0.42	−1.01
<i>R. rattus</i>	0.10	<b>0.41</b>	<b>0.21</b>	−0.20

species variation in abundance (variance = 1.84, SD = 1.36), though the direction of the effect varied among species (Table 2). The abundance of *M. musculus* and *R. norvegicus* was more strongly associated with winter (i.e., both were more abundant in winter), while *O. palustris* and *R. rattus* were more strongly associated with summer relative

**Table 3**

Weights and model averaged coefficients from top-selected models predicting rodent richness. Variables included in the top-selected models predicting rodent species richness, coefficients averages across all models within  $\Delta AIC \leq 2$ .

Variable	Sum of weights	N containing models	Model avg. coefficients
Land cover diversity	1	10	3.80
Vacant lots (low)	0.92	9	−0.67
Tree Cover	0.91	9	0.26
Population	0.9	9	−0.24
Unmain. vegetation	0.5	5	0.16
Season (winter)	0.16	2	0.13
Shrub richness	0.08	1	0.06
Med. household income	0.07	1	−0.05
Herb. Richness	0.07	1	0.04

to winter, and *S. hispidus* had little association with season (effect size = −0.04) (Table 2). The abundance of both *M. musculus* and *R. norvegicus* was higher in areas with greater unmaintained vegetation (coef. = 0.58, 0.78 respectively), less tree cover (coef. = −0.40, −0.43, respectively), and lower median household incomes (coef. = −0.51, −0.26). The abundance of *R. rattus* was greater in areas with unmaintained vegetation (coef. = 0.43) and in areas with greater median household income (coef. = 0.39). The abundance of both *S. hispidus* and *O. palustris* was greater in areas with more mature canopy cover (coef. = 0.93, 0.92 respectively) and in areas with more unmaintained vegetation (coef. = 0.74, 0.42, respectively).

#### 3.4. Socio-environmental predictors of total rodent richness

From coefficients averaged across the set ( $n = 10$ ) of top models (Table 3), we found that rodent richness was greatest in areas with increased land cover diversity (model avg. coef. = 3.80) and high levels of vacancy (model avg. coef. = −0.87, −0.10, respectively). Richness also was greater in areas with greater tree cover (coef. = 0.23), unmaintained vegetation (coef. = 0.16) and fewer residents (coef. = −0.24) (Table 3). Though several other variables were included in a few top-selected models, each exerted comparably low influence on rodent richness (Table 3).

#### 4. Discussion

Our findings indicate that rodent assemblage structure varies with counter-urbanization across post-Katrina New Orleans. As hypothesized, we found that rodent abundance and richness reflect features related to abandonment and infrastructure loss across the city. Rodent abundance was greater in residential areas burdened with higher levels of vacancy as well as higher levels of unmaintained vegetation, debris, and unmaintained buildings. We also found evidence that post-Katrina land management has influenced rodent assemblage structure, as abundance and richness were significantly greater in the Lower 9th Ward compared to adjacent St. Bernard Parish neighborhoods (Lewis et al., 2017). Notably, our modeling results indicate that rodent richness corresponds to land cover diversity, which provides some support for the hypothesis that ‘diversity begets diversity’. These findings further illustrate that counter-urbanization can reshape species assemblages and demonstrate that areas undergoing counter-urbanization can support a more diverse and abundant complement of host species capable of transmitting pathogens to humans (Eskew & Olival, 2018; Gulachenski et al., 2016; Rael et al., 2016).

Though similar to trends that have been observed for other taxa in urbanizing areas, patterns of rodent abundance across post-Katrina New Orleans reflect different underlying conditions. Notably, we found that rodent abundance was significantly lower in natural areas relative to residential areas that have sustained relatively high population loss triggered by Katrina-related flooding (e.g., the Lower 9th Ward study



area). We also found that rodent abundance was significantly lower in more densely populated residential areas with lower vacancy (e.g., the Uptown study area) relative to areas with higher vacancy and population loss (e.g., the Lower 9th Ward Study area). This finding runs contrary to the prevailing notion that rodent abundance closely mirrors human demography (i.e., the 'one rodent for every person' rule of thumb). Rather, it is more consistent with trends observed elsewhere indicating that the abundance of commensal fauna (e.g., lizards, birds, butterflies, mammals and several other arthropods) peaks at intermediate levels of urbanization (Blair, 1999; Germaine & Wakeling, 2001; McIntyre, 2000; Riem, Blair, Pennington, & Solomon, 2012). While prior studies have linked elevated abundance of commensal fauna to greater primary productivity in managed green spaces (Shochat, Warren, Faeth, McIntyre, & Hope, 2006), our findings indicate that unmanaged green spaces resulting from human population loss and vacancy (i.e., green blight) afford the resources and habitat necessary for rodents to become hyper-abundant. This is well illustrated by the finding that rodent abundance reflects the extent of unmaintained vegetation in residential areas with higher levels of vacancy. It is also notable that debris is a predictor of rodent abundance, particularly in winter when resources may otherwise be limiting (Table 1, Fig. 5) (Masi et al., 2010). Our findings also indicate that residential areas with more vacant lots and fewer people provide harborage for a greater number of rodent species, including less common native species. These results indicate that public health outcomes of green blight extend beyond well-recognized concerns such as crime, mental health and safety (Branas et al., 2018; Bogar & Beyer, 2015; Garvin et al., 2013; Troy et al., 2016) to include ecological hazards that can come from hyper-abundant pest and pathogen host species (LaDeau et al., 2013).

While important, vacancy was not the sole driver of rodent abundance. Our results indicate that land management acts in conjunction with vacancy to shape rodent assemblages, as demonstrated in comparisons of rodent abundance and assemblage composition between the Lower 9th Ward and adjacent blocks within St. Bernard Parish. The areas are spatially proximate to one another and exhibit comparable levels of vacancy but have been subject to contrasting land management policies since Hurricane Katrina. Publicly and privately owned lots have not been managed equivalently in the Lower 9th Ward neighborhood, which falls under the jurisdiction of Orleans Parish (Lewis et al., 2017). Whereas public lots are managed (e.g., regularly mowed and cleared) by the State and municipal government entities, private lot management falls to land owners, which has given rise to a heterogeneous patchwork of maintained and unmaintained areas in the neighborhood (Lewis et al., 2017). In contrast, nearly all vacant lots within St. Bernard Parish are regularly maintained by the Parish, regardless of ownership, resulting in relatively homogeneous vegetation (Lewis et al., 2017). Consistent with this, we found that the average proportion of unmaintained vegetation, the average number of debris piles and the number of unmaintained buildings at study sites across the Lower 9th Ward were more than twice as high as in study sites across St. Bernard Parish. The composition of the rodent assemblage also differed among the adjacent neighborhoods, likely reflecting shifts in habitat conditions. The correlogram of Mantel's  $r$  demonstrates that similarity among assemblages drops sharply over relatively small distances (Fig. 1A). For example, *R. norvegicus* was abundant and widely distributed across the Lower 9th Ward, but it was rarely encountered in the adjacent St. Bernard neighborhoods. The Parish boundary appears to be a one-way sieve, as all of the species detected in St. Bernard Parish were also found in the Lower 9th Ward. Maintenance of abandoned areas may thus be an effective strategy for reducing ecological hazards associated with particular commensal rodents like *R. norvegicus* (Peterson et al., 2017). This inference is consistent with the recommendation that managing public lands and reducing trash is a first line of defense against rodent infestation (Colvin & Jackson, 1999; Johnson, Bragdon, & Olson, 2014; Lambropoulos et al., 1999), as well

as appeals for greater coordination among municipal entities (e.g., trash management, land management, pest control, public health, etc.) to reduce hazards to human well-being (Corrigan, 2006).

Management to address public health concerns must account for species-specific responses to socio-environmental factors. Our results indicate that shifts in assemblage structure across New Orleans reflect differences in response to socio-environmental conditions. We were able to elucidate the socio-environmental features related to both total rodent abundance, as well as the abundance of individual species. Season was the most important predictor of among-species variation in abundance for most species, though the magnitude and direction of influence varied among species. Both *M. musculus* and *R. norvegicus* appear to be more sensitive to seasonality, as both species were more abundant in the winter compared to the summer season. Conversely, *O. palustris* and *R. rattus* were more abundant in the summer season, though features other than season were more strongly related to *R. rattus* abundance, suggesting that this species relies less on seasonally variable habitat or resources than its congener (Table 2). Similarly, tree cover and unmaintained vegetation were among the top predictors of abundance for both native species, with *S. hispidus* showing relatively low seasonal variation in abundance (Table 2). Further study of native species abundance is warranted, however, as both *S. hispidus* and *O. palustris* were only rarely captured in our study.

Notably, we found that *R. norvegicus*, *M. musculus*, and both native species were more abundant in lower-income areas, which is consistent with prior work suggesting that elevated rodent abundance in lower-income areas is likely due to infrastructure disinvestment and lower coping capacity of residents (Easterbrook, Shields, Klein, & Glass, 2005; Johnson et al., 2014; Rothenburger, 2017). Conversely, we found that the abundance of *R. rattus* was greater in higher-income areas (Table 2). This may be a reflection of the use of trees as habitat (and the use of trees to access elevated habitat like attic spaces in houses) by *R. rattus*, which is an arboreal species (Marsh, 1994). As in many cities (Grove, Locke, & O'Neil-Dunne, 2014; Schwarz et al., 2015), the prevalence and composition of tree cover varies across New Orleans, with higher-income areas supporting more trees and more native and culturally valuable tree species, in particular, relative to lower-income neighborhoods (Lewis et al., 2017). While tree cover was not among the strongest predictors of *R. rattus* abundance, the observed association between household income and *R. rattus* abundance suggests that native and cultivated trees are preferred habitat for *R. rattus*. Though further work is warranted to assess tree use by *R. rattus*, our findings indicate that public health risks associated with commensal rodents can transcend income disparities, and that one-size-fits-all approaches to managing risk are likely to prove unsuccessful in cities like New Orleans that harbor a diverse complement of commensal pests.

Interspecific interactions may also shape urban rodent assemblage structure. We found negative associations between *R. rattus* and *M. musculus* as well as between *R. rattus* and both native rodents. The relatively widespread distribution of *R. rattus* across the city suggests that *R. rattus* may displace native species, as has been demonstrated elsewhere (Stokes, Banks, Pech, & Williams, 2009). The negative association between *R. rattus* and *M. musculus* may also indicate direct or indirect competition or predation (Bridgman et al., 2013), but it may instead reflect spatial differences in preferred habitats across the city (Harper & Cabrera, 2010). While *R. norvegicus* are also thought to inhibit *M. musculus* (Brown, Moller, Innes, & Alterio, 1996; Ruscoe et al., 2011), we found a positive association between the two species across New Orleans, which is consistent with observations of similar habitat use in other cities (Cavia et al., 2009). This finding also offers further support for the hypothesis (Cavia et al., 2009) that abandonment and infrastructure decline result in sufficient resources to allow for species co-existence (Cavia et al., 2009).

The features that best predict rodent species richness mirror those that relate to abundance in post-Katrina New Orleans. Similar to abundance, rodent species richness was greater in areas with fewer

people and greater vacancy, tree cover, and unmaintained vegetation. Notably, we also found that land cover diversity was a strong predictor of rodent species richness. This is consistent with work done across agricultural-forest land cover gradients, which has shown that habitat heterogeneity, as measured by land cover diversity, strongly predicts rodent diversity (Horváth, March, & Wolf, 2001). Similar trends have been observed across other urban gradients (Cavia et al., 2009), indicating that land cover diversity is a consistent predictor of rodent diversity across urbanizing and counter-urbanizing cities.

Understanding patterns and drivers of rodent diversity can shed new light on zoonotic pathogen transmission risk, especially in areas like counter-urbanizing landscapes that can be novel human-wild land interfaces (Eskew & Olival, 2018). For example, we found evidence of local (i.e., within a study site) and regional (i.e., across a study area) species co-occurrence, which raises the possibility that non-host specific pathogens of concern could be transmitted by more than one host in a given area. Indeed, the zoonotic parasite *Angiostrongylus* sp. infects both *R. norvegicus* and *R. rattus* across the city (Rael et al., 2018). Notably, rodent richness and abundance appear to scale together in New Orleans, as both are highest in residential areas with high levels of vacancy, such as the Lower 9th Ward. Commensurate scaling of diversity and abundance of potential hosts is hypothesized to amplify zoonotic disease risk (Eskew & Olival, 2018; Mihaljevic et al., 2014), suggesting that lower-income areas burdened with greater abandonment and vacancy could be at a greater risk of zoonotic disease transmission. Though the total risk of zoonotic pathogens may be lower in counter-urbanizing areas like the Lower 9th Ward that support fewer residents, individual-level risk may nonetheless be greater for remaining residents. Moreover, the loss of access to critical infrastructure, like healthcare facilities, only exacerbates health risks in counter-urbanizing areas (Eskew & Olival, 2018; Gulachenski et al., 2016; Rael et al., 2016). Thus further study is warranted to determine whether pathogen loads track rodent abundance and diversity across the city.

## 5. Conclusion

The observed patterns of rodent abundance and richness illustrate

that counter-urbanization can engender and possibly exacerbate environmental justice concerns (Lewis et al., 2017) that may extend well beyond zoonotic disease risk. Our results suggest that lower-income areas burdened with features related to infrastructure loss and vacancy may be more at risk of zoonotic disease transmission. Recent work has also demonstrated, however, that mental health wellness is lower in residents of areas with greater rodent abundance (German & Latkin, 2016; Lam, Byers Kaylee, & Himsworth, 2018), especially in areas that are under-resourced (German & Latkin, 2016). Evidence that vacancy is disproportionately concentrated in areas of lower income in cities across the US (Gulachenski et al., 2016) suggests that the conditions found in post-Katrina New Orleans likely occur across many other cities. Importantly, our findings point to the prospects that interventions such as land management, removal of blighted buildings and vegetation, and debris removal can be executed to address disparities. Interventions that reduce blight can also serve to reduce real and perceived risk of crime (Branas et al., 2018) and improve mental health outcomes (Lam et al., 2018). We hypothesize that comparable interventions can similarly reduce concerns associated with rodents, including the risk of pathogen transmission to humans. Given the near global distribution of the three most commonly encountered rodent species (*R. rattus*, *R. norvegicus* and *M. musculus*) in post-Katrina New Orleans, we expect that interventions are likely to be broadly applicable and of increasing importance with the global progression of counter-urbanization.

## Acknowledgments

The Tulane-Xavier Center for Bioenvironmental Research, the Tulane ByWater Institute, the National Science Foundation (BCS-0948993, BCS-1313703), the Louisiana Board of Regents and the Tulane University Department of Ecology and Evolutionary Biology provided funding for this work. We would also like to acknowledge the following people for their contribution: R. Rael J. Childs, W. Zipperer, R. Hazen, A. Lesen, T. Madere, F. Bauder, T. Barre, A. Balliviero, P. Smith, A. Gulachenski, E. Ruda, S. Piper, H. Rahn, S. Sugarman, R. Wang, H. Patel, S. Triplett, A. Powell, and J. Haydel.

## Supplemental Table 1. Study area socio-environmental profiles

Mean  $\pm$  standard deviation of environmental variables averaged across all seasons and all focal study sites within each study area. Whole block data are variables collected for the entirety of the study site, including those calculated from satellite imagery. The environmental variables hypothesized to relate to rodent abundance differed significantly across study areas. Superscript letters that differ among rows represent significant differences among study areas ( $p < 0.05$ ).

	Uptown	Gentilly	Lower 9	St. Bernard	Natural Area
Total Population <sup>1</sup>	1862.9 <sup>a</sup> $\pm$ 872.13	2301.3 <sup>ac</sup> $\pm$ 653.64	729.2 <sup>b</sup> $\pm$ 480.53	1696.1 <sup>c</sup> $\pm$ 492.96	0.00 <sup>d</sup> $\pm$ 0.00
Median household income <sup>1</sup>	61378.7 <sup>a</sup> $\pm$ 24795.81	38169.7 <sup>b</sup> $\pm$ 10846.70	30221.7 <sup>bc</sup> $\pm$ 9338.63	39395 <sup>c</sup> $\pm$ 3818.58	0.00 <sup>d</sup> $\pm$ 0.00
Vacant lots (%) <sup>2</sup>	14.04 <sup>a</sup> $\pm$ 29.36	23.50 <sup>ab</sup> $\pm$ 28.42	62.58 <sup>c</sup> $\pm$ 24.26	50.93 <sup>bc</sup> $\pm$ 17.73	1.00 <sup>d</sup> $\pm$ 0.00
Grass cover (%) <sup>2</sup>	4.17 <sup>a</sup> $\pm$ 10.25	11.23 <sup>a</sup> $\pm$ 7.51	24.19 <sup>b</sup> $\pm$ 9.46	29.02 <sup>b</sup> $\pm$ 15.52	11.48 <sup>a</sup> $\pm$ 5.71
Tree cover (%) <sup>2</sup>	33.77 <sup>a</sup> $\pm$ 9.18	37.92 <sup>a</sup> $\pm$ 6.18	37.64 <sup>a</sup> $\pm$ 9.21	31.80 <sup>a</sup> $\pm$ 7.06	79.42 <sup>b</sup> $\pm$ 12.03
Urban surfaces (%) <sup>2</sup>	30.38 <sup>a</sup> $\pm$ 10.26	31.73 <sup>a</sup> $\pm$ 7.35	28.17 <sup>a</sup> $\pm$ 9.80	37.45 <sup>a</sup> $\pm$ 12.66	7.65 <sup>b</sup> $\pm$ 10.10
Buildings (%) <sup>2</sup>	30.87 <sup>a</sup> $\pm$ 10.14	18.96 <sup>b</sup> $\pm$ 7.73	10.00 <sup>c</sup> $\pm$ 5.13	1.60 <sup>d</sup> $\pm$ 4.92	0.05 <sup>d</sup> $\pm$ 0.09
Unmaintained vegetation (%) <sup>2</sup>	24.77 <sup>a</sup>	30.81 <sup>a</sup>	71.42 <sup>b</sup>	27.89 <sup>a</sup>	59.23 <sup>b</sup>
	3.57	18.44	20.48	10.25	16.89
Unmaintained buildings <sup>4</sup>	0.00 <sup>a</sup> $\pm$ 0.00	0.02 <sup>a</sup> $\pm$ 0.067	0.25 <sup>b</sup> $\pm$ 0.27	0.00 <sup>a</sup> $\pm$ 0.00	0.00 <sup>a</sup> $\pm$ 0.00
Debris piles <sup>4</sup>	0.47 <sup>a</sup> $\pm$ 0.49	0.78 <sup>a</sup> $\pm$ 0.67	1.84 <sup>b</sup> $\pm$ 0.69	0.70 <sup>a</sup> $\pm$ 0.69	1.05 <sup>a</sup> $\pm$ 1.40
Cement/asphalt <sup>3</sup>	26.75 <sup>a</sup> $\pm$ 15.30	11.79 <sup>b</sup> $\pm$ 9.25	8.89 <sup>bc</sup> $\pm$ 8.24	2.63 <sup>c</sup> $\pm$ 4.44	0.00 <sup>c</sup> $\pm$ 0.00
Bare dirt <sup>3</sup>	24.35 <sup>a</sup>	10.75 <sup>b</sup>	6.18 <sup>b</sup>	4.66 <sup>b</sup>	25.76 <sup>a</sup>
	11.00	8.99	8.42	6.4	27.38
Land cover diversity <sup>2</sup>	0.66 <sup>a</sup> $\pm$ 0.01	0.69 <sup>a</sup> $\pm$ 0.02	0.68 <sup>a</sup> $\pm$ 0.03	0.63 <sup>a</sup> $\pm$ 0.05	0.36 <sup>b</sup> $\pm$ 0.15
Tree richness <sup>5</sup>	1.50 <sup>a</sup> $\pm$ 1.04	0.70 <sup>a</sup> $\pm$ 0.79	0.80 <sup>a</sup> $\pm$ 0.76	0.30 <sup>a</sup> $\pm$ 0.47	2.50 <sup>b</sup> $\pm$ 1.29
Shrub richness <sup>5</sup>	3.00 <sup>a</sup> $\pm$ 2.35	1.00 <sup>abc</sup> $\pm$ 1.12	0.70 <sup>abc</sup> $\pm$ 0.79	0.40 <sup>b</sup> $\pm$ 0.20	1.83 <sup>ac</sup> $\pm$ 1.49
Herbaceous richness <sup>5</sup>	8.50 <sup>a</sup> $\pm$ 2.98	11.80 <sup>ab</sup> $\pm$ 5.08	14.48 <sup>b</sup> $\pm$ 3.88	12.10 <sup>ab</sup> $\pm$ 4.26	11.75 <sup>ab</sup> $\pm$ 2.86

<sup>1</sup>Data from U.S. 2010 Census

<sup>2</sup>Data calculated from satellite imagery, and represents values across entire study sites.

<sup>3</sup>Data represent % cover of within-site trapping areas, estimated during trapping.

<sup>4</sup>Number of buildings/debris piles counted within each focal within-site trapping area, divided by the total number of focal within-site trapping

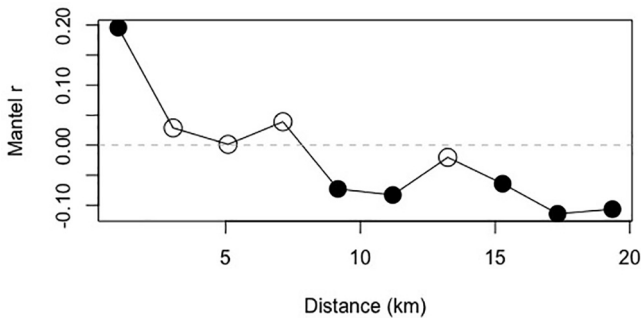
areas at a site, estimated during trapping.

<sup>5</sup>Data collected from circular vegetation plots randomly places within study sites.

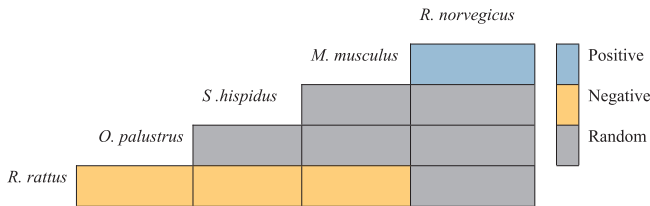
Supplemental Table 2. Variables included in the top three models predicting overall rodent abundance across the city of New Orleans, Louisiana and associated AICc and ΔAICc values

Model	1		2		3	
AICc	1989		1991		1992	
ΔAICc	0		2		3	
	Fixed effects		Random effects		Fixed effects	
Total population	X		X		X	
Vacant lots	X		X		X	
Season (winter)	X		X		X	
Debris	X		X		X	
Med. Income	X		X		X	
Tree cover	X		X		X	
Unmaintained buildings	X		X		X	
Unmaintained vegetation	X		X		X	
Vacant lots × Unm. Veg.	X		X		X	
Vacant lots × debris	X		X		X	
Debris × season	X		X		X	
Unm. Building × season	X		X			
Year		X		X		X

Supplemental Figure 1. Mantel’s r of community assemblage at increasing spatial lag. Open circles represent non-significant Mantel’s r values, while closed circles represent significant positive (above 0), or negative (below 0) spatial autocorrelation in rodent community assemblage



Supplemental Figure 2. Species co-occurrence matrix. Colors represent statistically significant positive or negative association between two species. Matrix includes animals captured in all years



Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2019.103710>.

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