Received: 4 September 2017 | Revised: 31 October 2017 | Accepted: 2 November 2017

DOI: 10.1111/mec.14437

ORIGINAL ARTICLE

WILEY MOLECULAR ECOLOGY

Spatial population genomics of the brown rat (*Rattus norvegicus*) in New York City

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Funding information
National Science Foundation, Grant/Award Number: DEB-1457523, DBI-1531639

Abstract

Human commensal species such as rodent pests are often widely distributed across cities and threaten both infrastructure and public health. Spatially explicit population genomic methods provide insights into movements for cryptic pests that drive evolutionary connectivity across multiple spatial scales. We examined spatial patterns of neutral genomewide variation in brown rats (*Rattus norvegicus*) across Manhattan, New York City (NYC), using 262 samples and 61,401 SNPs to understand (i) relatedness among nearby individuals and the extent of spatial genetic structure in a discrete urban landscape; (ii) the geographic origin of NYC rats, using a large, previously published data set of global rat genotypes; and (iii) heterogeneity in gene flow across the city, particularly deviations from isolation by distance. We found that rats separated by ≤200 m exhibit strong spatial autocorrelation (r = .3, p = .001) and the effects of localized genetic drift extend to a range of 1,400 m. Across Manhattan, rats exhibited a homogeneous population origin from rats that likely invaded from Great Britain. While traditional approaches identified a single evolutionary cluster with clinal structure across Manhattan, recently developed methods (e.g., fineSTRUCTURE, sPCA, EEMS) provided evidence of reduced dispersal across the island's less residential Midtown region resulting in fine-scale genetic structuring (F_{ST} = 0.01) and two evolutionary clusters (Uptown and Downtown Manhattan). Thus, while some urban populations of human commensals may appear to be continuously distributed, landscape heterogeneity within cities can drive differences in habitat quality and dispersal, with implications for the spatial distribution of genomic variation, population management and the study of widely distributed pests.

KEYWORDS
commensal, dispersal, gene flow, isolation by distance, rodent, spatial genetics

1 | INTRODUCTION

Urbanization rapidly alters the composition of landscapes, which strongly influences both the composition of urban wildlife communities (McKinney, 2006; Palomino & Carrascal, 2007; Shochat et al., 2010) and evolutionary processes governing urban-dwelling populations (Alberti, 2015; Hendry, Gotanda, & Svensson, 2017). The movement of individuals and their genes influences functional connectivity within and between populations and the spatial distribution of genetic variation (Slatkin, 1987), which is often used to understand contemporary dispersal processes (Broquet & Petit, 2009; Pinsky et al., 2016), ecological factors influencing dispersal success (Murphy, Evans, & Storfer, 2010; Robinson, Samuel, Lopez, & Shelton, 2012) and the potential for local adaptation (Lenormand, 2002; Munshi-South, Zolnik, & Harris, 2016). Variation at neutral loci is primarily governed by genetic drift, which causes the random loss

or fixation of alleles—thereby increasing differentiation among groups—and gene flow, which homogenizes groups linked by dispersal (Frankham, Biology, Issue, Soule, & Frankham, 1996; Slatkin, 1987; Waples & Gaggiotti, 2006). These opposing forces generate spatial patterns of genetic variation that depend both on phenotypic traits like dispersal or sociality and the abundance, quality and connectivity of suitable habitat across the landscape.

Urban landscapes have a substantial effect on the movement and genetic connectivity of many populations (Johnson & Munshi-South, 2017). For example, individuals in urban environments often move shorter distances (Adkins, 1998; Glass, Childs, Korch, & LeDuc, 1989) and exhibit higher relatedness (Chiappero, Panzetta-Dutari, Gomez, & Polop, 2011; Gortat et al., 2015) than those in nonurban environments. Studies on native wildlife in urban landscapes have generally reported declines in genetic variation within populations and strong genetic differentiation between populations in mammals (Magle, Ruell, Antolin, & Crooks, 2010; Munshi-South & Kharchenko, 2010; Wilson et al., 2016), amphibians (Littleford-Colquhoun, Clemente, Whiting, Ortiz-Barrientos, & Frere, 2017; Lourenco, Alvarez, Wang, & Velo-Antón, 2017; Noël & Lapointe, 2010), reptiles (Delaney, Riley, & Fisher, 2010) and arthropods (Desender, Small, Gaublomme, & Verdyck, 2005). Of particular interest are the processes that allow species to establish and maintain populations in cities. Some species exhibit source–sink dynamics, identified by asymmetric movement and gene flow into the city and among subpopulations (Björklund, Ruiz, & Senar, 2010), while others experience frequent gene flow with nonurban populations (Rutkowski, Rejt, Tereba, Gryczyńska-Siemiątkowska, & Janic, 2010) or persist in isolated populations through the maintenance of high population densities (Munshi-South & Kharchenko, 2010). Habitat availability is key to understanding patterns of genetic connectivity in urban populations (Lapoint, Balkenhol, Hale, Sadler, & van der Ree, 2015). For example, studies have found that gene flow in an urban wall lizard is influenced by the distribution of rocky substrates used for habitat (Beninde, Feldmeier, Werner, & Peroverde, 2016) and canopy cover predicts gene flow among urban white-footed mice (Munshi-South, 2012).

Non-native species are large components of urban communities (Mckinney, 2008; Riley et al., 2005) due to long-distance dispersal and establishment of urban populations through global networks of human trade (Armitage, 1993; Molnar, Gamboa, Revenga, & Spalding, 2008; Puckett et al., 2016; Saenz, Booth, Schal, & Vargo, 2012). Once introduced to cities, some species have traits that make them well suited to use certain features of the built environment as habitat, such as building exteriors, home interiors or underground infrastructure (Channon, Cole, & Cole, 2000; Martin et al., 2015; Osorio, Ze-Ze, Amaro, Nunes, & Alves, 2014; Sacchi, Gentilli, Razzetti, & Barbieri, 2002). These species are often human commensals and may be dependent on anthropogenic resources (i.e., anthrodependent, Hulme-Beaman, Dobney, Cucchi, & Searle, 2016). In contrast to native species that often occupy remnant patches of native habitat, human commensals inhabit an expanded realized niche in cities and thrive in the intervening urban matrix where habitat quality varies continuously across the landscape (Alberti et al., 2003). Here, we study the processes governing spatial genetic connectivity in a population of urban brown rats (*Rattus norvegicus*), an archetypical human commensal species and an abundant pest that poses considerable threats to public health and the structural integrity of the human environment (Feng & Himsworth, 2014; Firth et al., 2014; Himsworth, Parsons, Jardine, & Patrick, 2013; Johnson & Timm, 1987).

Patterns of anthropogenic disturbance, impervious surface and sharp contrasts in land use contribute to very high habitat heterogeneity in cities (Alberti, 2005; Cadenasso, Pickett, & Schwarz, 2007; Niemela, 1999). Commensal rodents rely on human resources that vary greatly across space and time, so population genetic outcomes for these species are likely influenced by the behavioural, socioeconomic and political forces that govern how humans design, build and occupy cities. Thus, while isolation by distance (IBD) is a useful null model of population structure for continuously distributed species (Meirmans, 2012; Wright, 1943), we expect the fine-scale heterogeneity of urban habitats to result in deviations from IBD. Recent advances in population genetic methods hold great promise for identifying fine-scale genetic structure (Galpern, Peres-Neto, Polfus, & Manseau, 2014; Jombart, Devillard, Dufour, & Pontier, 2008; Lawson, Hellenthal, Myers, & Falush, 2012) and the underlying drift and geneflow processes that create such patterns (Messina et al., 2016; Petkova, Novembre, & Stephens, 2014). These spatially explicit and individual-based models directly incorporate geographic locations or a network of spatial connectivity as prior information to highlight the portion of genetic variation that is spatially structured. Additionally, approaches that incorporate recombination and linkage throughout the genome can produce accurate estimates of fine-scale population structure using shared coancestry (Lawson et al., 2012; Leslie et al., 2015; Wallberg et al., 2014). These approaches have already demonstrated their utility for understanding connectivity in complex and human-modified landscapes (Grummer & Leaché, 2017; Richardson et al., 2017; Richmond et al., 2017; Rick, Moen, Erb, & Strasburg, 2017).

Interest in the population genetics of urban commensals has recently accelerated (Booth et al., 2012; Crissman et al., 2010; Richardson et al., 2017), but overall their evolutionary dynamics remain poorly understood. Previous research on brown rats and other urban commensals informs our predictions about the operation of gene flow and drift in NYC rats. Brown rats live in highly social colonies (Feng & Himsworth, 2014) and individuals use small home ranges throughout their life, rarely moving more than 150 m (Davis, 1953; Heiberg, Sluydts, & Leirs, 2012; Recht, 1988). In some urban areas, movement may be even more restricted due to higher rat population density (30–40 m; Davis, Emlen, & Stokes, 1948; Glass et al., 1989). Social interactions that promote colonial group structure, in combination with spatially restricted movements, can lead to rapid local differentiation in rodents as genetic drift occurs within the local genetic neighbourhood (Gauffre, Estoup, Bretagnolle, & Cosson, 2008; Neel et al., 2013). Thus, we expect a strong pattern of local spatial genetic structure between rats sampled within several hundred metres, as related individuals group together in space and alleles experience localized genetic drift over several generations.

Previous studies have found that only a small percentage of urban rats move between study sites, with greater movement identified by genetic methods (6.5%, Gardner-Santana et al., 2009; 6.8%, Kajdacsi et al., 2013) than capture–mark–recapture studies for rats caught above ground (0.003% between city blocks, Davis, 1953) or below ground (0.0% between sewer systems, Heiberg et al., 2012). Movements by adult males presumably maintain gene flow between nearby colonies (Costa et al., 2016; Glass, Klein, Norris, & Gardner, 2016), but results on sex-biased dispersal have been mixed (Gardner-Santana et al., 2009; Heiberg et al., 2012; Kajdacsi et al., 2013). However, urban rats are capable of moving several kilometres during relatively rare long-distance dispersal events (Creel, 1915), indicating the possibility of gene flow across entire cities. Consistent movement among adjacent colonies might produce a stepping-stone pattern of IBD (Kimura & Weiss, 1964), and a study of urban rats at 11 sites in Baltimore, MD, indeed suggested this model of population structure (Gardner-Santana et al., 2009). Yet, two other rat studies from Salvador, Brazil, indicate that stark differentiation into identifiable genetic clusters between rats can occur over short distances (Kajdacsi et al., 2013; Richardson et al., 2017). Thus, while we expect IBD at broad spatial scales, we hypothesize that local environmental heterogeneity will produce significant dispersal barriers between rats, leading to clear deviations from IBD and genetic structuring at fine spatial scales within the NYC landscape.

Brown rats have a nearly global distribution due to a complex history of range expansions and human-assisted movements (Puckett et al., 2016). Phylogeographic and population genetic analyses can untangle the recent migrations of human commensals and other invasive species (Anand, Boursot, Darviche, & Dad, 1996; Aplin et al., 2011; Darling, Bagley, Roman, Tepolt, & Geller, 2008; Novak & Mack, 2001; Puckett et al., 2016). While a recent study found that a small number of NYC rats exhibit ancestry primarily from Western European source populations, other cities harbour rat populations with multiple or admixed global origins (Puckett et al., 2016). Here, we expand on the study by Puckett et al. (2016) to include hundreds of NYC rats. Given NYC's history as a centre for global trade and human immigration over the last few centuries, we expect that the NYC population may contain recent migrants or rats of disparate or admixed origin, which might provide insight into contemporary patterns of genetic connectivity across the city's rat population.

For continuously distributed species, genetic discontinuities and patterns of relatedness are best identified with uniform, individual-based sampling across the entire landscape (Luximon, Petit, & Broquet, 2014; Prunier et al., 2013; Schwartz & McKelvey, 2009). Previous work on urban brown rats analysed a few clustered locations chosen a priori (Gardner-Santana et al., 2009) or relatively small portions of a city (Kajdacsi et al., 2013; Richardson et al., 2017), and all three studies used microsatellites. Here, we employ citywide individual-based sampling to examine three specific questions about neutral evolutionary processes in brown rats of New York City (NYC) using genomewide single nucleotide polymorphisms (SNPs) and spatial genetic approaches:

1. How does relatedness between rats and localized genetic drift change over fine spatial scales?
2. Do brown rats exhibit a continuous gradient of genetic variation over space best described by IBD, or do heterogeneous landscape effects on gene flow result in cryptic genetic structure?
3. Did brown rats in NYC originate from a single introduced lineage, or do they exhibit evidence of multiple invasions from distinct source populations?

We aim to understand how drift and gene flow influence the spatial genetic patterns of a highly commensal rodent occupying one of the most densely populated and developed cities in the world, and more broadly, to provide insight into the study and management of continuously distributed populations.

2 | METHODS

2.1 | Study site, species and sampling

We studied brown rats across the island of Manhattan in NYC, an intensely urbanized and densely populated landmass that hosts a large chronic rat population (Davis, 1950; Johnson, Bragdon, & Olson, 2016). Over 1.6 million permanent human residents live within the 59.1 km^2 island, and the local population increases to over 3.9 million with daily commuters (Moss & Qing, 2012). Rats likely invaded the southern tip of Manhattan between 1750 and 1770 (Armitage, 1993) and have since spread throughout the island. In a recent survey conducted by the NYC Department of Health and Mental Hygiene (DOHMH), 8.2% of all properties in Manhattan showed signs of rat activity (Johnson et al., 2016), but brown rats also inhabit other areas such as sewers, parks and subway tunnels that are not routinely surveyed. Manhattan is colloquially divided into three geographic regions that we use here for ease of communication (Figure 1a): Downtown ranges from the southern tip to 14th street and contains a mix of residential, commercial and office spaces; Midtown ranges between 14th and 59th street and contains higher proportions of office and commercial spaces with fewer residents, as well as several large transportation hubs; Uptown extends from 59th street to the northern tip of the island and is largely residential. Manhattan is further divided into 12 community board districts that we refer to here to describe geographic patterns (Figure 1a).

Rats typically use earthen space for burrowing, and we sampled rats on NYC Parks properties, as well as private properties with permission, throughout Manhattan in areas with evidence of burrowing or other rat activity. We used lethal snap traps baited with a mixture of peanut butter, oats and bacon, housed in bait stations (Bell Labs) and set for 24-hr periods. From each trapped rat, we stored 3–4 cm of tail tissue in 70% ethanol and recorded data on location, sex, weight and sexual maturity. To capture variation across the entire cityscape as well as at fine spatial scales, we aimed to maximize geographic coverage in our sampling. Between June 2014 and

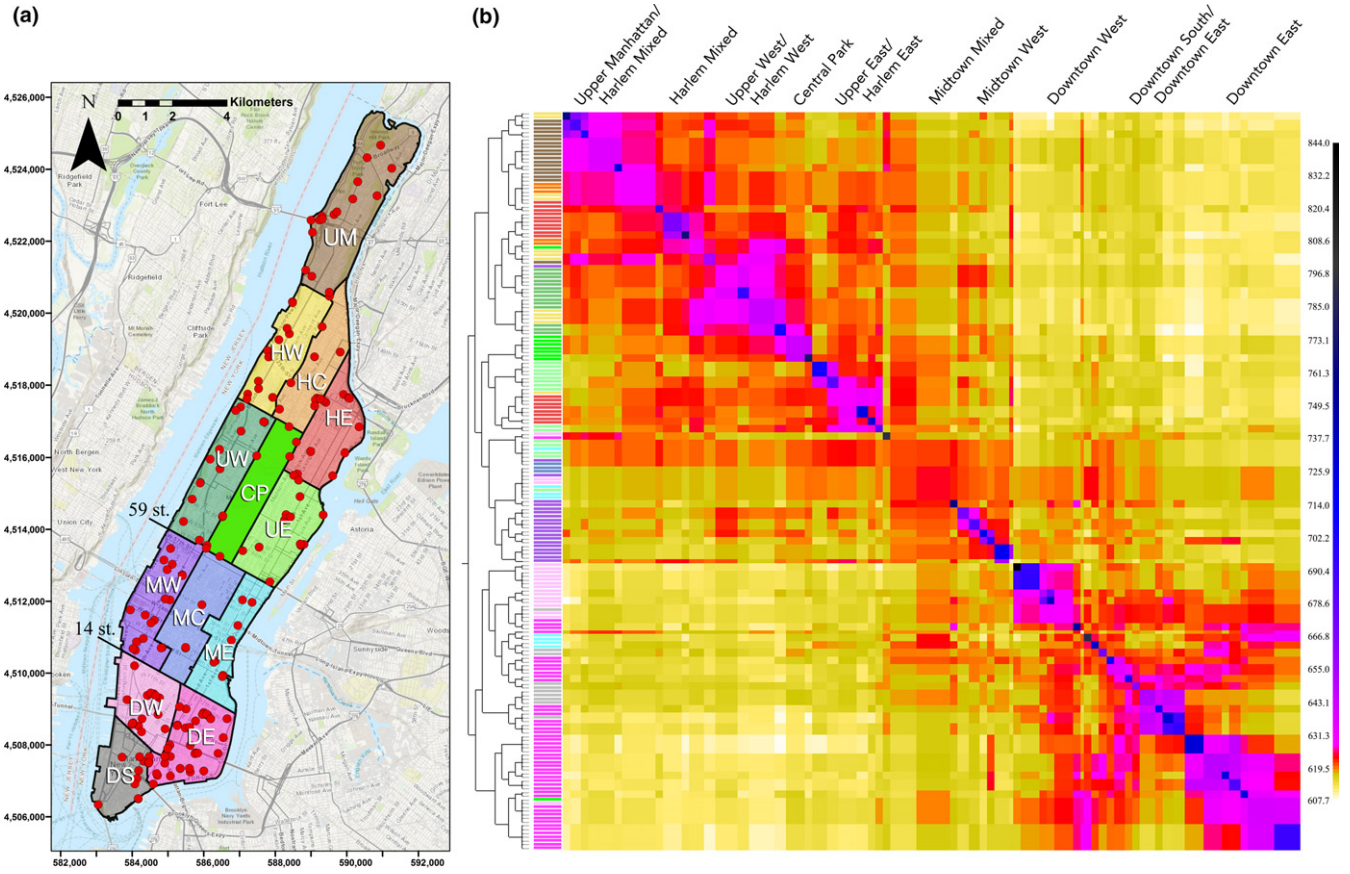

FIGURE 1 (a) Sampling map for brown rats (n = 198) in Manhattan, NYC. Red points are locations of rat samples. The island is separated into 12 community board districts labelled from south to north: DS, Downtown South; DW, Downtown West; DE, Downtown East; MW, Midtown West; MC, Midtown Central; ME, Midtown East; UW, Upper West; CP, Central Park; UE, Upper East; HW, Harlem West; HC, Harlem Central; HE, Harlem East; UM, Upper Manhattan. (b) Coancestry heatmap generated by fineSTRUCTURE analysis. Samples grouped along the heatmap's diagonal have common shared coancestry histories and pairwise comparisons outside the diagonal indicate level of shared coancestry between groups of rats. Lighter yellow colours represent lower shared coancestry and darker reds, purples and blues indicate progressively higher shared coancestry. Neighbourhood labels across the top describe the geographic area of clustered samples, and colours along the left side indicate the community board in which each rat was sampled [Colour figure can be viewed at wileyonlinelibrary.com]

December 2015, we collected 393 samples, of which 288 were chosen for sequencing that maximized geographic coverage.

2.2 | DNA sequencing and SNP genotyping

We extracted genomic DNA and prepared ddRADseq libraries for paired-end sequencing using the Peterson, Weber, Kay, Fisher, and Hoekstra (2012) protocol and then used STACKS v1.35 (Catchen, Hohenlohe, Bassham, Amores, & Cresko, 2013) to call and filter SNPs for a final data set of 61,401 polymorphic loci across 262 individuals. For detailed description of these methods, see Appendix S1.

Finally, we used the program BED2DIFFS_V1 (Petkova et al., 2014), to generate a matrix of average genetic dissimilarity based on allelic differences observed between samples, which is similar to Dps (i.e., proportion of shared alleles) but excludes loci where one sample contains missing data. Genetic distance estimates based directly on allelic differences are useful for assessing geneflow patterns among closely related samples (Bowcock & Minch, 1994; Takezaki & Nei, 1996).

2.3 | Genetic diversity and effective population size

We used the *populations* script in STACKS to calculate indices of genetic diversity for the entire Manhattan population, including expected (H_E) and observed (H_O) heterozygosity, nucleotide diversity (π) and inbreeding coefficient (F_{IS}). We also calculated these indices for the three major geographic regions of Manhattan (Downtown, Midtown and Uptown) to better understand the spatial distribution of genetic variation.

Lastly, we calculated effective population size (N_e) and 95% confidence interval (C.I.) using the linkage disequilibrium method in NEESTIMATOR v2 (Do et al., 2014) for all alleles. We calculated N_e for the full data set (n = 262), as well as for the Downtown, Midtown and Uptown regions separately to see how demographic processes varied across space.

2.4 | Local genetic structure and movement

We built a Mantel correlogram using our average genetic dissimilarity matrix and a matrix of Euclidean distance between NYC rats in the ECODIST R package to examine local genetic structure (also called fine-scale spatial genetic structure; Vekemans & Hardy, 2004; Dick, 2008) using the full data set of 26 individuals (Development Core Team 2011; Goslee & Urban, 2007). This analysis measured spatial autocorrelation between genetic and geographic distances, which results from IBD processes, for pairs of rats within different distance classes. We chose distance classes of 200 m because rats rarely move past this distance within a single generation (Davis et al., 1948; Heiberg et al., 2012). We only present comparisons at less than half the maximum pairwise geographic distance, because only individuals from the edges of sampling space were included in the larger distance classes, which can bias estimates (Wagner et al., 2005).

To quantify movements between related individuals, we studied the association between kinship and distance across all pairs of Manhattan rats. First, we generated within-family kinship coefficients (hereafter, kinship) for pairs of samples using the *genome* function in PLINKv1.07 (Purcell et al., 2007) and compared these values to their respective pairwise geographic distances. As first-order and second-order relationships have expected kinship values of 0.5 and 0.25, respectively, due to identity-by-descent, we binned related pairs by their "kinship class," which were centred around those expected values, to understand how geographic distance between rats changes as kinship decreases. Kinship classes were organized as follows: pairs with kinship $\geq$0.375 were considered first-order relatives (e.g., parent–offspring, full-siblings); pairs with 0.1875 $\geq$ kinship $>$ 0.375 were considered second-order relatives (e.g., grandparent–grandchild, half-siblings); pairs with 0.0 $>$ kinship $>$ 0.1875 were considered distantly related (e.g., cousins, second cousins or more distant); and pairs with kinship = 0 were considered unrelated. To quantify differences in geographic distance between pairs of rats with different kinship classes, we ran a one-way ANOVA ($\alpha = 0.05$) in R with a Tukey's post hoc test and calculated mean, median, standard deviation and maximum distance within each class.

We also created separate mantel correlograms for all rats identified as male ($n = 143$) and female ($n = 73$), to look for evidence of sex-biased dispersal, which can be detected through differences in patterns of spatial autocorrelation (Banks & Peakall, 2012). These correlograms used a lag size of 300 m to ensure at least 20 pairwise comparisons were included in each distance class.

2.5 | Citywide spatial population genomics

To understand the extent of genetic structuring and identify spatial genetic discontinuities across Manhattan, we used several related methods. Each is described in detail below, but briefly, we used (i) Bayesian clustering with BAPS v5.3 to test for the presence of multiple genetic populations under Hardy–Weinberg equilibrium (Corander, Sirén, & Arjas, 2008); (ii) simple mantel test (Mantel, 1967); (iii) principal components analysis (PCA) to identify major trends in the distribution of genomic variation through ordination; (iv) fineSTRUCTURE to assess genetic structuring through differences in shared coancestry (Lawson et al., 2012); (v) spatial principal components analysis (sPCA) to assess genetic structuring that captures patterns of both spatial autocorrelation and genetic variability across space (Jombart et al., 2008); and (vi) estimated effective migration surfaces (EEMS) to identify spatial regions that deviate from a null model of IBD (Petkova, Novembre, & Stephens, 2016).

When samples include multiple family groups alongside unrelated individuals, removing highly related pairs (e.g., full-siblings) allows more accurate quantification of population genetic structure and diversity (Goldberg & Waits, 2010; Waples & Anderson, 2017). We used the *genome* function in PLINK v1.07 (Purcell et al., 2007) to identify pairs of individuals with a kinship coefficient greater than 0.4. We removed whichever individual had more missing data, resulting in a filtered data set of 198 individuals that we used for all citywide population genomic analyses described in this subsection.

The program BAPS v5.3 determines the most likely number of putative populations (K) by maximizing HWE through a stochastic search algorithm that incorporates sample location as a spatial prior (Corander et al., 2008). We used the "spatial clustering of groups" module to examine values of *K* ranging from 1 to 10 in five independent iterations, using a reduced data set of 10,000 random SNPs for computational feasibility.

We ran a Mantel test within the ECODIST R package to test for IBD (Goslee & Urban, 2007) using matrices of average genetic dissimilarity and the natural log of geographic distance between all points (Rousset, 1997). The relationship between these variables was visualized using a scatterplot in R.

A PCA creates synthetic variables that maximize variation among samples, which we generated using the program FINESTRUCTURE (Lawson et al., 2012). Samples were labelled with a colour depicting their sampling location (NYC community board district), revealing geographic patterns of genetic variation. To further examine the association between genetic variation and geography, we compared individual scores from PC1 to latitude using a Spearman's rank correlation test.

The program FINESTRUCTURE harnesses the full power of reference-aligned and genomewide SNP data sets to fit a model of population structure estimating shared coancestry across recombination blocks on each individuals' chromosomes (Lawson et al., 2012). We first phased loci and imputed missing genotypes using FASTPHASE (Scheet & Stephens, 2006) and then ran FINESTRUCTURE using the unlinked model for 100,000 MCMC iterations and 20,000 tree building iterations, using a minimum of 500 SNPs and 10% of the genome for the expected maximization estimation, processing 10 individuals at a time. We inspected MCMC trace files to confirm model convergence, viewed and organized the resultant pairwise heatmap with the available FINESTRUCTURE GUI and labelled individuals based on their geographic origin.

sPCA is a spatially explicit ordination approach, implemented through the ADEGENET R package (Jombart & Ahmed, 2011), that

identifies eigenvectors that maximize both genetic variance and trends in spatial autocorrelation (Jombart et al., 2008). This analysis identifies both "global" structures, identified by positive autocorrelation and indicating clinal patterns, as well as "local" structures, characterized by negative autocorrelation that occurs as genetic distance changes rapidly over short spatial scales. We implemented the sPCA specific test for assessing statistical significance of spatial structure, used the Gabriel graph to create the spatial network within sPCA and calculated F_{ST} between identified clusters using STACKS (Catchen et al., 2013; Jombart et al., 2008). Studies of population genetic structure and connectivity often adopt a hierarchical approach to identify subtle genetic patterns, by repeating analyses on subsets of individuals that are found to be differentiated in analysis of the full data set (Barr et al., 2015; Ruiz-Lopez et al., 2015). We repeated our sPCA on the two major genetic clusters identified by sPCA to distinguish any minor genetic clusters within Manhattan rats. We removed one spatial outlier that was >6 km away from all other rats in the Downtown-only analysis.

EEMS was developed specifically to investigate gene flow in systems driven broadly, but not completely, by IBD (Petkova et al., 2014). It uses a stepping-stone model (Kimura & Weiss, 1964) to assess whether migration rates between adjacent demes are higher or lower than expected and interpolates these estimates to produce a migration surface that illustrates barriers and corridors for movement across the landscape. We chose to represent the landscape across 60 demes to ensure we capture signatures of long-distance gene flow, as distance between demes would be many times the distance of normal home range movements (Davis et al., 1948; Glass et al., 1989; Heiberg et al., 2012). To run EEMS, we first adjusted parameters until each gave the recommended acceptance proportion of 20%–30% and then ran the analysis for 1×10^7 iterations, sampling every 5,000 iterations after 1×10^6 burn-in iterations. We plotted results using the REEMSPLOTS package in R (Petkova et al., 2014).

2.6 | Global origins of NYC rats

To understand the evolutionary origins of the NYC rat population and examine whether NYC harbours recent migrants, we compared the full NYC rat data set (n = 262) to a global data set of 314 brown rats sampled from around the world and sequenced with the same ddRAD-Seq approached used in this article (Puckett et al., 2016; NCBI SRA PRJNA344413). We first extracted genomic loci from the NYC samples using the mpileup function in SAMTOOLS v1.2 (Li et al., 2009), using the position list for 32,127 SNPs analysed for the global analysis (Puckett et al., 2016). We sought to place NYC rats in context to the major global trends of genomic variation so we first ran a PCA in EIGENSOFT v5.0.2 (Patterson, Price, & Reich, 2006) using the global samples as controls and then projected all NYC samples into the PC space. For a more detailed analysis, we reran the PCA and projection excluding Asian samples because NYC rats did not show evidence of recent Asian ancestry.

3 | RESULTS

3.1 | Genetic diversity and effective population size

Across Manhattan, we estimated summary values of H_O = 0.212, H_E = 0.266, π = 0.267 and F_{IS} = 0.205 for the full data set and found regional differences in genetic diversity across Manhattan (Table 1). Most notably, rats in the Midtown region exhibit increased inbreeding coefficients and reduced observed heterozygosity, but show higher levels of expected heterozygosity and nucleotide diversity, compared to rats in Downtown or Uptown.

We estimated an effective population size of 259.6 (95% C.I.: 259.1–260.1) for the full Manhattan data set, but also observed clear regional differences in N_e across the city (Table 1). The estimated N_e of Downtown rats was 122.4 (95% C.I.: 122.1–122.7) and the estimated N_e of Uptown rats was 147.4 (95% C.I.: 147.0–147.7), but the estimated N_e of Midtown rats was only 42.3 (95% C.I.: 42.4–42.4).

3.2 | Local spatial genetic structure and movement

The Mantel correlogram and kinship analyses identified a strong pattern of localized spatial genetic structure. Spatial autocorrelation was positive and significant among rats to a range of 1,400 m, with particularly high correlation between pairs within 0–200 m (r = .30, p = .001; Figure 2). The signature of spatial structure dropped sharply in the second distance class (200–400 m) then decreased steadily, dropping below zero beyond 1,400 m, past which rats were effectively no more related than they would be at random (i.e., spatially independent), with the exception of a significant but low value between 1,800 and 2,000 m.

At shorter geographic distances, pairs of rats exhibited increased kinship values (Table 2). ANOVA indicated significant differences in geographic distance between rats of different kinship classes ($F_{1, 195}$ = 21.88, p < .0001). Tukey's post hoc test indicated that geographic distances between first- and second-order-related rats were

TABLE 1 Genetic diversity summary statistics and effective population size estimation for the full data set of Manhattan, NYC, brown rats and for each of the three major geographic regions of Manhattan

Data set	n	H_O (±StdErr)	H_E (±StdErr)	Pi (±StdErr)	F_{IS} (±StdErr)	N_e (95% C.I.)
Full NYC	262	0.212 (0.001)	0.266 (0.001)	0.267 (0.001)	0.205 (0.077)	259.6 (259.1–260.1)
Downtown only	89	0.207 (0.023)	0.251 (0.026)	0.252 (0.026)	0.168 (0.048)	122.4 (122.1–122.7)
Midtown only	50	0.200 (0.022)	0.260 (0.026)	0.264 (0.026)	0.221 (0.073)	42.3 (42.4–42.4)
Uptown only	123	0.204 (0.024)	0.245 (0.027)	0.246 (0.027)	0.159 (0.043)	147.4 (147.0–147.7)

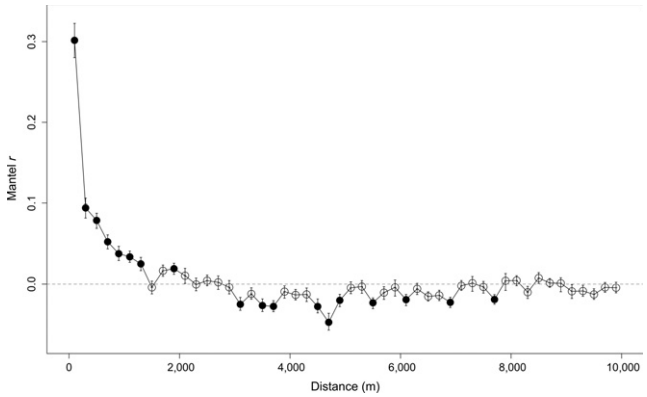

FIGURE 2 Mantel correlogram depicting the association between genetic distance and geographic distance among pairs of samples within each distance class of 200 m (n = 262). Error bars show 95% confidence intervals and were calculated using 999 bootstrapped replicates. Significant associations (α = 0.05) are represented by filled circles

not significantly different (p = .87), although both groups differed significantly from distantly related pairs of rats (p < .001 for both comparisons). First-order relatives were separated by a mean distance of 45 m (SD = 83 m, median = 14 m) but exhibited a maximum observed distance of 539 m. Second-order relatives were separated by larger distances, but were also often found in proximity to each other (mean = 139 m, SD = 256 m, median = 24 m). Distantly related rats were separated by a mean distance of over 1,259 (SD = 2,402, median = 328 m). Many pairs of rats with kinship coefficients of zero were identified at all distances (Figure S1).

Across Manhattan, patterns of spatial autocorrelation for male and female rats show an overall similar pattern with increasing geographic distance (Figure S2). While both sexes exhibit strong positive spatial autocorrelation across the first distance class, males show a slightly higher mantel r value (Males = 0.40, Females = 0.26), which may be in part due to a difference in sample size.

3.3 | Citywide spatial population genomics

Model-based clustering with BAPS indicated that NYC rats are best described as a single genetic population; the probability of K = 1 was 1 (for log likelihood values Table S1). All further citywide analyses thus represent within-population processes and patterns.

The simple Mantel test showed evidence of moderate IBD across the cityscape (r = .27, p = .001; Figure S3). The PCA indicated a clinal pattern in genetic variation across Manhattan, where PC1 was highly correlated with latitude and presented a near continuous distribution of samples (Figure 3; r^2 = .83). The second PC axis indicated differentiation between rats in Downtown East and Downtown West.

We also identified clear signals of within-population differentiation using three methods intended to identify fine-scale genetic structuring and deviations from IBD. Together, fineSTRUCTURE (Figure 1b), sPCA (Figure 4a) and EEMS (Figure 4d) indicated reduced gene flow across the Midtown region, leading to the presence of Uptown and Downtown genetic clusters. The fineSTRUCTURE analysis identified 58 groups among 198 samples (grouped tips on the bifurcating population tree) with indistinguishable patterns of shared coancestry that we interpret as members of the same or closely related colonies. Pairwise comparisons among these groups reveal patterns of shared coancestry across the city. Notably, despite evidence of ample gene flow within both the Uptown and Downtown clusters separately, rats exhibit very low coancestry between the two regions. Rats within Midtown and particularly Midtown West show only moderate levels of shared coancestry with each other, indicating less gene flow within the region.

The first axis of our sPCA indicated the same break in genetic connectivity between Uptown and Downtown rats, stretching across the Midtown region from SW to NE, suggesting two major genetic clusters of rats within the Manhattan population. This axis clearly identified the largest proportion of genetic variance and spatial autocorrelation (Figure S4). The sPCA global test confirmed that this genetic discontinuity was statistically significant (p = .001) and the fixation index calculated between these clusters indicated fine-scale structuring (F_{ST} = 0.01). The migration surface produced by EEMS indicated that long-distance migration rates deviated from IBD (Figure 4d), with the most striking feature being a band of decreased migration stretching across the Midtown region and to the southwest. This area broadly overlaps the discontinuity identified by sPCA that separates the observed Uptown and Downtown clusters as well as the region of reduced diversity identified by sGD.

We also observed a subtle pattern of hierarchical genetic structuring (i.e., minor genetic clusters observable within the major clusters). This was present in both the fineSTRUCTURE plot, as geographically proximate samples that share relatively high

TABLE 2 Summary of geographic distance measurements for pairs of rats within kinship classes determined through kinship analysis in PLINK. A Tukey's post hoc test for a significant one-way ANOVA indicated significant statistical differences between first-order related and distantly related rats (p < .001) and between second-order related and distantly related rats (p < .001)

Kinship class	Relatedness	n	Average geographic distance (m)	Median geographic distance (m)	Maximum geographic distance (m)
$k \geq 0.375$	First order	91	45.3 (±82.5)	14.3	538.6
$0.375 > k \geq 0.1875$	Second order	76	139.1 (±256.0)	24.3	1,201.7
$0.1875 > k > 0.0$	Distantly related	30	1,259.1 (±2,402.1)	328.1	10,006.8

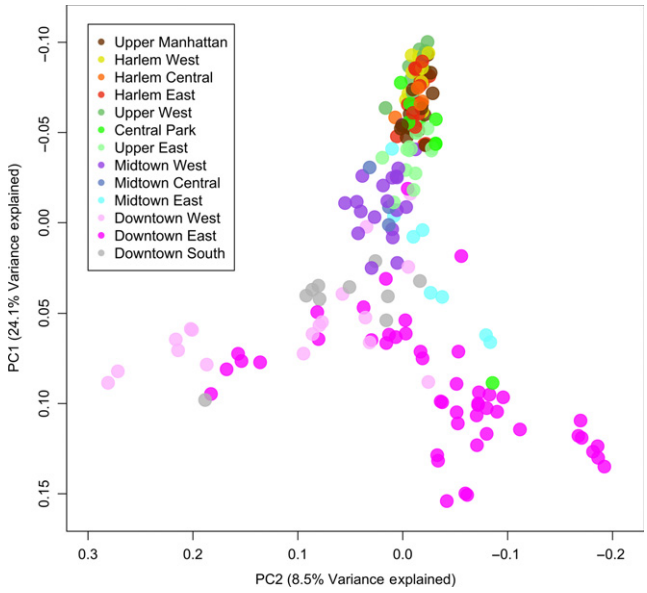

FIGURE 3 Principal components analysis generated by fineSTRUCTURE for $n = 198$ Manhattan rats. Samples are coloured based on the community district from which they were collected and axes have been flipped to best recapitulate geography. PC1 is highly correlated with latitude ($\rho = 0.86$) [Colour figure can be viewed at wileyonlinelibrary.com]

coancestry, as well as within our sPCA, when we analysed each major cluster separately (Figure 4b,c). The presence of genetic discontinuities was significant for both Uptown ($p = .02$) and Downtown ($p = .001$) sPCA. Within the Uptown cluster, rats in Upper Manhattan and the northern portion of Harlem West and Harlem Central were differentiated from those in the Upper West, Upper East and Harlem East (Figures 1b and 4b). EEMS also identified a band of reduced migration that partially explained this break in connectivity (Figure 4d). Rats in Upper West and Upper East were lightly differentiated, with Upper East appearing to share more gene flow with Midtown in both sPCA and fineSTRUCTURE (Figures 1b and 4b). Within the Downtown cluster, rats in Downtown West, Downtown South and Downtown East all appear spatially structured, with Downtown East and West sharing more gene flow with Downtown South than with one another (Figures 1b and 4c).

3.4 | Global origins of NYC rats

In our global PCA projections, all rats from NYC were tightly clustered with Western European populations, which likely indicates a population origin in Western Europe (Figure S5A). The first and fifth PCs were the most informative for understanding the global origins of NYC rats. The first PC separated the cluster containing Asian,

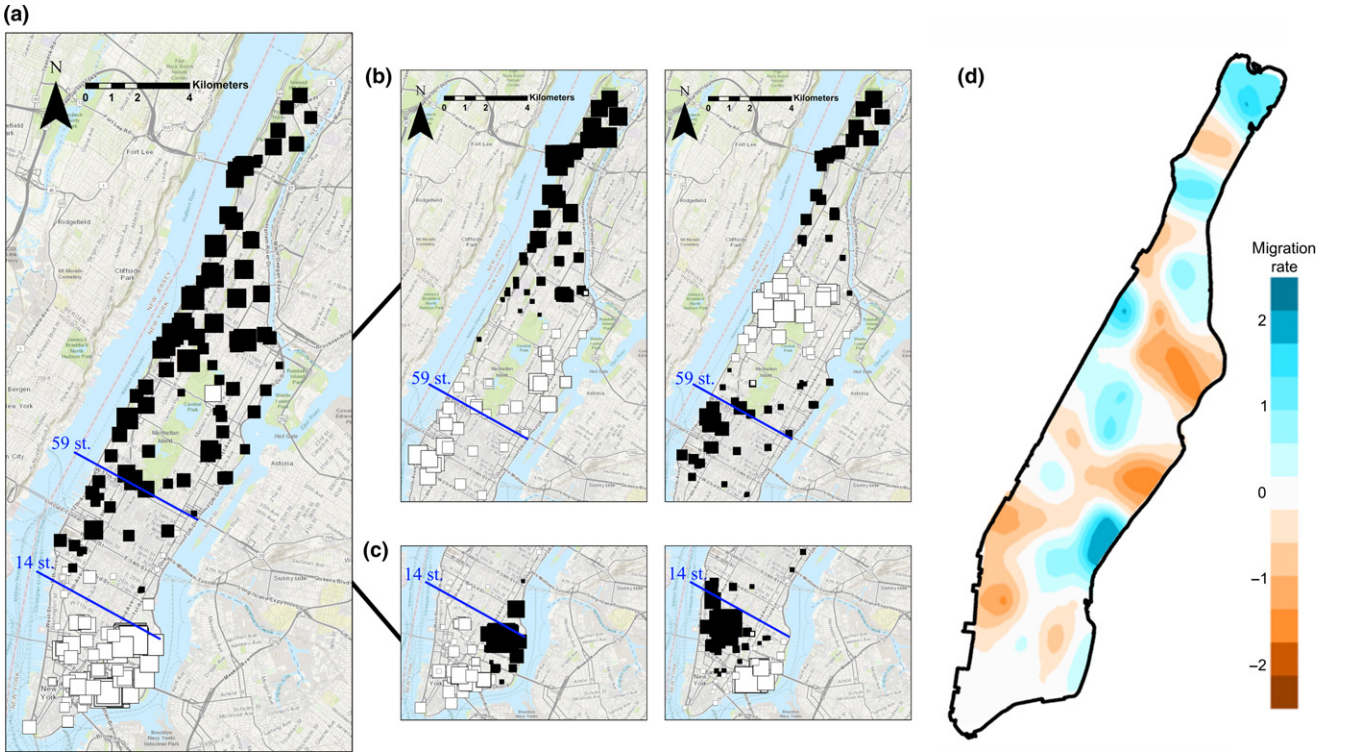

FIGURE 4 (a) First global axis scores from full landscape sPCA ($n = 198$). Each georeferenced rat is depicted with a square, where colour represents assignment to one of the two major spatial genetic clusters of rats, and size describes the magnitude of differentiation (eigenvalue) between groups. Street markings in blue denote boundaries between the Downtown, Midtown and Uptown regions. (b) The first two global eigenvectors representing spatial genetic clustering within only the Uptown rats identified in the full landscape analysis. (c) The first two global eigenvectors representing spatial genetic clustering within only the Downtown rats identified in the full island analysis. (d) Estimated migration rate surface produced by EEMS analysis depicting deviations from estimates of continuous long-distance gene flow. Darker reds indicate reduced migration across those areas, and darker blues indicate higher migration rate than expected. Migration was calculated across 60 putative demes in a stepping-stone lattice model [Colour figure can be viewed at wileyonlinelibrary.com]

Alaskan and Western U.S. samples from the non-Asian cluster, while the fifth PC maximized spread of the non-Asian samples (Figure S5B). NYC rats were consistently projected near samples from Great Britain, France and Spain, as well as several Central and South American samples. When projected into PC space generated using only the non-Asian samples, NYC rats remained tightly clustered with Western European populations (Figure S6), particularly with samples from Great Britain and France. Several samples from Brazil, Argentina and New Orleans, USA, also overlap with the projected NYC cluster. Samples from Baltimore, MD, USA, did not overlap with the NYC samples despite the proximity of these two cities on the east coast of North America (Figure S6B).

4 | DISCUSSION

Brown rats in Manhattan, NYC, compose a single genetic cluster with a Western European origin and a moderate clinal pattern of genetic variation across the island's north–south axis. Despite the lack of divergence into distinct populations, we detected significant departures from IBD across specific regions of the landscape, including reduced gene flow across Midtown Manhattan. A clear split between major Uptown and Downtown genetic clusters as well as minor spatial genetic structuring within those areas suggests heterogeneity in the extent of gene flow and drift across the urban landscape. We also identified strong spatial autocorrelation at fine geographic scales driven by limited spatial dispersion of related individuals, suggesting that genetic drift outweighs the effects of gene flow at a distance of 1,400 m, past which rats are spatially independent. This study is the first on urban rats to use evenly distributed and individual-based sampling across a city as well as dense SNP genotyping. These advances provide much higher resolution of the evolutionary processes and movement ecology driving the spatial distribution of neutral variation for this globally important urban invader.

4.1 | Genetic diversity and effective population size

Through differences in genetic diversity and N_e estimated across the Downtown, Midtown and Uptown regions of Manhattan, we can infer heterogeneity in local connectivity among rats and the demographic processes they experience. While it is notoriously difficult to determine the true census population size from N_e estimates (Frankham, 1995; Luikart, Ryman, Tallmon, Schwartz, & Allendorf, 2010), the relative values of N_e between regions of Manhattan indicate that Midtown supports a smaller population of rats and provides less suitable habitat, compared to Downtown and Uptown Manhattan. Pest management may also be more intense in the Midtown region. The reduced H_O and increased F_{IS} also suggest more limited gene flow among rats living within the Midtown region. In contrast, Midtown rats show elevated H_E and π, which reflects our expectation that this region receives immigrant rats from both Uptown and Downtown.

4.2 | Local spatial genetic structure and movement

We used spatial autocorrelation and kinship analyses to identify a strong pattern of localized spatial genetic structure (Dick, 2008; Epperson, 1995; Hardy & Vekemans, 1999) driven by limited dispersal of related individuals across the urban landscape. Brown rats live in social colony groups (Barnett, 1958; Feng & Himsworth, 2014), and the strong Mantel correlation within the first 200 m captures space use patterns among closely related individuals, likely driven by social interactions (Gauffre et al., 2008). Although the signature of spatial structure weakens with increased distances, it extends well past the boundaries of a single colony to a range of 1,400 m.

Natal and mating dispersal (i.e., adult dispersal) are known drivers of gene flow (Bohonak, 1999; Broquet & Petit, 2009; Phillipsen, Kirk, Bogan, Mims, & Julian, 2015), but despite several studies on home range and movement, dispersal distance in brown rats is not well known. Rats have been observed moving over 150 m in a day (Glass et al., 1989; Recht, 1988), but their home range is often as small as 30–40 m in urban settings (Davis et al., 1948). Additionally, paternity tests (Costa et al., 2016; Glass et al., 2016) and radio tracking (Taylor & Quy, 1978) indicate that male rats regularly expand their range of movement to find mates, often moving hundreds of metres. Our study describes distances separating related pairs of individuals that may be due to dispersal or regular home range movement by one or both rats in each dyad. It is unclear whether rats in this study mated after moving long distances, but while socially dominant males are known to antagonize unfamiliar male rats (Davis & Christian, 1956), subordinate male rats regularly mate and sire offspring (Macdonald, Mathews, & Berdoy, 1999). Despite these above-mentioned gene flow mechanisms, a pattern of male-biased dispersal is not ubiquitous in urban rat populations (Gardner-Santana et al., 2009) and was not identified in this study (Figure S2), indicating that female rats may contribute considerably to local gene flow dynamics.

Our results on fine-scale structure and movement provide several key insights on movement ecology of brown rats: (i) urban brown rats remain spatially clustered over several generations, but experience gene flow with adjacent colonies due to a small number of rats moving larger distances. These patterns lead to local genetic structure as alleles drift in spatial patches over multiple generations (Endler, 1977; Turner, 1982); (ii) rats separated by a distance larger than 1,400 m experience genetic drift independently, indicating the potential for within-population genetic clustering in NYC that we identified using citywide analyses; (iii) many unrelated rats exist at very short distances (Figure S1) suggesting that rats observed in the same location are not necessarily highly related, due to dispersal and inbreeding avoidance (Schwartz & Armitage, 1980; Vignieri, 2007).

Together these findings suggest that while rats exhibit spatially restricted dispersal, local genetic variation is not completely governed by social interactions and strict territoriality among nearby rats. Consistent gene flow from outside the immediate colony area, paired with the high turnover rate for urban rats (>90% per year; Davis, 1953), may allow brown rats to avoid the negative effects of inbreeding and cause spatial structure to extend beyond the bounds

of a single colony. Several species of anthrodependent arthropods also experience gene flow into adjacent areas, but these species usually move much shorter distances than rats (e.g., between apartments in a building) and often tolerate elevated inbreeding (Booth et al., 2012; Crissman et al., 2010).

The presence of localized spatial genetic structure in urban rats works to maintain high population-wide genetic diversity as alleles drift differently in different geographic locations (Nunney, 2016) and ensures overall population persistence in the case of local disturbance or eradication of individual colonies (Ray, 2001). Gene flow among adjacent rat colonies supports a stepping-stone model of IBD, which promotes gene flow across the entire urban landscape over many successive generations of short distance dispersal. This pattern was also inferred within the Baltimore rat population (Gardner-Santana et al., 2009). Nevertheless, habitat quality differs across the diverse urban landscape matrix, which can alter dispersal dynamics, potentially creating stark differences in genetic connectivity over very short distances (Richardson et al., 2017), rather than gradual decrease in structure indicated by our correlogram.

4.3 | Citywide spatial population genomics

Rats in Manhattan show clear departures from panmixia, including hierarchical structuring into major and minor genetic clusters (Figures 1b and 4) and clinal variation along the island's linear north–south axis (Figure 3). We also identified substantial deviations from our null hypothesis of citywide IBD; a band of reduced migration across the Midtown region divides the major Uptown and Downtown clusters. Methods that take full advantage of reference-aligned genomic data (e.g., fineSTRUCTURE), and/or incorporate a model of IBD (e.g., spatial autocorrelation in sPCA), can reveal important fine-scale spatial genetic discontinuities, even when the populations under study are not comprised of strongly differentiated clusters.

We used IBD as a null model given that brown rats have an expansive realized niche in cities (Alberti et al., 2003), readily disperse through dense urban landscapes (Feng & Himsworth, 2014; Gardner-Santana et al., 2009), and are widely distributed in Manhattan (NYC DOHMH 2013). Our results indicating a clinal pattern of genetic variation and moderate IBD suggest that *Rattus norvegicus* has a much greater ability to maintain genetic connectivity across urban landscapes compared to other native rodents, which exhibit considerable genetic differentiation between populations in isolated urban habitat patches (*Peromyscus leucopus*, Munshi-South & Kharchenko, 2010; *Apodemus flavicollis*, Gortat, Rutkowski, Gryczynska, Kozakiewicz, & Kozakiewicz, 2016). Yet, we also observed heterogeneity in gene flow across the landscape when we accounted for IBD, which supports our hypothesis that genetic structuring will be influenced by areas of reduced dispersal, rather than by continuous gene flow driven by IBD alone. This likely reflects variations in habitat quality and dispersal success that fluctuate in conjunction with natural, cultural and structural heterogeneity across the city known to influence rat habitat (van Adrichem, Buijs, Goedhart, & Verboom, 2013; Colvin, Degregorio, & Fleetwood, 1996; Johnson et al., 2016; Traweger, Travnitzky, Moser, Walzer, & Bernatzky, 2006; Walsh, 2014).

To better understand why the Midtown region acts as a moderate barrier to gene flow within NYC, we considered the patterns of land use and human activity that characterize those spaces. Every neighbourhood in Manhattan supports the presence of rats to some degree (NYC DOHMH 2013), but microhabitat conditions driven by variation in the way humans use, inhabit and maintain individual properties dictate the distribution of urban commensals like the brown rat (Davis, 1953; Johnson et al., 2016). Midtown is largely a centre of commerce and tourism and Midtown West contains several massive transportation hubs, a convention centre and many commercial and industrial use properties. Both have lower densities of permanent human residents compared to surrounding neighbourhoods to the north and south (United States Census Bureau 2010), and rats in these areas displayed decreased H_O and N_e. The combination of less anthropogenic food waste resources and increased levels of disturbance likely make these areas lower quality-habitat for rats that act as a genetic sink, supporting fewer arriving immigrants and producing fewer emigrating dispersers and resulting in lower rates of gene flow across the region (Pulliam, 1988).

In a study of urban habitat occupancy among small mammals, Cavia, Cueto, and Suárez (2009) found that *R. norvegicus* was less common in the industrial urban core than surrounding areas and recent rat activity surveys in NYC indicate relatively fewer rats in Midtown Central and Midtown West (NYC DOHMH 2013). Spatial variability in abundance can lead to local heterogeneity in gene flow (Berthier, Galan, Foltête, Charbonnel, & Cosson, 2005), and lower density can result in effective migration barriers (Petkova et al., 2014). Together with our results on citywide spatial patterns of genetic variation and effective population size differences across Manhattan, we are led to conclude that while brown rats thrive in urban landscapes, differences in long-distance gene flow depend on fluctuations in local habitat quality that ultimately affect demographic parameters like local population density and persistence (Shirk & Cushman, 2014).

In continuous populations under strong IBD, analyses can falsely identify genetic clusters from clinal genetic structures (Frantz, Cellina, Krier, Schley, & Burke, 2009; Meirmans, 2012). While the two major clusters we identified may be partially driven by the background of clinal variation, we observed reduced migration rates across the Midtown region and lower estimates of effective population size as well as geographically clustered patterns of shared coancestry with fineSTRUCTURE. Therefore, we interpret the observed clustering pattern as driven by a combination of distance and landscape attributes, rather than by distance alone. We have several hypotheses about how landscape features might influence the observed major and minor clustering. For example, we expect less gene flow through areas of lower human population density, greater gene flow among low-income areas (Masi et al., 2010) and greater gene flow through brick-lined sewer systems (Johnson et al., 2016). Future landscape genetic analysis may help distinguish between the influence of distance and the natural, social and

structural components of the cityscape (Manel, Schwartz, Luikart, & Taberlet, 2003; Wagner & Fortin, 2012).

4.4 | Global origins of NYC rats

Using a data set of global rat genotypes, we found that NYC's brown rat population was most closely related to rats from Western Europe, particularly Great Britain and France, and showed no signs of multiple introductions from disparate geographic locations. These results reflect the early historical roots of colonization, trade and immigration in New York City. Brown rats first arrived in New York City between 1750 and 1780, when the city was still part of a British colony, and the contemporary population was likely founded by rats crossing on ships between continents (Armitage, 1993; Puckett et al., 2016). Our results build on those of Puckett et al. (2016) by analysing rats from throughout the entire Manhattan landscape, which all share a similar population genetic history.

Rats from eastern North America, South America, Africa and Australasia have similar genomic signatures to those in Western Europe (Puckett et al., 2016), likely due to European colonialism from the 1600s to 1900s. The global reach of the British Empire and other European colonial powers may explain why samples from South America also clustered near NYC. Those rat populations were likely derived from the same historical wave of migrations out of Western Europe, although we cannot discount the possibility of introductions into cities following New World colonization (i.e., NYC to South America or vice versa).

Given NYC's 300-year history as a centre of commerce and port-of-call for immigrants from around the world, we expected that NYC rats would show evidence of multiple recent invasions. However, the global signature of rats appeared largely homogeneous when examined against a background of global genetic diversity. This pattern may be due to ecological priority effects, which would allow an initial wave of invaders to occupy the cityscape and limit the successful establishment of later arrivals (Fraser et al., 2014; Puckett et al., 2016). Additionally, we note that while Manhattan was historically a port city, much of the port activity now occurs in nearby Essex county and Hudson county, New Jersey, or in the NYC boroughs of Brooklyn and Staten Island (Notteboom & Rodrigue, 2005; Rodrigue, 2004). Therefore, there may be limited opportunity for long-distance migration of rats into Manhattan and we may expect differences in global genetic diversity between low- and high-volume port cities and nonport cities.

4.5 | Applications to urban pest management

Results from population genetic studies provide actionable information for pest management professionals, particularly in terms of understanding movement ecology in this cryptic urban pest (Piertney et al., 2016; Richardson et al., 2017; Robins, Miller, Russell, Harper, & Fewster, 2016). Reinvasion post-treatment is a major concern in cities and elsewhere and using evidence of local structuring can help design eradication units (Richardson et al., 2017; Russell et al., 2010; Spurr, O'Connor, Morriss, & Turner, 2006). In Manhattan, rats generally experience gene flow from rats within a 1,400 m radius, so eradication units of this size would likely limit rapid reinvasion by dispersers. Alternatively, because minor genetic clusters aligned fairly well to community board district divisions, these boundaries might provide directly actionable units for municipal management efforts, although effective management of rats always requires habitat modification and reduction of accessible resources (Corrigan, 2011; Lambert, Quy, Smith, & Cowan, 2008; Singleton, Leirs, Hinds, & Zhang, 1999). Our results also highlight the utility of population genetics for identifying recent migrants and the potential source of new rat invasions across fine and global spatial scales (Gardner-Santana et al., 2009; Puckett et al., 2016). For example, in Manhattan, our PCA and sPCA clearly identified an individual in Central Park that was most genetically similar to rats in Downtown East (Figures 3 and 4a), although it is unclear whether this individual moved ~7.5 km independently or by human-mediated dispersal.

5 | CONCLUSION

Urban landscapes create unique ecosystems, with wildlife species responding differently depending on resource availability and dispersal characteristics (Alberti et al., 2003; McKinney, 2006). We described movement dynamics and resultant spatial genetic variation in a continuously distributed and commensal urban exploiter species, the brown rat. We have shown that (i) related individuals often remain highly associated in space, leading to localized spatial genetic structure that is strong at short distances but detectable well beyond a single colony; (ii) rats in Manhattan experience sufficient citywide gene flow to prevent differentiation into multiple isolated populations, but exhibit fine-scale structuring into Uptown and Downtown genetic clusters due to landscape effects that cause deviations from IBD; (iii) rats in Manhattan exhibit a single common population origin with no clear signs of multiple introductions or recent migrants, when compared against a panel of global genetic diversity. Overall, this study uncovers the ongoing evolutionary processes shaping one of the world's most prolific human pests in human-dominated environments and suggests that even continuously distributed populations in urban landscapes may exhibit cryptic genetic discontinuities and fine-scale structuring in response to urban landscape heterogeneity.

ACKNOWLEDGEMENTS

We thank three anonymous reviewers for helpful comments that improved this manuscript. This work was supported by grants from the National Science Foundation (DEB-1457523 and DBI-1531639). We thank Sonia Bernal, David Forlano, Brittney Kajdacsi, Nicholas Rapillo, Matt Wollman and Otis Wood, and the Ryders Alley Trencher-Fed Society (R.A.T.S.) for help with sample collection, and also we thank Jane Park and Ian Hayes for laboratory work support and to Elizabeth Carlen, Nicole Fusco, Arbel Harpak and Carol Henger

for thoughtful comments on early drafts. Thank you to the City of New York Department of Parks and Recreation for trapping permits.

DATA ACCESSIBILITY

Illumina reads are available on the NCBI SRA, accession PRJNA414893.

AUTHOR CONTRIBUTION

M.C. wrote the manuscript, conducted fieldwork and conducted lab-work; M.C., E.E.P., D.M. and J.R. performed analyses; J.M.S. directed and conceived of project; All authors contributed to draft and final versions of the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Combs M, Puckett EE, Richardson J, Mims D, Munshi-South J. Spatial population genomics of the brown rat (*Rattus norvegicus*) in New York City. *Mol Ecol*. 2018;27:83–98. https://doi.org/10.1111/mec.14437