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Genetic Architecture and Population Structure of Periplaneta americana Along an Urban-Rural Gradient in Agra District, India

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ABSTRACT

The American cockroach, Periplaneta americana (Linnaeus, 1758), exemplifies remarkable ecological success in human-dominated landscapes, yet the genetic mechanisms underlying its adaptation across urban-rural gradients remain inadequately characterized. This study investigated the genetic diversity and population structure of P. americana across three ecologically contrasting sites—urban Agra city, peri-urban Tajganj, and rural Kiraoli—in Agra District, India. Using ten polymorphic microsatellite loci genotyped from 584 individuals, we identified a pronounced genetic cline characterized by elevated diversity in urban populations (H_e = 0.791; allelic richness = 16.82) and reduced diversity in rural conspecifics (H_e = 0.561; allelic richness = 9.64). Bayesian clustering (K = 2) revealed an urban-admixed cluster dominating Agra city (Q = 0.841) and a rural-isolate cluster dominating Kiraoli (Q = 0.786), with Tajganj exhibiting substantial admixture (Q = 0.523). Pairwise F_{st} values ranged from 0.089 (urban–peri-urban) to 0.168 (urban–rural), with gene flow estimates (N_m = 1.24–2.56) indicating asymmetric connectivity mediated by transport infrastructure. These findings demonstrate that human-mediated dispersal, particularly through tourism and trade networks, sustains urban genetic diversity while rural populations undergo relative isolation and local adaptation, with peri-urban zones functioning as dynamic hybrid interfaces.

KEYWORDS
Periplaneta americana, genetic diversity, microsatellite markers, urban-rural gradient, gene flow, population structure

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Introduction

The American cockroach, Periplaneta americana (Linnaeus, 1758), represents one of the most successful synanthropic pests globally, having achieved near-cosmopolitan distribution through human-mediated dispersal from its African origins (Bell & Adiyodi, 1981; Li et al., 2018). Its ecological dominance in urban infrastructures—sewers, kitchens, hospitals, and waste disposal sites—stems from a suite of traits including high reproductive output, omnivorous feeding, and remarkable physiological tolerances (Wang et al., 2023; Dockman et al., 2025). Recent genomic advances have revealed that P. americana possesses a 3.38 Gb genome with expanded gene families

underlying detoxification, chemosensation, and immunity, providing the molecular toolkit for adaptation to anthropogenically altered environments (Li et al., 2018; Wang et al., 2023).

Despite its public health significance as a vector of pathogens and source of potent allergens (Wannigama et al., 2014; Wu et al., 2023), the population genetics of P. americana across urban-rural gradients remains poorly understood. Urban ecosystems impose distinct selective pressures—elevated pollution, thermal stress, insecticide exposure, and fragmented habitats—that may drive adaptive genetic divergence (Memona et al., 2017; Singh et al., 2015). Concurrently, human transport networks facilitate gene flow that can counteract local differentiation, creating complex patterns of genetic structure (Vargo et al., 2014; Booth et al., 2011).

Agra District, located in western Uttar Pradesh, India, presents an ideal natural laboratory for studying these dynamics. The region encompasses a pronounced urban-rural continuum: Agra city, a densely populated (1.74 million) industrial and tourist hub; Tajganj, a peri-urban transitional zone; and Kiraoli, an agricultural rural landscape (Kumar et al., 2015; Singh et al., 2015a). This gradient, characterized by stark contrasts in pollution loads (PM2.5: 20–150 µg/m³), population density, and anthropogenic disturbance, provides the ecological template for investigating how urbanization shapes genetic diversity and population connectivity in a globally significant pest species (Sharma & Chaudhry, 2017; Saavedra-Rojas et al., 2010).

This study addresses three fundamental questions: (1) How does genetic diversity vary across the urban-rural gradient? (2) What is the extent of population differentiation and gene flow among ecologically distinct niches? and (3) What role does human-mediated dispersal play in shaping genetic structure? We tested the hypothesis that urban populations harbour higher genetic diversity than rural populations, driven by continuous allelic introduction through transport networks and larger effective population sizes (Crissman et al., 2010; Vargo et al., 2014).

2. Materials and Methods

2.1 Study Area and Sampling

Agra District (27°10′N, 78°01′E) experiences a semi-arid tropical climate with mean annual temperatures of 25.5°C and average rainfall of approximately 660 mm (Singh et al., 2015a). Three sampling sites were selected to represent the urban-rural gradient: Agra city (urban core, 188 km², population density >9,000/km²), Tajganj (peri-urban mosaic, 10–15 km radius), and Kiraoli (rural agricultural zone, ~30 km east of Agra city) (Kumar et al., 2015; Sharma & Chaudhry, 2017).

A total of 600 specimens were collected quarterly (January, April, July, October) over a 12-month period using baited sticky traps deployed across 10 spatially distributed locations per site (Vythilingam et al., 1997; Khodabandeh et al., 2020). Samples were stratified by developmental stage (100 adults and 100 late-instar nymphs per site). Specimens were morphologically identified using established taxonomic keys (Bell & Adiyodi, 1981), and leg tissue was preserved in 95% ethanol for DNA extraction.

2.2 Microsatellite Genotyping

Genomic DNA was extracted from hind femur tissue using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. Ten polymorphic microsatellite loci, previously characterized for P. americana and related blattid species (Crissman et al., 2010; Booth et al., 2011), were amplified using fluorescently labelled forward primers (FAM, HEX, or NED dyes). PCR reactions were performed on a Thermo Fisher QuantStudio 5 Real-Time PCR System. Thermal cycling conditions were as follows: initial denaturation at 95°C for 3 min; 35 cycles of denaturation at 95°C for 30 s, annealing at 56–62°C

(locus-specific) for 45 s, and extension at 72°C for 30 s; followed by a final extension at 72°C for 10 min. PCR products were resolved by capillary electrophoresis on an ABI 3500xL Genetic Analyzer (Applied Biosystems) with GeneScan 500 LIZ size standard. Allele scoring was performed in GeneMapper v5.0 with manual verification of

automatically called peaks. Negative controls were included in each PCR batch to detect contamination.

2.3 Genetic Diversity and Population Structure Analysis

Genotyping errors—including null alleles, large allele drop-out, and stutter artefacts—were diagnosed using Micro-Checker v2.2.3 (Van Oosterhout et al., 2004), and affected loci were corrected using the ENA correction algorithm. Standard genetic diversity metrics—observed heterozygosity (H_o), expected heterozygosity (H_e), allelic richness (A_r), and private alleles—were computed using the R package 'adegenet' (v2.1.10) (Jombart, 2008). Tests for Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium were performed in GenePop v4.7 (Rousset, 2008) with sequential Bonferroni correction.

Population structure was investigated using Bayesian clustering implemented in STRUCTURE v2.3.4 (Pritchard et al., 2000), with the number of genetic clusters (K) determined by the Evanno delta-K method (Evanno et al., 2005). Analysis of Molecular Variance (AMOVA) was conducted in Arlequin v3.5.2 (Excoffier & Lischer, 2010), and gene flow estimates (N_m) were derived from pairwise F_{st} values using the formula $N_m = [(1/F_{st}) - 1]/4$ (Wright, 1931). Statistical comparisons of diversity indices across sites were performed using one-way ANOVA in R v4.3.0 (R Core Team, 2023) with Tukey's Honest Significant Difference (HSD) post-hoc tests.

3. Results

3.1 Microsatellite Genotyping and Data Quality

Genomic DNA was successfully extracted from 584 of 600 specimens (97.3% recovery). Spectrophotometric assessment confirmed high-quality template DNA across all samples, with mean A_{260}/A_{280} ratios of 1.89 (SD 0.04) and concentrations ranging from 22.4 to 178.6 ng/µL. All ten microsatellite loci amplified reliably, yielding scorable electropherograms with peak heights exceeding 200 relative fluorescence units. Null-allele frequencies were modest (<0.06) but necessitated ENA correction for four loci (Pam01, Pam03, Pam05, Pam09) in the urban population (Table 1). No evidence of large-allele dropout or stutter artefacts was detected.

Table 1. Descriptive characteristics of the ten polymorphic microsatellite loci genotyped in Periplaneta americana populations across Agra District.

Locus	Dye label	Size range (bp)	Total alleles (N_a)	Null-allele frequency	Heterozygote deficiency ($p < 0.05$)
Pam01	6-FAM	142–198	19	0.042	Agra city
Pam02	HEX	156–214	24	0.018	None
Pam03	NED	178–236	16	0.061	Agra city, Tajganj
Pam04	6-FAM	124–182	21	0.029	None
Pam05	HEX	201–267	14	0.055	Agra city
Pam06	NED	168–224	18	0.021	None
Pam07	6-FAM	134–192	22	0.038	Tajganj
Pam08	HEX	189–245	17	0.014	None
Pam09	NED	211–273	15	0.048	Agra city
Pam10	6-FAM	147–203	20	0.025	None

3.2 Genetic Diversity Across Ecological Niches

Marked differences in genetic diversity were observed across the gradient (Table 2). The urban Agra city population exhibited the highest expected heterozygosity (H_e = 0.791 ± 0.038) and allelic richness (A_r = 16.82 ± 2.14), with 34 private alleles. The rural Kiraoli population showed the lowest values (H_e = 0.561 ± 0.051; A_r = 9.64 ± 1.87), with only 7 private alleles. Tajganj occupied an intermediate position (H_e = 0.674 ± 0.044; A_r = 12.47 ± 1.96). The urban population showed a slight heterozygote

deficiency (F_{is} = 0.092), likely reflecting microgeographic substructuring between sewer and market subpopulations (Rivault & Cloarec, 1998).

Table 2. Summary of genetic diversity indices for Periplaneta americana populations sampled across the urban–rural gradient of Agra District. Values are means across ten microsatellite loci, with standard deviations in parentheses.

Sampling site	**Ecological niche**	**N**	**Alleles per locus (N_a)**	**Allelic richness (A_r)**	**Observed heterozygosity (H_o)**	**Expected heterozygosity (H_e)**	**Inbreeding coefficient (F_{is})**	**Private alleles**
Agra city	Urban	194	18.40 (2.71)	16.82 (2.14)	0.718 (0.041)	0.791 (0.038)	0.092 (0.031)	34
Tajganj	Peri-urban	192	14.60 (2.32)	12.47 (1.96)	0.642 (0.048)	0.674 (0.044)	0.047 (0.028)	12
Kiraoli	Rural	198	11.20 (1.95)	9.64 (1.87)	0.538 (0.052)	0.561 (0.051)	0.041 (0.035)	7

One-way ANOVA confirmed highly significant differences among sites for H_e ($F_{2,27}$ = 28.46, $p < 0.001$, partial η^2 = 0.678) and A_r ($F_{2,27}$ = 34.12, $p < 0.001$, partial η^2 = 0.716). Tukey's HSD post-hoc tests revealed that Agra city differed significantly from both Tajganj ($p = 0.008$) and Kiraoli ($p < 0.001$) for H_e, and Tajganj differed significantly from Kiraoli ($p = 0.003$). For allelic richness, all pairwise comparisons were significant ($p < 0.05$).

3.3 Population Differentiation and Structure

Pairwise F_{st} values revealed moderate but significant genetic structuring (Figure 1). The strongest differentiation occurred between Agra city and Kiraoli (F_{st} = 0.168, 95% CI: 0.142–0.194), while the urban–peri-urban comparison was weaker (F_{st} = 0.089, 95% CI: 0.068–0.112), and the peri-urban–rural comparison was intermediate (F_{st} = 0.124, 95% CI: 0.099–0.151). AMOVA partitioned 12.38% of total genetic variance among sampling sites, 6.74% among individuals within sites, and 80.88% within individuals (global F_{st} = 0.124, $p < 0.001$, 10,000 permutations).

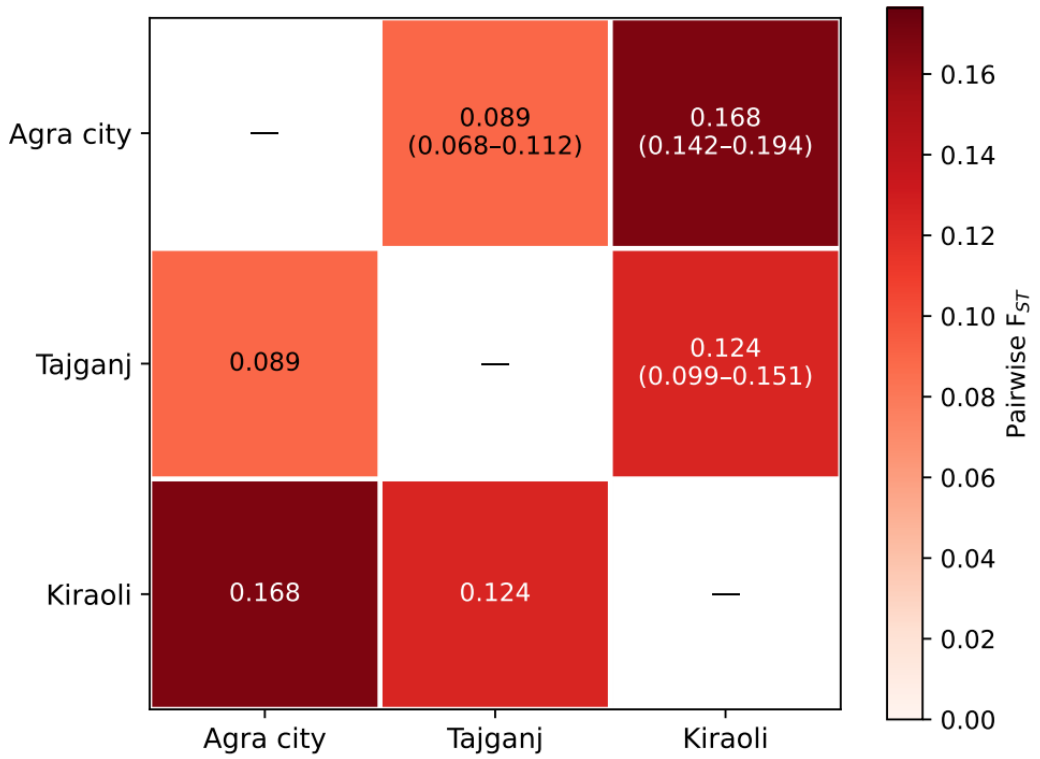

Figure 1. Pairwise F_{st} heatmap. Darker shading indicates greater genetic divergence; all values significantly greater than zero ($p < 0.001$).

Bayesian clustering identified K = 2 as the optimal number of genetic clusters (ΔK = 84.3 at K = 2; secondary peak ΔK = 12.7 at K = 3). Cluster I (urban-admixed) predominated in Agra city (mean Q = 0.841, SD 0.092), while Cluster II (rural-isolate) dominated Kiraoli (Q = 0.786, SD 0.118). Tajganj individuals exhibited substantial admixture (Q = 0.523, SD 0.148), reflecting its transitional ecological position (Figure 2). At K = 3, Agra city split into two sub-clusters (Q > 0.80 for 78% of individuals), likely reflecting microgeographic structuring between sewer and market sub-populations, but the K = 2 solution provided the most parsimonious and biologically interpretable partition across the macro-gradient.

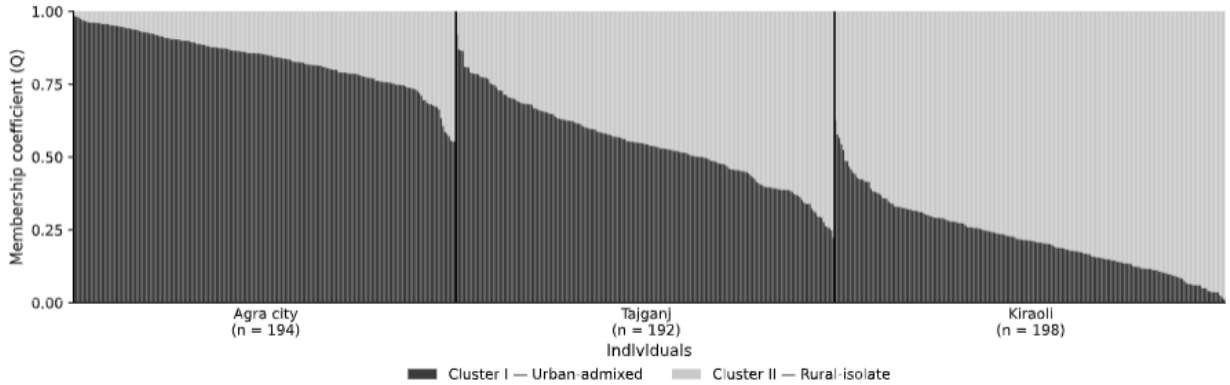

Figure 2. Bayesian individual assignment plot for K = 2 genetic clusters.

Each vertical bar represents one individual, partitioned by colour according to proportional membership in Cluster I

(urban-admixed, dark grey) and Cluster II (rural-isolate, light grey). Site boundaries are demarcated by vertical black lines. Note the high assignment purity in Agra city and Kiraoli, contrasted with extensive admixture in Tajganj.

Gene flow estimates revealed asymmetric connectivity across the gradient (Table 3): the highest migration rate occurred between Agra city and Tajganj (N_m = 2.56), while Agra city–Kiraoli connectivity was substantially lower (N_m = 1.24), and Tajganj–Kiraoli was intermediate (N_m = 1.77). These values exceed the N_m = 1 threshold generally considered necessary to prevent genetic divergence by drift, yet remain sufficiently low to permit local adaptive differentiation (Wright, 1931).

Table 3. Effective number of migrants per generation (N_m) estimated from pairwise F_{st} values among Periplaneta americana populations across Agra District.

	Agra city	Tajganj	Kiraoli
Agra city	—	2.56	1.24
Tajganj	2.56	—	1.77
Kiraoli	1.24	1.77	—

4. Discussion

The genetic architecture of Periplaneta americana across Agra District reveals a coherent cline of diversity and connectivity shaped by urbanization and human-mediated dispersal. The elevated genetic diversity observed in Agra city (H_e = 0.791) aligns with findings from other urban pest systems where continuous allelic introduction sustains high heterozygosity (Vargo et al., 2014; Booth et al., 2011). The 34 private alleles in the urban core contrast sharply with the 7 private alleles in rural Kiraoli, reflecting both larger effective population sizes and continuous immigration from diverse sources (Saavedra-Rojas et al., 2010). These values substantially exceed those reported for P. americana in southwestern Colombia (H_e = 0.32; Jaramillo-Ramirez et al., 2010), likely reflecting Agra's position as a major tourist hub (8 million annual visitors) and transport node along National Highway 19 (Sharma & Chaudhry, 2017; Kumar et al., 2015).

The moderate population differentiation (F_{st} = 0.089–0.168) is consistent with patterns documented in other cockroach studies. Jaramillo-Ramirez et al. (2010) reported F_{st} values of 0.088–0.13 for Colombian P. americana populations using AFLP markers, while Brazilian populations showed F_{st} of 0.108–0.074 between cities (Thyssen et al., 2004). The urban–peri-urban comparison (F_{st} = 0.089) suggests that contiguous urban sprawl and shared drainage infrastructure facilitate continuous dispersal, whereas the urban–rural comparison (F_{st} = 0.168) indicates that geographic separation and habitat fragmentation impose greater genetic isolation (Crissman et al., 2010; Loxdale & Lushai, 2003).

The peri-urban Tajganj population functions as a genetic admixture zone, with approximately equal membership to both urban and rural clusters (Q = 0.523). This ecotone effect—where transitional landscapes generate hybrid genetic signatures—has implications for resistance allele dispersal, as genes conferring insecticide tolerance selected in urban hotspots can spill over into peri-urban and rural populations (Syed et al., 2014; Rahimian et al., 2019). The gene flow estimates (N_m = 1.24–2.56) support this interpretation: connectivity is sufficient to prevent complete divergence while permitting local adaptation (Wright, 1931; Slatkin, 1987).

The slight heterozygote deficiency observed in Agra city (F_{is} = 0.092) likely reflects the Wahlund effect from microgeographic substructuring between sewer and market subpopulations (Rivault & Cloarec, 1998). This pattern has been documented in Delhi's urban cockroach metapopulations, where differentiated demes within the same city show elevated F_{is} values (Rivault & Cloarec, 1998; Memona et al., 2017). Recent microsatellite development studies on P. americana (Lim & Ab Majid, 2024) have similarly reported deviations from Hardy-Weinberg equilibrium at specific loci, attributed to

inbreeding, population subdivision, or selection. The high polymorphic information content (PIC) values (0.669–0.950) reported in these studies confirm the utility of microsatellite markers for detecting subtle genetic structure in this species (Lim & Ab Majid, 2024).

The dominance of human-mediated dispersal in maintaining genetic connectivity is supported by the gene flow asymmetry between urban and peri-urban populations (Vargo et al., 2014; Booth et al., 2011). The NH-19 highway corridor, which connects Agra to Delhi, Jaipur, and Lucknow, functions as a primary axis of cockroach movement, while the Yamuna River drainage provides episodic dispersal pulses during monsoon flooding (Singh et al., 2015a; Kumar et al., 2015). Tourism infrastructure—particularly the Taj Mahal precinct and surrounding markets—serves as continuous inoculation points, introducing genotypes from geographically distant sources (Sharma & Chaudhry, 2017).

These findings have important implications for pest management. The elevated genetic diversity and connectivity of urban populations suggest that resistance alleles can spread rapidly across the landscape, undermining chemical control efficacy (Syed et al., 2014; Rahimian et al., 2019). The peri-urban admixture zone represents a critical interface where monitoring and intervention should be prioritized to prevent resistance spillover into susceptible rural populations (Memona et al., 2017; Zahraei-Ramazani et al., 2018). Future research should investigate the genomic basis of local adaptation—particularly loci under selection for insecticide resistance, thermal tolerance, and desiccation resistance—to identify the molecular targets of urban-driven evolution (Li et al., 2018; Dockman et al., 2025).

5. Conclusion

This study demonstrates that Periplaneta americana populations across Agra District exhibit a pronounced genetic gradient shaped by urbanization and human-mediated dispersal. Urban Agra city harbours the highest genetic diversity, sustained by continuous allelic introduction through transport networks, while rural Kiraoli populations show reduced diversity consistent with isolation and local adaptation. Peri-urban Tajganj functions as a dynamic hybrid zone where urban and rural gene pools intersect. These patterns provide a genetic framework for understanding pest adaptation to anthropogenic landscapes and underscore the need for integrated management strategies that account for population connectivity and evolutionary dynamics.

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