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URBAN FORESTS AS RESERVOIRS OF CRYPTIC DIVERSITY IN FRUIT FLIES *Bactrocera* spp. WITH CONSEQUENCES FOR BIOSECURITY

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ABSTRACT

Fruit flies of the genus *Bactrocera* Macquart, 1835 are among the most damaging horticultural pests in tropical regions; however, their genetic diversity in urban forest ecosystems remains poorly characterized. Urban forests in Wallacea, Indonesia, may serve as reservoirs of biodiversity and potential monitoring sites for emerging pest lineages. This study assessed the mitochondrial genetic diversity and population structure of *Bactrocera* spp. in urban forest ecosystems in Makassar, Sulawesi. Forty individuals were collected using methyl eugenol–baited Steiner traps and analyzed based on partial *COI* gene sequences to identify haplotypes, estimate genetic diversity, and reconstruct phylogenetic relationships. Eight haplotypes were identified, with high haplotype diversity (Hd = 0.872) but low nucleotide diversity ($\pi = 0.0087$). Most haplotypes clustered within a main clade, whereas Hap_8 showed notable divergence (>3% genetic distance). AMOVA indicated that 92.4% of genetic variation occurred within populations. Neutrality tests yielded negative values, consistent with recent demographic expansion or selective processes, although interpretation should be cautious given unresolved species boundaries. Phylogenetic and haplotype network analyses revealed a star-like topology cantered on dominant haplotypes. While based on limited temporal and spatial sampling, these findings provide baseline molecular information on genetic heterogeneity within urban forest *Bactrocera* populations. Broader geographic sampling and integrative taxonomic approaches will be necessary to clarify species boundaries and assess the ecological significance of divergent lineages in Wallacea.

Keywords: *Bactrocera* biosecurity; cryptic species; urban biodiversity; Wallacea

ABSTRAK

Lalat buah daripada genus *Bactrocera* Macquart, 1835 merupakan antara perosak hortikultur yang paling merosakkan di kawasan tropika; namun demikian, kepelbagaian genetiknya dalam ekosistem hutan bandar masih kurang dicirikan. Hutan bandar di Wallacea, Indonesia berpotensi berfungsi sebagai takungan biodiversiti serta lokasi pemantauan bagi garis keturunan perosak yang baharu muncul. Kajian ini menilai kepelbagaian genetik mitokondria dan struktur populasi *Bactrocera* spp. dalam ekosistem hutan bandar di Makassar, Sulawesi. Sebanyak 40 individu telah dikumpulkan menggunakan perangkap Steiner berumpan metil eugenol dan dianalisis berdasarkan jujukan separa gen *COI* bagi mengenal pasti haplotip, menganggar kepelbagaian genetik, serta membina semula hubungan filogenetik. Sebanyak lapan haplotip telah dikenal pasti dengan kepelbagaian haplotip yang tinggi (Hd = 0.872), tetapi kepelbagaian nukleotida yang rendah ($\pi = 0.0087$). Kebanyakan haplotip mengelompok dalam satu klad utama, manakala Hap_8 menunjukkan perbezaan ketara (>3% jarak genetik). Analisis AMOVA menunjukkan bahawa 92.4% variasi genetik berlaku dalam populasi. Ujian keneutralan menghasilkan nilai negatif, selaras dengan pengembangan demografi terkini atau proses pemilihan, walau bagaimanapun tafsiran perlu dibuat secara berhati-hati memandangkan sempadan spesies yang masih belum jelas. Analisis filogenetik dan rangkaian haplotip menunjukkan topologi berbentuk bintang yang berpusat pada haplotip dominan. Walaupun berdasarkan persampelan temporal dan spatial yang terhad, dapatan ini menyediakan maklumat molekul asas mengenai heterogeniti genetik dalam populasi *Bactrocera* di hutan bandar. Persampelan geografi yang lebih meluas serta pendekatan taksonomi integratif diperlukan untuk memperjelas sempadan spesies dan menilai kepentingan ekologi garis keturunan yang berbeza di Wallacea.

Kata kunci: Biosekuriti *Bactrocera*; spesies kriptik; biodiversiti bandar; Wallacea

INTRODUCTION

Fruit flies of the genus *Bactrocera* Macquart, 1835 (Diptera: Tephritidae) are one of the most significant insect groups impacting tropical and subtropical horticultural systems, infesting a wide range of fruit crops and posing severe biosecurity threats (Jaleel et al. 2018; Badii et al. 2015; Vargas et al. 2015). Species such as *B. dorsalis*, *B. zonata*, and *B. carambolae* are internationally regulated invasive pests because of their capacity to undermine local fruit yields, disrupt international trade, and generate substantial economic losses. Their polyphagous feeding behavior, broad host range, and adaptability to diverse climatic conditions exacerbate their impact, whereas global trade and human-mediated dispersal facilitate their rapid spread across borders (Zhao et al. 2024; Mutamiswa et al. 2021; Raza et al. 2020). These ecological and evolutionary traits make *Bactrocera* not only a serious agricultural pest but also a model organism for examining how anthropogenic landscapes shape the dynamics of invasive species.

In Indonesia, fruit flies remain a persistent and costly challenge to horticultural production, particularly in biodiversity-rich regions such as Wallacea (Nahas et al. 2025; Hidayat et al. 2023; Hudiwaku et al. 2021). However, molecular and population-level studies that could inform integrated management remain sparse. Urban green spaces, often overlooked in pest research, may act as biodiversity refugia and ecological corridors. In the case of highly mobile insects such as *Bactrocera*, fragmented urban forests can harbor cryptic genetic diversity, sustain resident populations, and serve as gateways for invasive lineages (Wee & Jalaluddin 2025). Anthropogenic disturbance, heterogeneous vegetation mosaics, and fruit availability within these ecosystems create microhabitat conditions that may drive localized genetic divergence distinct from agricultural landscapes, where homogenizing gene flow predominates (Fischbein & Corley 2022; Fountain 2022; Pizzolotto et al. 2018). Understanding these dynamics is critical for tropical conservation science, as urban ecosystems are increasingly central to biodiversity management and biosecurity.

Conventional fruit fly control in Indonesia still relies heavily on synthetic insecticides and chemical traps (Pretty & Bharucha 2015). However, such approaches are often unsustainable, environmentally damaging, and limited in their long-term effectiveness. Molecular population genetics provides an alternative, evidence-based pathway to strengthen Integrated Pest Management (IPM), enabling the identification of invasion sources, detection of cryptic or novel lineages, and monitoring of dispersal routes (Damos 2015; Legros et al. 2021). The mitochondrial cytochrome oxidase I (COI) gene, widely validated for DNA barcoding and phylogeography, offers a reliable tool for disentangling fine-scale genetic variation within *Bactrocera* populations (Chen et al. 2023; Doorenweerd et al. 2020b; Phillips et al. 2019; Pentinsaari et al. 2016). Such approaches have proven useful for detecting demographic expansions, invasion histories, and cryptic species boundaries, which directly inform conservation and pest management decisions.

Despite extensive research across Asia and Oceania (Zhang et al. 2023; Deschepper et al. 2023; Catullo et al. 2019; Zeng et al. 2019;), genetic data from Indonesia, particularly Sulawesi, remain limited. Sulawesi occupies a central position in Wallacea, a globally recognized biodiversity hotspot with a complex geological history and high levels of endemism (Suhri et al. 2021, 2025; Ali & Heaney 2021). Therefore, it is plausible that *Bactrocera* populations in this region harbor unique or cryptic genetic signatures that remain undocumented. This gap represents not only a taxonomic and ecological frontier but also a pressing conservation and biosecurity concern, given that invasive fruit flies threaten both agroecosystem stability and native biodiversity.

This study investigated the genetic diversity of *Bactrocera* spp. within the Makassar urban forest ecosystem, embedded within a rapidly growing metropolitan area. By focusing on COI-derived haplotype variation, genetic diversity indices, and phylogenetic reconstruction, we aimed to clarify the population structure and demographic history of local fruit fly populations. Beyond molecular characterization, this study emphasizes the role of urban forests as reservoirs of cryptic diversity and sentinel landscapes for monitoring invasive pests. Linking molecular ecology and conservation science is critical for advancing biosecurity and biodiversity resilience in tropical regions.

MATERIALS AND METHODS

Study Sites and Sampling

Adult fruit flies *Bactrocera* spp. was collected from 1st to 7th April 2025 using Steiner traps baited with methyl eugenol. Sampling was conducted in two urban forest ecosystems in Makassar, South Sulawesi, Indonesia: (1) a mangrove ecosystem dominated by *Rhizophora mucronata* and *Avicennia marina*, and (2) the urban forest of Hasanuddin University Campus (5°08'S, 119°29'E), a semi-natural forest fragment characterized by *Samanea saman*, *Ficus* spp., and *Swietenia mahagoni*.

Three sampling stations were established within each ecosystem (mangrove and urban forest), resulting in six stations in total. Stations within each ecosystem were spaced ≥200 m apart to ensure spatial independence. A total of 30 Steiner traps were deployed, with five traps installed at each station. Traps were suspended at a height of approximately 1.5–2.0 m above ground level in shaded microhabitats to maximize capture efficiency. Each trap was baited with 2 mL of commercially available methyl eugenol (800 g/L formulation, undiluted) (Wee & Hee 2018), applied directly to the lure substrate following standard field protocols for male Tephritid attraction. Traps were inspected daily during the sampling period, and captured specimens were retrieved and immediately preserved in 96% ethanol to maintain DNA integrity.

The total sampling area encompassed approximately 500 m^2 per ecosystem (approximately 1000 m^2 in total across both ecosystems). A total of 40 adult individuals were selected for subsequent mitochondrial genetic analysis. Each specimen was labeled with a collection date and station code, and voucher specimens were deposited in the Zoology Laboratory, Department of Biology, Hasanuddin University.

Morphological and Molecular Identification

Specimens were initially identified to genus level (*Bactrocera*) based on external morphological characteristics following standard diagnostic keys for Tephritidae. Due to morphological similarity among closely related taxa and potential species complexes within *Bactrocera*, species-level delimitation was further assessed using mitochondrial *COI* sequence analysis. Molecular clustering and genetic distance patterns were used to evaluate whether the sampled individuals represented a single species with intraspecific variation or multiple closely related taxa.

DNA Extraction

Genomic DNA was extracted from thoracic muscle tissue using the Geneaid Tissue DNA Kit (Geneaid Biotech Ltd.) following the manufacturer's protocol. The concentration and purity of extracted DNA were assessed using a Nanodrop spectrophotometer.

COI Gene Amplification and Sequencing

A fragment of the mitochondrial *COI* gene (~650–700 bp) was amplified using universal primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3'). PCR was performed in a total volume of 25 µL, consisting of 12.7 µL DNase-free water, 2.5 µL 10× PCR buffer, 3.0 µL $MgCl_2$ (25 mM), 2.5 µL dNTP mix (100 mM), 1 µL of each primer (20 µM), 2 U Taq polymerase, and ~20 ng of DNA template. Thermal cycling conditions were as follows: initial denaturation at 94°C for 3 minutes; 35 cycles of 94°C for 30 seconds, 50°C for 30 seconds, 72°C for 1 minute; and a final extension at 72°C for 5 minutes. PCR products were visualized on agarose gel, purified, and bidirectionally sequenced by a commercial sequencing service.

Genetic Diversity Analysis

Haplotype groups were defined based on nucleotide variation in the *COI* sequences. Genetic diversity indices were calculated using DnaSP version 6, including haplotype diversity (Hd), nucleotide diversity (π), and average number of nucleotide differences (k). Population structure was analyzed using Arlequin v3.5 through Analysis of Molecular Variance (AMOVA) to evaluate genetic variance within and among groups, and neutrality tests including Tajima's D and Fu's Fs. A distance-based phylogenetic tree (Neighbor-Joining) was constructed in MEGA using the Kimura 2-parameter model and supported with 1000 bootstrap replicates.

RESULTS AND DISCUSSION

Haplotype and Genetic Diversity Analysis

Analysis of mitochondrial *COI* sequences from 40 *Bactrocera* specimens collected from the Makassar urban forest revealed eight distinct haplotypes (Hap_1–Hap_8) (Table 1). Haplotype Hap_1 was the most common (30% of individuals), whereas Hap_5–Hap_8 were each found at lower frequencies. Overall, haplotype diversity was high (Hd = 0.872±0.064), whereas nucleotide diversity was relatively low (π = 0.0087±0.0005). The mean number of nucleotide differences among the individuals was 5.24.

Table 1. Haplotype distribution of *Bactrocera* spp. based on *COI* sequence data

Haplotype	Number of Individuals	Frequency (%)
Hap_1	10	30.0
Hap_2	7	15.0
Hap_3	7	15.0
Hap_4	4	10.0
Hap_5	3	5.0
Hap_6	3	5.0
Hap_7	3	5.0
Hap_8	3	5.0
Total	40	100.0

Table 1 shows that Hap_1 was the most common haplotype (30% of individuals), while the remaining haplotypes occurred at lower frequencies, each ranging from 5% to 15%. This distribution indicates that the population is dominated by a single haplotype, accompanied by several rare haplotypes that contribute to the overall high haplotype diversity. The coexistence of common and rare haplotypes suggests a dynamic population history within the urban forest. Our findings revealed that *Bactrocera* populations in the Makassar urban forest exhibit a paradoxical genetic signature: high haplotype diversity (Hd = 0.872) and low nucleotide diversity (π = 0.0087). This pattern is consistent with recent demographic expansion from limited founder stocks, as previously observed in invasive *Tephritidae* (Doorenweerd et al. 2020a), yet it also raises important questions for conservation and biosecurity. The coexistence of multiple rare haplotypes with shallow overall divergence suggests that both evolutionary and anthropogenic processes shape population dynamics in urban habitats. Notably, the detection of two divergent haplotypes (≥2–3% divergence) surpasses the commonly accepted intraspecific threshold for *Bactrocera* (Kunprom & Pramual 2019), supporting two plausible scenarios: (1) the presence of cryptic diversity linked to Wallacea's complex biogeographic history (Ali & Heaney 2021; Doorenweerd et al. 2020a) or (2) human-mediated introductions facilitated by fruit trade and urbanization (Manawaduge et al. 2023).

Population Structure and Neutrality Analysis

Analysis of Molecular Variance (AMOVA) indicated that 92.4% of genetic variation occurred within populations, while only 7.6% was attributable to differences among groups (Figure 1). Neutrality tests yielded significantly negative values, with Tajima's D = –1.85 (*P<0.05*) and Fu's Fs = –4.72 (*P<0.02*), consistent with scenarios of population expansion or purifying selection. The neutrality tests yielded a Tajima's D of –1.85 (*P<0.05*) and a Fu's Fs of –4.72 (*P<0.02*). These significantly negative values indicate two possible scenarios: (1) a recent population expansion, or (2) purifying selection reducing the frequency of rare alleles.

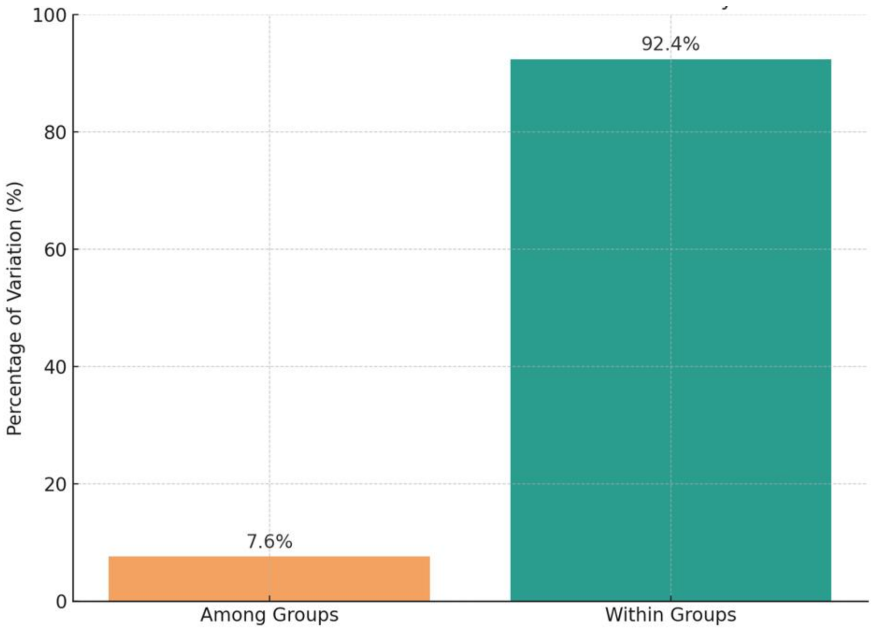

Figure 1. Genetic variation structure based on AMOVA analysis

The AMOVA results (Figure 1) demonstrate that the majority of genetic variation (92.4%) is contained within populations, with limited differentiation among groups (7.6%). This pattern reflects a high level of intrapopulation gene flow. Neutrality tests (Figure 2) yielded significantly negative Tajima's D and Fu's Fs values, consistent with either recent population expansion or selective processes acting on the populations. Together, these findings highlight demographic instability that may be linked to ecological or anthropogenic drivers in the study site.

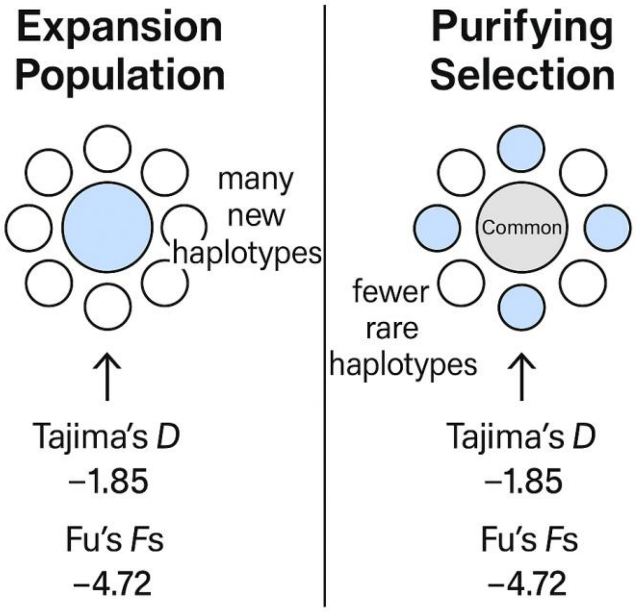

Figure 2. Evolutionary scenarios in Bactrocera spp. inferred from Tajima's D and Fu's Fs neutrality tests

Urban forests are increasingly recognized as multifunctional landscapes that serve as biodiversity refugia, ecological corridors, and socioecological spaces in tropical cities. In this study, the urban forest harbored genetically diverse *Bactrocera* populations despite its limited size and fragmentation. This suggests that even small urban green spaces may sustain insect diversity and provide critical “stepping stones” for insect dispersal. However, this ecological role comes with trade-offs, as such habitats may simultaneously act as reservoirs for pest lineages and gateways for invasive genotypes. Similar patterns have been observed in *Bactrocera umbrosa* across the Indo-Australian Archipelago, where fruit trade and anthropogenic dispersal obscure fine-scale phylogeographic signals (San Jose et al. 2023; Krosch et al. 2019). Thus, urban ecosystems are not merely passive refuges but are active nodes in regional biodiversity and invasion networks.

The dominance patterns observed at certain stations, where a few haplotypes or species accounted for a disproportionate abundance, also have ecological significance. High dominance and low evenness, as recorded at Station 2, indicate reduced functional redundancy and potential instability in insect communities (Leblanc et al. 2021; Wimp et al. 2019; Schlinkert et al. 2016). From a conservation standpoint, this highlights the need to promote habitat heterogeneity and ecological resilience in urban forests. Greater evenness is generally associated with higher ecosystem stability and resistance to invasions. Habitat management strategies, such as maintaining diverse vegetation mosaics or supporting natural enemies, can therefore serve the dual goal of conserving biodiversity while mitigating pest risks (Fountain 2022).

Phylogeny and Haplotype Relationships

The Neighbor-Joining phylogenetic tree constructed with the Kimura 2-parameter model grouped five haplotypes (Hap_2, Hap_3, Hap_4, Hap_6, and Hap_7) into a single clade with 78% bootstrap support. Hap_1 and Hap_5 formed a separate subclade, while Hap_8 emerged as the most divergent lineage, showing >3% genetic distance from other haplotypes (Figure 4). The median-joining haplotype network showed a star-like topology centered on Hap_2–Hap_7, separated by one to two mutational steps. Hap_5 diverged by ≥2% from its nearest haplotype, while Hap_8 diverged by >3%, forming a distinct lineage (Figure 5).

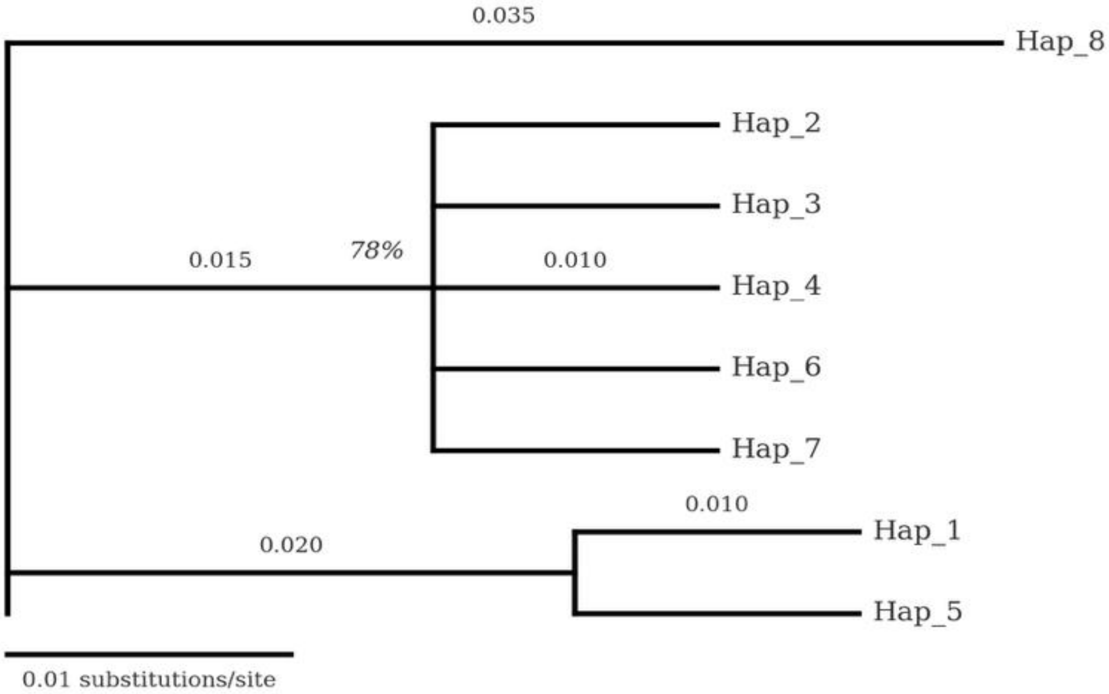

Figure 4. Neighbor-Joining phylogenetic tree of eight Bactrocera haplotypes (Hap_1–Hap_8) based on *COI* sequences using the Kimura 2-parameter model. Bootstrap values (>70%) shown at nodes

The phylogenetic tree (Figure 4) grouped Hap_2–Hap_7 into a main clade, with Hap_1 and Hap_5 forming a subclade and Hap_8 emerging as the most divergent lineage (>3% genetic distance). These results indicate that, while most haplotypes are closely related, a subset exhibits notable genetic divergence. The haplotype network (Figure 5) further supports this pattern, showing a star-like structure centered on Hap_2–Hap_7, with Hap_5 and Hap_8 separated by multiple mutation steps. Such divergence may reflect historical differentiation within Wallacea or other evolutionary processes. However, direct comparison with international sequence databases was not conducted in the present study; therefore, correspondence with globally reported invasive or widespread *Bactrocera* lineages cannot be confirmed. The interpretation of divergence drivers is consequently presented as a working hypothesis rather than a definitive conclusion. The observed genetic differentiation may represent intraspecific variation within a single species, the presence of a species complex, or potential cryptic species. Because species-level morphological identification was not fully resolved, neutrality tests such as Tajima's D should be interpreted cautiously, as their assumptions typically apply to single, panmictic populations. Further integrative taxonomic approaches combining detailed morphology and multilocus molecular data would be required to delimit species boundaries more conclusively. Within these limitations, the detected genetic heterogeneity provides baseline molecular information for understanding genetic structure in urban forest *Bactrocera* populations.

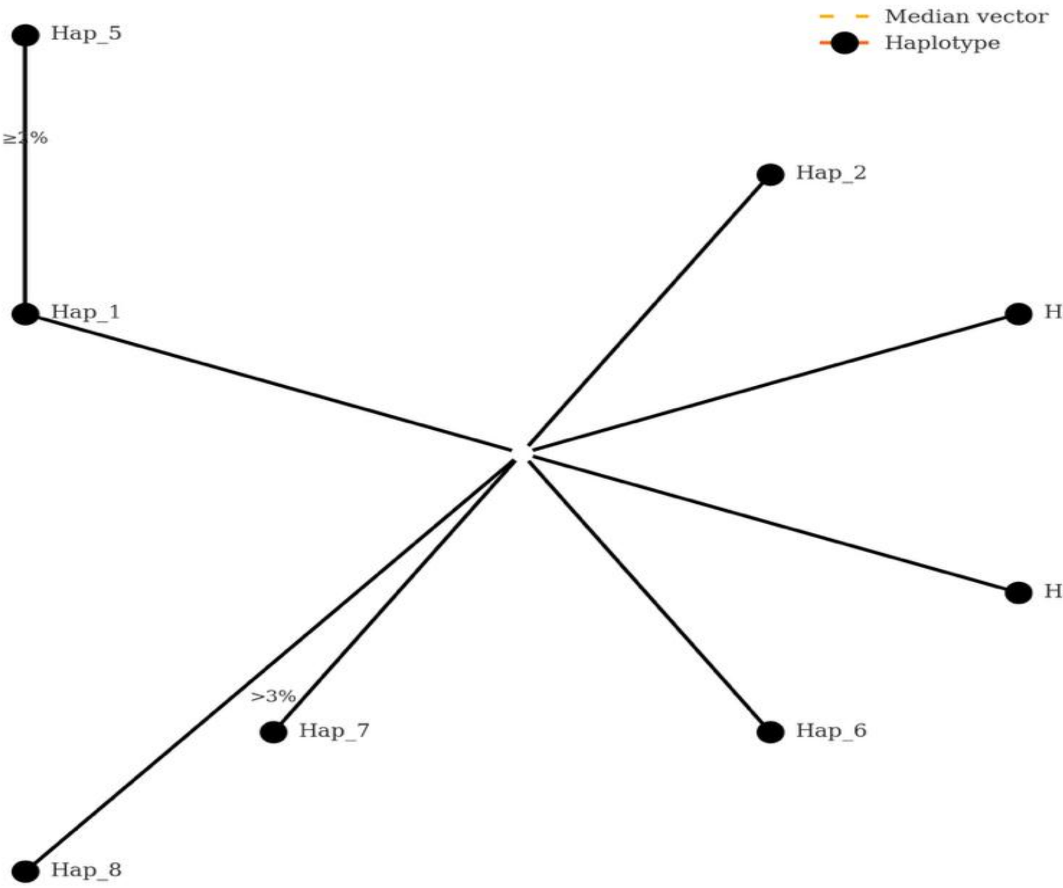

Figure 5. Median-joining haplotype network of eight Bactrocera haplotypes (Hap_1–Hap_8). Circle size indicates haplotype frequency; hatch marks show mutational steps

At the policy level, this study emphasizes the strategic role of urban forests in tropical biodiversity governance. Urban green spaces are increasingly recognized as frontlines for monitoring invasive species and conserving remnant biodiversity. In Wallacea, a region of exceptional biogeographic complexity and vulnerability (Ali & Heaney 2021), urban forests such as the Hasanuddin University campus provide both conservation opportunities and early warning systems. The detection of divergent haplotypes within such landscapes highlights the urgency of embedding molecular monitoring into national and regional biosecurity frameworks. Aligning local research with broader conservation policies can strengthen resilience to biological invasions, safeguard food security, and protect the ecological integrity of the biodiversity hotspots.

This study is based on 40 individuals, which is sufficient for an initial assessment of mitochondrial genetic diversity within the sampled urban forest sites. However, this sampling depth may not fully capture the complete spectrum of genetic variation present across the broader urban forest ecosystem, particularly rare haplotypes or additional cryptic lineages. Expanding sample size and spatial coverage in future investigations would provide a more comprehensive understanding of population structure and hidden diversity. Nevertheless, the current findings provide important baseline molecular evidence highlighting the role of urban forests as reservoirs of genetic diversity with potential biosecurity implications.

The detected genetic heterogeneity within *Bactrocera* populations of Makassar's urban forests reflects underlying evolutionary processes operating within complex tropical landscapes. While the present study is based on limited temporal and spatial sampling, the observed divergence provides preliminary baseline molecular information for future monitoring initiatives. These findings should be interpreted as an initial molecular snapshot rather than definitive evidence for immediate biodiversity policy intervention. Future studies incorporating broader geographic coverage, longer sampling periods, nuclear markers, and integrative taxonomic approaches will be necessary to more fully resolve species boundaries and evaluate population dynamics in urban forest systems.

CONCLUSIONS

This study provides the first evidence of high haplotype diversity coupled with shallow nucleotide divergence in *Bactrocera* populations inhabiting an urban tropical forest in Sulawesi. The discovery of two divergent haplotypes exceeding established intraspecific thresholds underscores the potential presence of cryptic diversity or recent anthropogenic introductions within Wallacea. These findings highlight the dual role of urban forests: they act both as reservoirs of biodiversity and as sentinel landscapes for invasive species detection. Beyond their relevance to pest ecology, our results demonstrate the value of integrating molecular tools into conservation science and biosecurity frameworks. Urban forests should be recognized not only as green infrastructure but also as frontline systems for monitoring invasive pests and protecting biodiversity. Embedding molecular surveillance within conservation and agricultural policies in biodiversity hotspots such as Wallacea will strengthen ecosystem resilience, safeguard food security, and provide early-warning capacity against biological invasions.

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AUTHORS DECLARATIONS

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This research was conducted without any external financial support, and no funding was received for the publication of this work.

Conflict of Interest

The authors declare that there is no conflict of interest regarding the conduct of this research or the publication of this article.

Ethics Declarations

This study involved the trapping of fruit flies (invertebrates); therefore, no formal ethical approval was required.

Data Availability Statements

The data supporting the findings of this study are available within the article

Author Contribution

Fitha Febrilia Ruli and Andi Gita Maulidyah Indraswari Suhri conceived and designed the study, supervised all research activities, and led the manuscript writing. Full name Nurul Amalia., Fausia., Asti Khaerani., and Markiah conducted field sampling, trap deployment, and specimen preservation. Septiantina Dyah Riendriasari. performed data organization, biodiversity index calculation, and contributed to figure and table preparation. Ambeng, supported laboratory curation, voucher specimen documentation, and reference management. All authors contributed to data interpretation, critically reviewed the manuscript, and approved the final version for submission.

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