

DOI 10.15407/zoo2026.02.127

UDC: 595.78:712.253 (410 West London)

FINE-SCALE BUTTERFLY COMMUNITY AND TRAIT DIVERSITY IN A STRUCTURALLY COMPLEX URBAN GREEN SPACE IN WEST LONDON

R. Bangay

Department of Biological Sciences, Royal Holloway, University of London,
Egham Hill, Egham, Surrey TW20 0EX, United Kingdom

Current affiliation: Division of Natural System, Graduate School of Natural Science &
Technology, Kanazawa University, Kanazawa, Ishikawa, 920-1192, Japan

E-mail: rohitbangay@gmail.com

R. Bangay (<https://orcid.org/0000-0002-4292-5912>)

urn:lsid:zoobank.org:pub:2D3C3F30-4C03-44F6-8B8B-F6AD8CC72D65

Fine-scale butterfly community and trait diversity in a structurally complex urban green space in West London. Bangay, R. — Urban and peri-urban landscapes represent increasingly important reservoirs for biodiversity conservation, yet our understanding of community structure and genetic variation maintenance in these fragmented environments remains limited. I investigated butterfly communities and wing pattern polymorphism across four structurally distinct habitats (grassland, hedgerow, woodland edge, and woodland) within a 10ha peri-urban site in West London. Over two summer months, standardized transect surveys recorded 2,786 individuals representing 23 species. Woodland edge and hedgerow habitats supported the highest diversity (21 species each), while grassland and woodland showed lower richness (17 and 13 species respectively). Five species dominated the community, with *Maniola jurtina* (Meadow Brown) and *Aphantopus hyperantus* (Ringlet) comprising 51% of total abundance. Mendelian analysis of wing spot polymorphism in these focal species revealed inheritance patterns consistent with dihybrid F2 expectations, independent of habitat context but showing significant sexual dimorphism in *M. jurtina*. These findings demonstrate that small, structurally complex peri-urban habitats can maintain both species-level and genetic diversity, highlighting their conservation value and the importance of preserving habitat heterogeneity in urban planning strategies.

Key words: urban ecology, Lepidoptera, biodiversity, phenotype, species richness.

© Publisher Publishing House “Akademperiodyka” of the NAS of Ukraine, 2026. The article is published under an open access license CC BY-NC-ND (<https://creativecommons.org/licenses/by-nc-nd/4.0/>)

ISSN 2707-725X. Zoodiversity. 2026. Vol. 60, No. 2

Introduction

The transformation of natural landscapes into urban and peri-urban mosaics represents one of the most significant global environmental changes of the 21st century. While urbanization has traditionally been viewed as detrimental to biodiversity, there is growing recognition that urban environments can serve as important refugia for species and maintain ecological processes when appropriately managed. This paradigm shift is particularly relevant for invertebrate communities, which often exhibit high diversity in urban green spaces and contribute substantially to ecosystem functioning.

Butterflies serve as excellent indicators of ecosystem health and habitat quality due to their sensitivity to environmental changes, specific habitat requirements, and relatively well-understood ecology (Pollard & Yates, 1993). In the United Kingdom, butterfly populations have experienced substantial declines over recent decades, with habitat loss, fragmentation, and climate change identified as primary drivers (McDermott Long et al., 2017). Despite these broader trends, urban and peri-urban environments may provide important stepping-stones and refugia for butterfly populations, particularly when they contain diverse microhabitats that can support different ecological requirements (Dennis et al., 2013).

The maintenance of both species-level and genetic diversity in fragmented landscapes depends critically on habitat structure and connectivity (Dunning et al., 1992). Edge habitats, in particular, have been recognized for their potential to support high biodiversity by providing transitional zones between different habitat types. However, the mechanisms underlying community assembly and genetic diversity maintenance in these environments remain poorly understood, particularly at the fine spatial scales relevant to urban planning and management (Saccheri et al., 1998).

Meadow Brown — *Maniola jurtina* (Linnaeus, 1758) and Ringlet — *Aphantopus hyperantus* (Linnaeus, 1758), are among the most widespread and abundant butterfly species in the UK, characterized by notable wing spot polymorphisms that have been extensively studied in rural and island populations (Brakefield & French, 1993; Brakefield, 1979). These polymorphisms follow Mendelian inheritance patterns and provide an excellent system for investigating how urbanization and habitat fragmentation influence genetic diversity maintenance (Creed et al., 1964; Newland et al., 2015). Previous research has focused primarily on large-scale geographical variation or isolated populations (Dowdeswell et al., 1960; Creed et al., 1970, Baerwaerts et al., 1998), leaving gaps in our understanding of genetic variation at the scale of individual urban sites.

This study addresses two primary questions: (1) How do butterfly abundance and species richness vary across structurally distinct habitats within a small peri-urban landscape? (2) Are classic Mendelian wing spot polymorphisms maintained in urban butterfly populations, and do they show habitat-specific or sex-linked variation? By integrating community-level surveys with phenotypic genetic analysis, I provide insights into both ecological and evolutionary processes operating in urban environments.

Material and Methods

Study Site and Habitat Classification. Research was conducted at a 10 ha site in Heston, West London (51°29' N, 0°22' W), adjacent to Osterley Park (National Trust) and surrounded by agricultural land, residential areas, and transport infrastructure and the M4, one of the busiest motorways in the UK. The site represents a typical peri-urban mosaic containing multiple habitat types within close proximity. Four distinct habitats were identified based on vegetation structure (Fig. 1, *a*), canopy cover, and management history: (1) Grassland — open areas dominated by grasses and herbs with <10% tree cover (Fig. 1, *b*); (2) Hedgerow — linear woody features comprising mixed native shrubs and trees, 2–5 m wide; (3) Woodland edge — transitional zones between woodland and open areas, characterized by partial canopy cover (30–70%) and high structural diversity; (4) Woodland — closed canopy areas with > 80% tree cover and sparse understory vegetation.

Butterfly Surveys. Between 29 June and 30 August 2019, standardized line transects were conducted in each habitat type. Twenty-five surveys were completed per habitat (100 total surveys), with each transect comprising six stops at 50m intervals along a predetermined route (Fig. 1, *a*). At each stop, all butterflies observed within a 4m radius during a 2-minute observation period were recorded, identified to species level, and photographed for verification when necessary.

Surveys were conducted between 10:00 and 16:00 hours on days with suitable weather conditions (temperature >15 °C, wind speed < Beaufort scale 4, no precipitation). Climatic variables (temperature, cloud cover percentage, wind strength) were recorded at each survey to assess their influence on butterfly activity and detectability.

Plant Community Assessment. Concurrently with butterfly surveys, all flowering vascular plants within each transect were identified and recorded to provide context for nectar resource availability and habitat characterization. Plant diversity indices were calculated to examine relationships between plant and butterfly community structure.

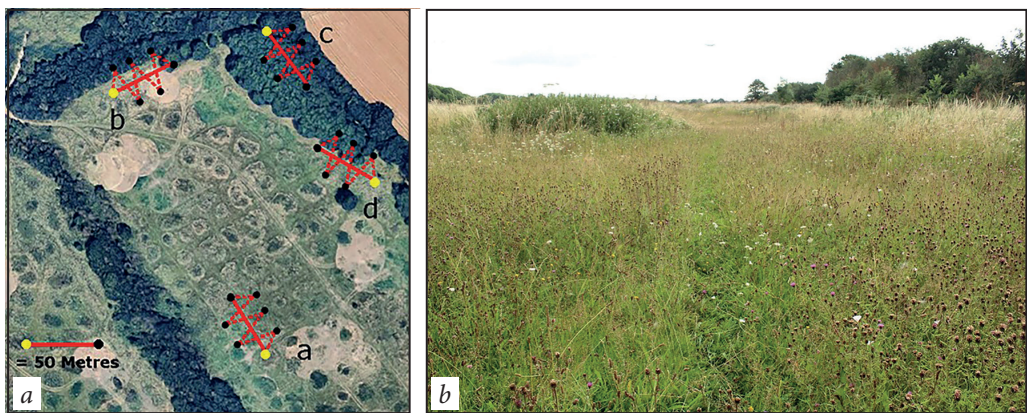


Fig. 1. Butterfly sampling habitats and transects: *a* — map of areas surveyed for each habitat. Lines indicating layout of transects and yellow dots indicate starting positions (*a* — grassland, *b* — hedgerow, *c* — woodland, *d* — woodland edge). © Google maps; *b* — grassland habitat dominated by grasses and wildflowers

Phenotypic Data Collection. Adult *M. jurtina* (n = 80) and *A. hyperantus* (n = 51) were captured using sweep netting during survey periods. Each individual was sexed, photographed to record ventral wing spot patterns, and measured for left forewing length using digital calipers (± 0.01 mm). All captured individuals were marked with small dots of non-toxic paint and immediately released at the point of capture to prevent re-sampling.

Wing spot patterns were scored according to established protocols, with *M. jurtina* assessed for forewing (0–2 spots) and hindwing (0–3 spots) spot counts, and *A. hyperantus* assessed for forewing (2–3 spots) and hindwing (5–6 spots) combinations. Digital photographs were analyzed using ImageJ software to ensure accurate spot counting and provide permanent records.

Statistical Analysis. Community-level analyses examined habitat differences in butterfly abundance and species richness using one-way ANOVA when assumptions were met (verified using Shapiro-Wilk and Levene's tests), or Kruskal-Wallis tests when assumptions were violated. Post hoc comparisons used Tukey's HSD or Dunn's tests as appropriate. Diversity indices (Shannon-Weiner, Simpson's, Berger-Parker dominance) and community similarity (Bray-Curtis dissimilarity) were calculated from species abundance matrices. The effects of climatic variables on community metrics were assessed using linear regression.

Wing spot polymorphism frequencies were compared to expected Mendelian dihybrid F2 ratios (9:3:3:1) using chi-square goodness-of-fit tests. Habitat and sex effects on spot patterns were analyzed using Pearson's chi-square or Fisher's exact tests depending on sample sizes. Sexual size dimorphism was assessed using two-way ANOVA with sex and habitat as factors. All analyses were conducted in R version 4.0.3, with significance set at $\alpha = 0.05$.

Results

Community Structure and Diversity. A total of 2,786 butterflies representing 23 species were recorded across all surveys. Species richness was highest in woodland edge and hedgerow habitats (21 species each), intermediate in grassland (17 species), and lowest in woodland (13 species). Total abundance showed a similar pattern, with woodland edge recording the highest numbers (1,029 individuals), followed by grassland (775), hedgerow (676), and woodland (306).

Five species dominated the community, accounting for approximately 85% of all observations (Fig. 2, a): *M. jurtina* (33.3%), *A. hyperantus* (18.0%), Skipper species complex (17.2%), *Pyronia tithonus* (Linnaeus, 1771; Gatekeeper, 11.1%) and *Pararge aegeria* (Linnaeus, 1758; Speckled Wood, 6.5%). This dominance pattern resulted in low community evenness across all habitats, as indicated by high Berger-Parker dominance values (Table 1).

Significant differences in abundance were detected among habitats ($F_{3,96} = 15.2$, $P < 0.001$), with woodland supporting significantly fewer individuals than all other habitat types (Fig. 2, b). Species richness per survey also varied significantly among habitats ($H = 18.7$, $P < 0.001$), with woodland edge and hedgerow supporting higher diversity than grassland and woodland (Fig. 2, c).

Seasonal patterns showed peak abundance and richness in July, with a sharp decline in August (Supplementary Fig. S1a & b). Temperature showed a weak negative relationship with both abundance ($R^2 = 0.26, P < 0.05$) and richness across habitats (Supplementary Fig. S3), while cloud cover positively influenced species richness in hedgerow habitats ($R^2 = 0.16, P < 0.05$) (Supplementary Fig. S5).

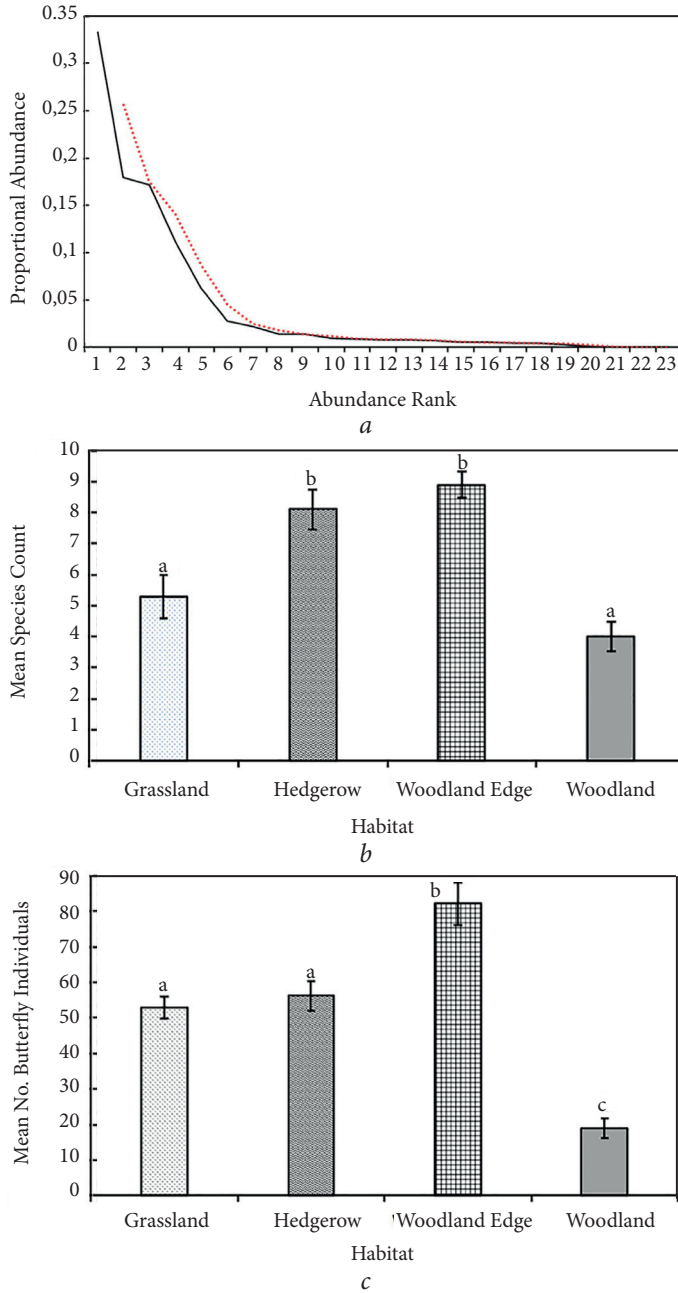


Fig. 2. Butterfly community composition across habitats: *a* — ranking of butterfly species based on proportional abundance from the total of 2786 butterflies recorded; *b* — mean butterfly abundance per survey for each habitat. Standard errors for each habitat are represented by bars; *c* — mean species count per survey calculated from 25 surveys of each habitat. Single letters (a–c) indicate significant differences between means. Habitats with common letters signify non-significant differences

Plant community diversity followed similar patterns to butterfly diversity, with woodland edge supporting the highest floral richness (27 species) and woodland the lowest (14 species). Bray-Curtis dissimilarity revealed that grassland and woodland had the most dissimilar species compositions (89.9% dissimilarity), while woodland edge and hedgerow showed the highest similarity (74.6% similarity) (Table 2).

Wing Spot Polymorphism and Genetics. Eight distinct forewing/hindwing spot combinations were observed in *M. jurtina*, and four combinations in

Table 1. Overall species abundance and rank order for each species identified throughout the survey. Berger-Parker Dominance shows the proportion of dominance of each species from the total butterfly abundance

Species	Latin Name	Abundance	Rank	Berger-Parker Dominance Proportion
Meadow Brown	<i>Maniola jurtina</i>	927	1	0.33
Ringlet	<i>Aphantopus hyperantus</i>	501	2	0.18
Skippers (Large, Small, Essex)	<i>Ochlodes sylvanus</i> (Esper, 1777); <i>Thymelicus sylvestris</i> (Poda, 1761); <i>Thymelicus lineola</i> (Ochsenheimer, 1808)	478	3	0.17
Gatekeeper	<i>Pyronia tithonus</i>	309	4	0.11
Speckled Wood	<i>Pararge aegeria</i>	180	5	0.06
Brown Argus	<i>Aricia agestis</i> (Denis & Schiffermüller, 1775)	77	6	0.03
Green Veined White	<i>Pieris napi</i> (Linnaeus, 1758)	60	7	0.02
Common Blue	<i>Polyommatus icarus</i> (Rottemburg, 1775)	39	8	0.01
Small White	<i>Pieris rapae</i> (Linnaeus, 1758)	38	9	0.01
White Letter Hairstreak (UKBAP Priority, EN)	<i>Satyrium w-album</i> (Knoch, 1782)	28	10	0.01
Comma	<i>Polygonia c-album</i> (Linnaeus, 1758)	24	11	0.01
Red Admiral	<i>Vanessa atalanta</i> (Linnaeus, 1758)	23	12	0.01
Peacock	<i>Aglais io</i> (Linnaeus, 1758)	22	13	0.01
Purple Hairstreak (Protected)	<i>Favonius quercus</i> (Linnaeus, 1758)	19	14	0.01
Holly Blue (Protected)	<i>Celastrina argiolus</i> (Linnaeus, 1758)	14	15	0.01
Small Tortoiseshell	<i>Aglais urticae</i> (Linnaeus, 1758)	14	16	0.01
Large White	<i>Pieris brassicae</i> (Linnaeus, 1758)	13	17	0.00
Small Copper	<i>Lycaena phlaeas</i> (Linnaeus, 1761)	12	18	0.00
Painted Lady	<i>Vanessa cardui</i> (Linnaeus, 1758)	5	19	0.00
Marbled White	<i>Melanargia galathea</i> (Linnaeus, 1758)	2	20	0.00
Small Heath (UKBAP priority, NT, Protected)	<i>Coenonympha pamphilus</i> (Linnaeus, 1758)	1	21	0.00
Total		2786		1

Table 2. Bray-Curtis index indicating similarity in species composition between each habitat

Bray-Curtis Index	Hedgerow, %	Woodland, %	W. Edge, %
Grassland	46.42	10.10	45.55
W. Edge	74.59	28.81	
Woodland	42.42		

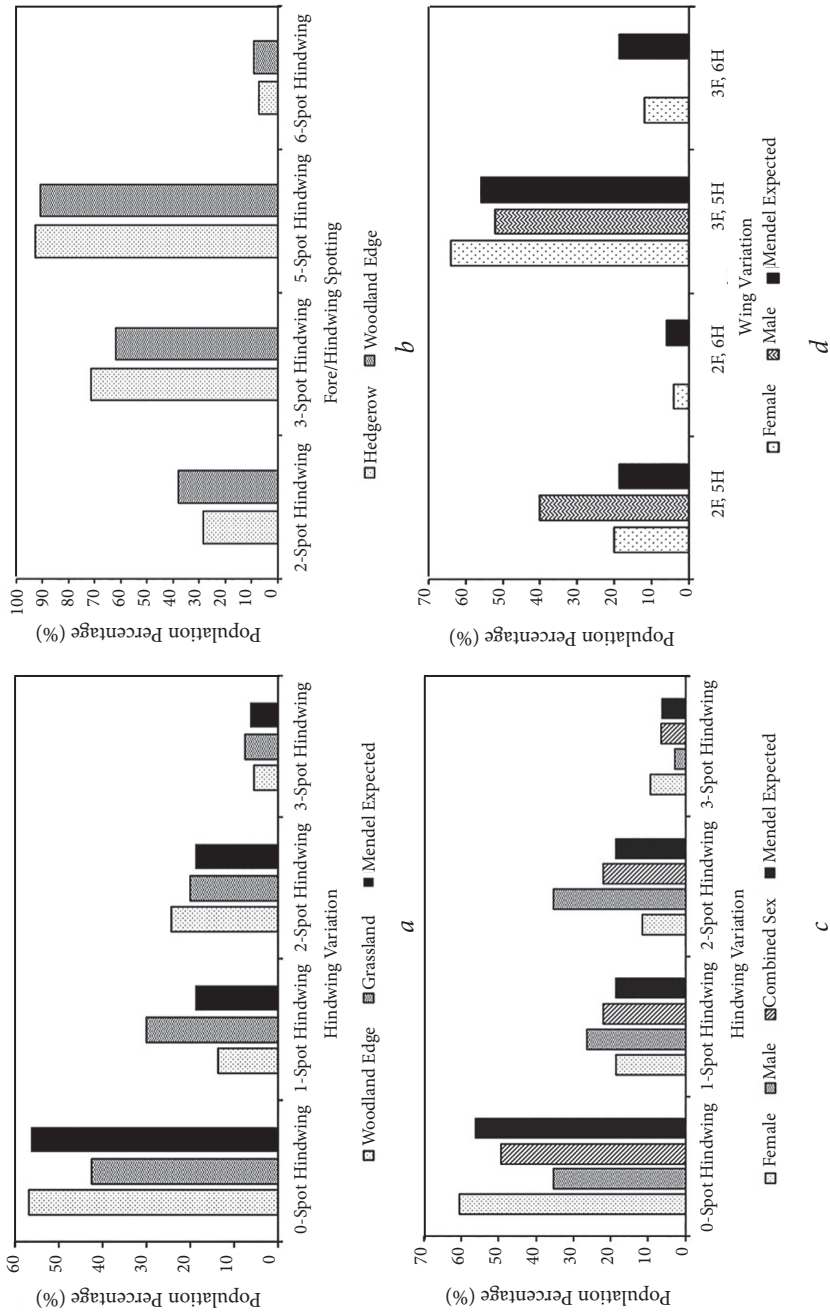


Fig. 3. Wing-spot phenotypes with Mendelian comparisons across habitats and sexes: *a* — comparison of percentage of individuals identified with specific hindwing variations between individuals from woodland edge and grassland habitats irrespective of forewing spotting. The 'Mendel expected' column is based upon Mendel's Law of independent assortment of alleles and the expected proportion of combinations of the F2 generation; *b* — comparison of percentage of spotting on forewing and hindwing based upon *A. hyperantus* individuals collected from hedgerow and woodland edge; *c* — comparison of percentage of individuals identified with specific hindwing variations between male and female of the overall *M. jurtina* population sampled. The 'Combined Sex' column is the sum of both male and female individuals; *d* — composition of wing variations between the sexes within *A. hyperantus* populations (F= forewing, H = hindwing)

A. hyperantus. In both species, observed frequency distributions did not differ significantly from expected Mendelian dihybrid F2 ratios, indicating strong genetic control of spot patterns independent of environmental influences (Fig. 3, *a, b*).

For *M. jurtina*, no significant habitat effects on spot distribution were detected ($\chi^2 = 0.61$, $df = 1$, $P > 0.05$). However, significant sexual dimorphism was observed, with males more likely than females to possess two hindwing spots (Fisher's exact test, $P < 0.05$) (Fig. 3, *c*). The observed pattern closely matched theoretical expectations for sex-linked inheritance of spot number traits.

A. hyperantus showed no significant habitat (Fisher's exact test, $P > 0.05$) or sex effects (Fisher's exact test, $P > 0.05$) on wing spot patterns, with frequencies closely approximating expected Mendelian ratios across all categories (Fig. 3, *d*).

Sexual Size Dimorphism. Both species exhibited significant sexual size dimorphism, with females displaying longer forewings than males. In *M. jurtina*, females averaged 25.08 mm compared to males at 23.70 mm ($F_{1,76} = 28.67$, $P < 0.001$). Similarly, *A. hyperantus* females averaged 23.00 mm versus males at 21.12 mm ($F_{1,47} = 58.17$, $P < 0.001$). No significant habitat effects or sex-by-habitat interactions were detected for wing size in either species (Fig. 4, *a, b*).

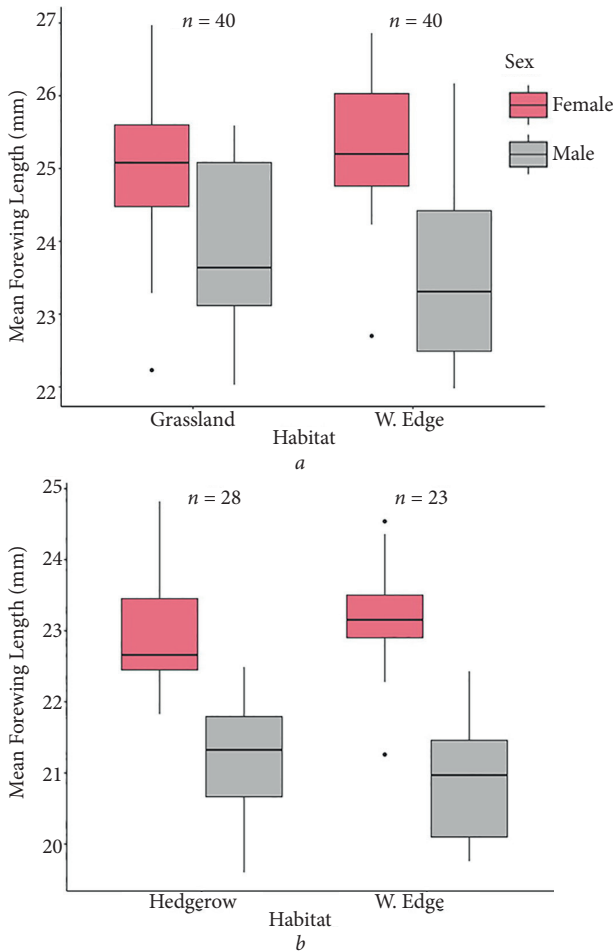


Fig. 4. Sexual size dimorphism in forewing length across habitats: *a* — forewing size of *M. jurtina* comparison between males and females collected in grassland and woodland edge; *b* — forewing size of *A. hyperantus* comparison between males and females collected from hedgerow and woodland edge

Discussion

This study provides compelling evidence that small peri-urban habitats can support substantial butterfly diversity and maintain genetic polymorphisms at fine spatial scales. The observed patterns highlight the conservation value of structurally complex urban environments and provide insights into community assembly processes in fragmented landscapes (Dennis et al., 2013; Van Dyck & Baguette, 2005).

Habitat Structure and Community Assembly. The higher diversity and abundance in woodland edge and hedgerow habitats reflects the importance of structural complexity and resource heterogeneity in supporting butterfly communities (Lebeau et al., 2015; Essens et al., 2017). These transitional habitats provide diverse microclimates, increased floral resources, and varied microhabitats that can support species with different ecological requirements. The edge effect creates favorable conditions for both woodland specialists and open-habitat species, effectively expanding the realized niche space available within the site (Shapiro & Carde, 1970).

The dominance of generalist species like *M. jurtina* and *A. hyperantus* is characteristic of fragmented urban environments where habitat specialists may be filtered out by limited patch size or connectivity. However, the presence of conservation priority species demonstrates that even small urban sites can contribute to regional conservation efforts.

Genetic Diversity Maintenance. The maintenance of Mendelian wing spot polymorphisms in both focal species, with frequencies closely matching theoretical expectations, indicates that urban populations retain substantial genetic diversity despite potential demographic constraints (Brakefield & French, 1993; Sepänen, 1981). The absence of habitat-specific deviations from expected ratios suggests that local selection pressures are insufficient to override genetic effects, or that gene flow maintains genetic variation across the site.

The sex-linked differences in *M. jurtina* spot patterns are consistent with previous research on this species and reflect the genetic architecture of spot determination rather than environmental influences (Creed et al., 1964). The preservation of these sex-specific patterns in urban populations indicates that fundamental genetic processes remain intact despite the potentially stressful urban environment.

Conservation Implications. These findings have several important implications for urban conservation and planning. First, they demonstrate that relatively small peri-urban sites can serve as significant reservoirs of both species and genetic diversity when they contain appropriate habitat heterogeneity. The 10ha study site supported 23 butterfly species, representing approximately 40% of British butterfly fauna, highlighting the disproportionate conservation value of well-designed urban green spaces.

Second, the superior performance of edge and hedgerow habitats emphasizes the importance of maintaining structural complexity in urban environments (Van Dyck & Baguette, 2005). Linear features like hedgerows can provide connectivity between habitat patches while supporting high local diversity. Urban planners should prioritize the creation and maintenance of such transitional habitats rather than focusing solely on large homogeneous green spaces.

Climatic Influences and Phenology. The weak effects of climatic variables over the study period suggest that habitat structure plays a more important role than short-term weather variation in determining community patterns (Kharouba & Vellend, 2015). The negative relationship between temperature and abundance may reflect behavioural responses to thermal stress, while the positive influence of cloud cover on hedgerow richness could indicate extended activity periods under more favourable microclimatic conditions (Bennie et al., 2008).

The sharp decline in abundance and richness from July to August highlights the importance of phenological synchrony between butterfly emergence and resource availability (McDermott Long et al., 2017). This pattern emphasizes the need for urban habitat management that maintains diverse flowering resources throughout the butterfly activity season.

Sexual Size Dimorphism Patterns. The pronounced sexual size dimorphism observed in both species, with females consistently larger than males, is consistent with established patterns in Satyrinae butterflies and reflects evolutionary pressures related to fecundity and reproductive success (Wiklund & Karlsson, 1988; Gilchrist, 1990). The absence of habitat effects on size dimorphism suggests that this trait is primarily under genetic rather than environmental control, even in heterogeneous urban environments.

Limitations and Future Directions. This study's temporal and spatial scope, while intensive within its bounds, limits the generalizability of findings. Longer-term monitoring would provide insights into population stability and the temporal persistence of genetic polymorphisms. Additionally, expanding the study to multiple urban sites would allow assessment of regional patterns and the role of connectivity in maintaining diversity.

Future research should also investigate the demographic processes underlying the observed patterns, including dispersal rates, reproductive success, and survival across different urban habitat types. Molecular genetic approaches could provide more detailed insights into gene flow and population structure at both local and regional scales.

Conclusions

This study demonstrates that peri-urban habitats, particularly those with high structural complexity such as woodland edges and hedgerows, can support remarkable butterfly diversity and maintain important genetic polymorphisms. The close correspondence between observed and expected Mendelian ratios for wing spot traits, combined with the preservation of sexual dimorphism patterns, indicates that fundamental evolutionary processes remain intact in these urban environments.

The findings strongly support the conservation value of maintaining habitat heterogeneity in urban planning and highlight the potential for relatively small green spaces to contribute meaningfully to regional biodiversity conservation. As urbanization continues to accelerate globally, understanding and optimizing the ecological function of urban habitats becomes increasingly critical for maintaining both species diversity and evolutionary potential.

The integration of community ecology and population genetics approaches employed here provides a robust framework for evaluating urban habitat quality and should be considered in future assessments of urban biodiversity conservation strategies. By demonstrating that urban environments can maintain both ecological and genetic diversity, this work contributes to the growing recognition that cities and their surrounding landscapes represent important frontiers for 21st-century conservation.

Acknowledgements. I am grateful for the support of Prof. Alan. C. Gange and the help of Chris Arnold. This research received no specific funding from any agency in the public, commercial, or not-for-profit sectors. Language editing in this manuscript was assisted by AI-based tools to improve grammar and clarity; all content was reviewed and finalised by the author.

Data Availability Statement. Raw data supporting this study, including species abundance matrices, wing spot scoring data, and morphometric measurements, are available from the corresponding author upon reasonable request. Summary data tables are provided in the supplementary material.

Conflicts of Interest. The author declares no conflicts of interest.

REFERENCES

- Baerwaerts, K., VanDyck, H., VanDongen, S. & Matthysen, E. 1998. Morphological and genetic variation in the Speckled Wood butterfly (*Pararge aegeria* L.) among differently fragmented landscapes. *Netherlands Journal of Ecology*, **48** (3), 241–253.
- Bennie, J., Huntley, B., Wiltshire, A., Hill, M. O. & Baxter, R. 2008. Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling*, **216** (1), 47–59.
- Brakefield, P. M. 1979. Spot-number in *Maniola jurtina*—variation between generations and selection in marginal populations. *Heredity*, **42** (2), 259–266.
- Brakefield, P. M. & French, V. 1993. Butterfly wing patterns. *Acta Biotheoretica*, **41** (4), 447–468.
- Creed, E. R., Ford, E. B. & McWhirter, K. G. 1964. Evolutionary studies on *Maniola jurtina*: The Isles of Scilly, 1958–59. *Heredity*, **19** (3), 471–488.
- Creed, E. R., Dowdeswell, W. H., Ford, E. B. & McWhirter, K. G. 1970. Evolutionary studies on *Maniola jurtina* Lepidoptera: Satyridae: the ‘boundary phenomenon’ in southern England. In: Hecht, M. K. & Steere, W. C., eds. *Essays in Evolution and Genetics*. Appleton Century Crofts, New York, 263–287.
- Denis, M. & Schiffermüller, I. 1775. *Ankündigung eines systematischen Werkes von den Schmetterlingen der Wienergegend*. Bernardi, Vienna, 1–322.
- Dennis, R. L. H., Dapporto, L., Dover, J. W. & Shreeve, T. G. 2013. Corridors and barriers in biodiversity conservation: a novel resource-based habitat perspective for butterflies. *Biodiversity and Conservation*, **22** (12), 2709–2734.
- Dowdeswell, W. H., Ford, E. B. & McWhirter, K. G. 1960. Further studies on the evolution of *Maniola jurtina* in the Isles of Scilly. *Heredity*, **14** (3), 333–364.
- Dunning, J. B., Danielson, B. J. & Pulliam, H. R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos*, **65**, 169–175.
- Esper, E.J.C. 1777. *Die Schmetterlinge in Abbildungen nach der Natur mit Beschreibungen. Theil 1, Band 1*. Wolfgang Walther, Erlangen, 1–388.

- Essens, T., van Langevelde, F., Vos, R. A., van Swaay, C. A. M. & WallisDeVries, M. F. 2017. Ecological determinants of butterfly vulnerability across the European continent. *Journal of Insect Conservation*, **21** (3), 439–450.
- Gilchrist, G. 1990. The consequences of sexual dimorphism in body size for butterfly flight and thermoregulation. *Functional Ecology*, **4**, 475–487.
- Kharouba, H. M. & Vellend, M. 2015. Flowering time of butterfly nectar food plants is more sensitive to temperature than the timing of butterfly adult flight. *Journal of Animal Ecology*, **84** (5), 1311–1321.
- Knoch, A.W. 1782. *Beiträge zur Insectenfauna von Teutschland. Zweiter Band.* Friedrich Wilhelm Iversen, Leipzig, 1–124.
- Lebeau, J., Wesselingh, R. A. & Van Dyck, H. 2015. Butterfly density and behaviour in uncut hay meadow strips: behavioural ecological consequences of an agri-environmental scheme. *PLoS ONE*, **10** (8), e0134945.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th Edition, Volume I.* Laurentius Salvius, Holmiae (Stockholm), 1–824.
- Linnaeus, C. 1761. *Fauna Svecica. Second edition.* Laurentius Salvius, Stockholm, 1–578 .
- Linnaeus, C. 1771. *Mantissa Plantarum Altera.* Laurentius Salvius, Holmiae (Stockholm), 1–588.
- McDermott Long, O., Warren, R., Price, J., Brereton, T. M., Botham, M. S. & Franco, A. M. A. 2017. Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? *Journal of Animal Ecology*, **86** (1), 108–116.
- Newland, D., Still, R., Swash, A. & Tomlinson, D. 2015. *Britain's Butterflies: A Field Guide to the Butterflies of Britain and Ireland. 3rd ed.* WILDGuides Ltd, Old Basing, 1–240.
- Ochsenheimer, F. 1808. *Die Schmetterlinge von Europa. Band 2.* Gerhard Fleischer dem Jüngeren, Leipzig, 1–288.
- Poda von Neuhaus, N. 1761. *Insecta Musei Graecensis.* Widmanstad, Grätz, 1–127.
- Pollard, E. & Yates, T. J. 1993. *Monitoring Butterflies for Ecology and Conservation.* Chapman and Hall, London, 1–274.
- Rottemburg, S.A. von 1775. Anmerkungen zu den Hufnagelischen Tabellen. 6. Die Papillons. *Der Naturforscher*, **6**, 1–34.
- Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature*, **392** (6675), 491–494.
- Seppänen, R. 1981. Differences in spotting pattern between populations of *Aphantopus hyperantus* Lepidoptera, Satyridae in southern Finland. *Annales Zoologici Fennici*, **18**, 1–36.
- Shapiro, A. M. & Carde, R. T. 1970. Habitat selection and competition among sibling species of satyrid butterflies. *Evolution*, **24**, 48–54.
- Van Dyck, H. & Baguette, M. 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? *Basic and Applied Ecology*, **6** (6), 535–545.
- Wiklund, C. & Karlsson, B. 1988. Sexual size dimorphism in relation to fecundity in some Swedish Satyrid butterflies. *The American Naturalist*, **131** (1), 132–138.

Received 8 October 2025

Accepted 22 April 2026