What defines an urban butterfly? Life history traits and habitat associations of butterflies in urban environments

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Abstract

Urban areas are encroaching onto semi-natural areas the world over, driving species assemblages into homogenisation. A better understanding of the life history and habitat association traits can help support management efforts to improve urban biodiversity. Urban areas present an ecological filter, limiting the number of species present compared to the wider countryside. What characteristics help define an urban species may also aid in conservation efforts and improve urban biodiversity. Our research aims to identify the subset of butterflies associated with urban areas based on published information about life history traits and broad habitat associations of butterflies in the United Kingdom to define their characteristics. Principal component analysis revealed a group of thirty butterfly species with traits associated with urban areas. This represents 51% of all British species, including 3 habitat specialists. Urban butterflies were closely associated with preference for woodland glades, a habitat that is mirrored in urban areas by the presence of hedgerows and grassland/woodland edges around urban woodlands. Life history traits associated with urban species included negative association with egg laying on short turfs and herbs, perhaps because of the intensive nature of much urban grassland management, and positive correlations with multivoltinism, the latter of which is closely associated with effective dispersal capability and habitat generalism. This research highlights the characteristics of some butterflies which make them suited to urban environments and points towards habitat management that might support these species as well as identifying opportunities for management to broaden the diversity of urban butterflies.

Introduction

The importance of urban nature is becoming increasingly recognised (Dearborn and Kark, 2010; Botzat, Fischer and Kowarik, 2016). Yet, it is characteristic of urban spaces to be under intense management, for example, being mown regularly, which negatively impacts botanical diversity (Rudolph *et al.*, 2017; Chollet *et al.*, 2018; Proske, Lokatis and Rolff, 2022). Management of "weeds", sometimes with herbicides that have the potential to indiscriminately harm all plant species is common, with cascading effects on biodiversity (Ignatieva *et al.*, 2020). It is widely recognised that urbanisation has a negative impact on biodiversity (Aronson *et al.*, 2014) but urban areas can be designed and managed to support it through the use of green spaces and connective habitat networks (Faeth, Bang and Saari, 2011; Nilon, 2011) with well managed urban woodlands being particularly important for butterflies (Neal, Araya and Wheeler, 2024). Urban areas are also under unique pressures including high degrees of fragmentation (Ramalho *et al.*, 2014), which negatively effects dispersal (Gorton and Shaw, 2023), and often a patchy structure on the landscape scale with small, potentially isolated fragments. Therefore, species that are tolerant of the urban landscape likely fall into a subset of butterflies that are highly dispersal-capable and tolerant of disturbance (Wood and Pullin, 2002). To inform management practices and bolster urban biodiversity, it is increasingly important that we understand the characteristics of species that occur in urban areas.

Butterflies are designated in the United Kingdom as 'state indicators' for insect species by the UK's Joint Nature Conservation Committee (JNCC) based on their use of resources on small spatial scales and their rapid response to habitat management and environmental change (JNCC, 2023). Indicator species such as these can reflect population trends of other, less well recorded groups and are therefore vital to study them (Thomas, 2005). Their detectability, diverse habitat preferences, and varied dispersal capabilities are well studied outside of the urban context, and the habitat associations and life history traits of many species are well known, making them an ideal focus for conservation management efforts.

As butterfly declines are most prominent in urban areas (Dennis *et al.*, 2017), understanding how urbanisation impacts butterflies is important. Increasing demand for housing and the resulting loss of natural and semi-natural habitats means it is pertinent to know which species of butterflies occur in urban areas and how to manage remnant patches habitats for them. This may aid in improving or arresting some of the rapid decline of butterflies (Fox *et al.*, 2023), but also potentially improve or create habitat for some species that are not commonly detected in urban areas. Similarly, examining life-history traits helps the understanding of not just where a butterfly occurs, but the behaviours and ecological requirements that also must be present for a patch to function as habitat or resource. Much urban green space may not be able to support the entire lifecycle of butterflies and may only provide nectar resources, for example in gardens, which may not be suitable breeding habitat but offer significant nectar resources depending on the species present (Olivier *et al.*, 2016).

Understanding how and why some butterflies persist within an urban landscape can support adaptations to the design or management of towns and cities for butterflies more generally and highlight which parts of urban greenspace are especially valuable for creation or restoration. Conservation of butterflies has valuable ecosystem benefits, ranging from human-nature connections and wellbeing (Butler *et al.*, 2024) to supporting broader biodiversity and thereby reinforcing ecosystem stability in the face of future climatic and environment shocks (Johnson *et al.*, 2015).

Methods

Habitat associations of all 59 species of British butterflies were recorded from contemporary literature, largely from field identification guides written by authoritative authors to provide a summary of expert opinions on butterfly habitat preferences (Asher *et al.*, 2001; Fox *et al.*, 2006; Thomas and Lewington, 2016; Eeles, 2019; Newland *et al.*, 2020; Oates, 2020). These sources were chosen over primary literature due to a lack of literature on urban butterfly communities generally, and a similar lack of literature that considers the breadth of urban habitats. Furthermore, the use of such guides provides an aggregation of information from a variety of sources, such as individual species records and expert knowledge, not generally reported in primary literature. This approach provides a qualitative ‘presence-absence‘ assessment of habitat association, rather than a quantitative one which might include measures of density. As a result, there may be species infrequently found habitats which are not reported as being associated with these habitats.

25 different habitat categories were identified from the literature (Table 1) and were recorded in binary (1 for recorded presence, 0 for no recorded presence). Terms in the literature including “parks”, “public recreation areas”, “urban green spaces”, or simply “urban” were used loosely, and therefore grouped together as a single ‘urban’ category. Each category was grouped into one of 4 general habitats and one miscellaneous category. Industrial sites include railways and brownfield sites, with grassland including any grassland-type designation including field margins. The woodland category considers both the woodland type (deciduous or coniferous) and the location within the woodland, for example arboreal species would fit into “woodland canopy.” Finally, the miscellaneous category includes

anything that does not fit into the previous four, which includes unique habitats such as heath, bracken and various elements of coastal environments.

The general urban group includes garden butterflies but are used as a separate category as some urban species do not occur in gardens: all garden butterflies are urban, but not all urban butterflies are found in gardens. Road verges are not considered an exclusive urban feature as roads cut through large parts of the countryside as well and are therefore independent of urban areas, although clearly part of them.

Table 1 - Habitat types collected from the literature.

Urban	Industrial	Grassland	Woodland	Misc.
Urban	Disused railway	Grassland (general)	Woodland (general)	Heath
Garden	Brownfield site	Field margin	Deciduous woodland	Coastal
		Roadside verge	Coniferous woodland	Coastal cliff
		Damp grassland	Oak woodland	Sand dune
		Acid grassland	Woodland canopy	Bracken
		Chalk grassland	Woodland clearing	
		Limestone grassland	Woodland edge	
			Woodland rides	
			Woodland glade	

Traits-based analysis

Traits were separated into two distinct categories: habitat associations and life histories. Habitat associations were derived from the literature described previously and show the general habitat a species can be found in. Life history traits encompass the ways a species interacts with its habitat, such as egg-laying sites, nectar resource preferences, and seasonal activity patterns and other similar activities or specific elements of their lifecycle. These data were sourced from a database created by Middleton-Welling et al. (2020), which describes 25 traits with 217 variables and sub-states of various elements of butterfly life histories. The database covers 542 butterfly species across Europe and the Maghreb (northwest Africa). All the 59 British species were selected for this study.

Completing the urban butterflies list

To determine if the literature gave a complete picture of the potential butterflies in urban areas, a PCA was plotted using each species' habitat association traits and the designation of urban or non-urban. Both groupings were surrounded by a 75% ellipse to determine the range of each grouping. Where species listed as non-urban (or not considered urban in the literature) appear outside of the non-urban ellipse and within the urban ellipse, they are considered urban associated species by trait-association. Species which are at an edge of the ellipse of urban butterflies are not considered urban.

For the purpose of this analysis, the species which occurred in every habitat according to the literature were removed as they all clustered on the same point due to occurring either every or almost every habitat type, which skewed the analysis. These species are *Colias crocea, Aglais io, Aglais urticae, Pieris brassicae, Pieris napi, Pieris rapae, Vanessa atalanta* and

Vanessa cardui. Most of these species are very common or migratory species that can be found in a wide variety of habitats, including urban areas.

Statistical analysis

Once the habitat associations, traits and urban associated species through the literature and PCA had been declined, GLM models were produced to determine which traits can help define an urban butterfly. As there are many terms, Fisher's exact test was used to test for relationships between the urban group and each individual trait, which formed the terms for GLMs.

All analyses were conducted using R version 4.5.0 (2025-04-11 ucrt) "How About a Twenty-Six" R (R Core Team, 2022) using the glm() function with a binomial error term to account for the binary nature of the traits data. All model assumptions were tested by a variety of quantitative assessments including collinearity that was validated using Variance Inflation Factor (VIF), with variables returning values greater than a value of 2 rejected (Hair *et al.*, 2019). The Breusch-Pagan test was used to diagnose heteroscedasticity, and the Shapiro-Wilk test was used to assess normality of the residuals. We tested for overdispersion by calculating the ratio of the sum of squared Pearson residuals to the residual degrees of freedom. Additionally, we assessed overall goodness of fit using the Hosmer–Lemeshow test (Lele and Keim, 2006). This test compares observed and expected frequencies across groups of fitted values. A non-significant result ($p > 0.05$) indicates that the model fits the data adequately, with no evidence of systematic lack of fit.

Non-significant terms were only removed if retaining them had a negative impact on model fit which was measured using Tjur's R^2, and fitted models compared using Akaike Information Criterion (AIC).

In a GLM with a binomial error term, odds ratios help interpret how different habitat traits influence whether a butterfly species is classified as urban-associated or not. Since the response variable is binary (urban-associated = 1, not urban-associated = 0), the model uses a logistic link function, making it a logistic regression model. The odds ratio compares how the odds of urban association change with different habitat traits. It quantifies the effect of each habitat variable on the likelihood that a butterfly is found in urban areas. For example, a significant correlation better the urban butterfly group and woodland would suggest that if a butterfly is associated with woodland, then there is a significant probability that it also occurs in urban areas.

The process of using field guides and life history traits to investigate which traits are strongly associated with urban butterflies is shown in Figure 1.

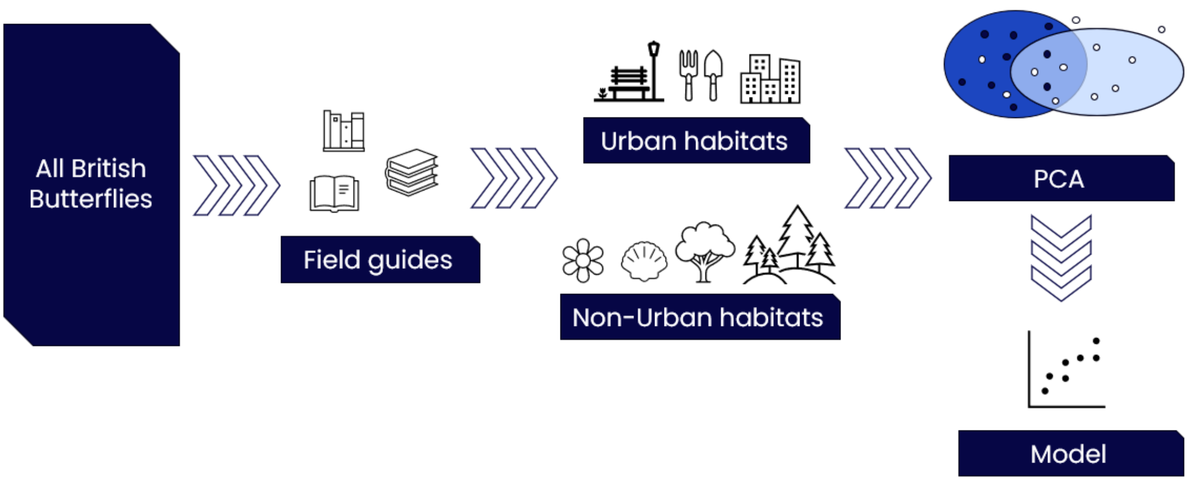

Figure 1 - A process diagram of the methods used to understand the traits of urban British butterflies.

Results

Deriving the urban group

Table 2 shows the species of butterflies that occur in urban areas as described in the literature with the associated references. Additionally, it shows the designation of each species in the British Red List for Butterflies (Fox *et al.*, 2022).

Table 2 - Butterfly species that are 'urban' butterflies by specific mention in the literature cited British Red List from supplementary material in Fox et al. (2022)**.**

Species	Common name	Family	Reference	British Red List Status
Aglais io	Peacock	Nymphalidae	(Asher *et al.*, 2001; Warren and Fox, 2001; Thomas and Lewington, 2016; Eeles, 2019; Newland *et al.*, 2020)	Least concern
Aglais urticae	Small Tortoiseshell	Nymphalidae	(Asher *et al.*, 2001; Warren and Fox, 2001; Thomas and Lewington, 2016; Eeles, 2019; Newland *et al.*, 2020)	Least concern
Anthocharis cardamines	Orange-tip	Pieridae	(Asher *et al.*, 2001; Warren and Fox, 2001; Thomas and Lewington,	Least concern

			2016; Eeles, 2019; Newland *et al.*, 2020)	
Apatura iris	Purple Emperor	Nymphalidae	(Oates, 2020)	Least concern
Aphantopus hyperantus	Ringlet	Nymphalidae	(Lewington and Thompson, 2019)	Least concern
Aricia agestis	Brown Argus	Lycaenidae	(Lewington and Thompson, 2019)	Least concern
Celastrina argiolus	Holly Blue	Lycaenidae	(Thomas and Lewington, 2016; Eeles, 2019)	Least concern
Colias crocea	Clouded Yellow	Pieridae	(Eeles, 2019; Newland *et al.*, 2020)	Least concern
Favonius quercus	Purple Hairstreak	Lycaenidae	(Eeles, 2019; Newland *et al.*, 2020)	Least concern
Gonepteryx rhamni	Brimstone	Pieridae	(Eeles, 2019; Newland *et al.*, 2020)	Least concern
Lasiommata megera	Wall Brown	Nymphalidae	(Thomas and Lewington, 2016)	**Endangered**
Lycaena phlaeas	Small Copper	Lycaenidae	(Eeles, 2019; Newland *et al.*, 2020)	Least concern
Maniola jurtina	Meadow Brown	Nymphalidae	(Eeles, 2019; Newland *et al.*, 2020)	Least concern
Ochlodes sylvanus	Large Skipper	Hesperiidae	(Eeles, 2019; Newland *et al.*, 2020)	Least concern
Pararge aegeria	Speckled Wood	Nymphalidae	(Warren and Fox, 2001; Eeles, 2019; Newland *et al.*, 2020)	Least concern
Pieris brassicae	Large White	Pieridae	(Warren and Fox, 2001; Eeles, 2019; Newland *et al.*, 2020)	Least concern
Pieris napi	Green-veined White	Pieridae	(Warren and Fox, 2001; Eeles, 2019; Newland *et al.*, 2020)	Least concern

Pieris rapae	Small White	Pieridae	(Warren and Fox, 2001; Eeles, 2019; Newland *et al.*, 2020)	Least concern
Polygonia c-album	Comma	Nymphalidae	(Warren and Fox, 2001; Eeles, 2019; Newland *et al.*, 2020)	Least concern
Polyommatus icarus	Common Blue	Lycaenidae	(Lewington and Thompson, 2019)	Least concern
Pyronia tithonus	Gatekeeper	Nymphalidae	(Warren and Fox, 2001; Eeles, 2019; Newland *et al.*, 2020)	Least concern
Satyrium w-album	White-letter Hairstreak	Lycaenidae	(Eeles, 2019)	**Vulnerable**
Thymelicus sylvestris	Small Skipper	Hesperiidae	(Thomas and Lewington, 2016; Lewington and Thompson, 2019)	Least concern
Vanessa atalanta	Red Admiral	Nymphalidae	(Asher *et al.*, 2001; Warren and Fox, 2001; Thomas and Lewington, 2016; Eeles, 2019; Newland *et al.*, 2020)	Least concern
Vanessa cardui	Painted Lady	Nymphalidae	(Asher *et al.*, 2001; Warren and Fox, 2001; Thomas and Lewington, 2016; Eeles, 2019; Newland *et al.*, 2020)	Least concern

Figure 2 shows the results of a PCA with all UK butterflies (except those excluded mentioned in the method section) and their habitat associations separated into urban (red) and non-urban (black) species.

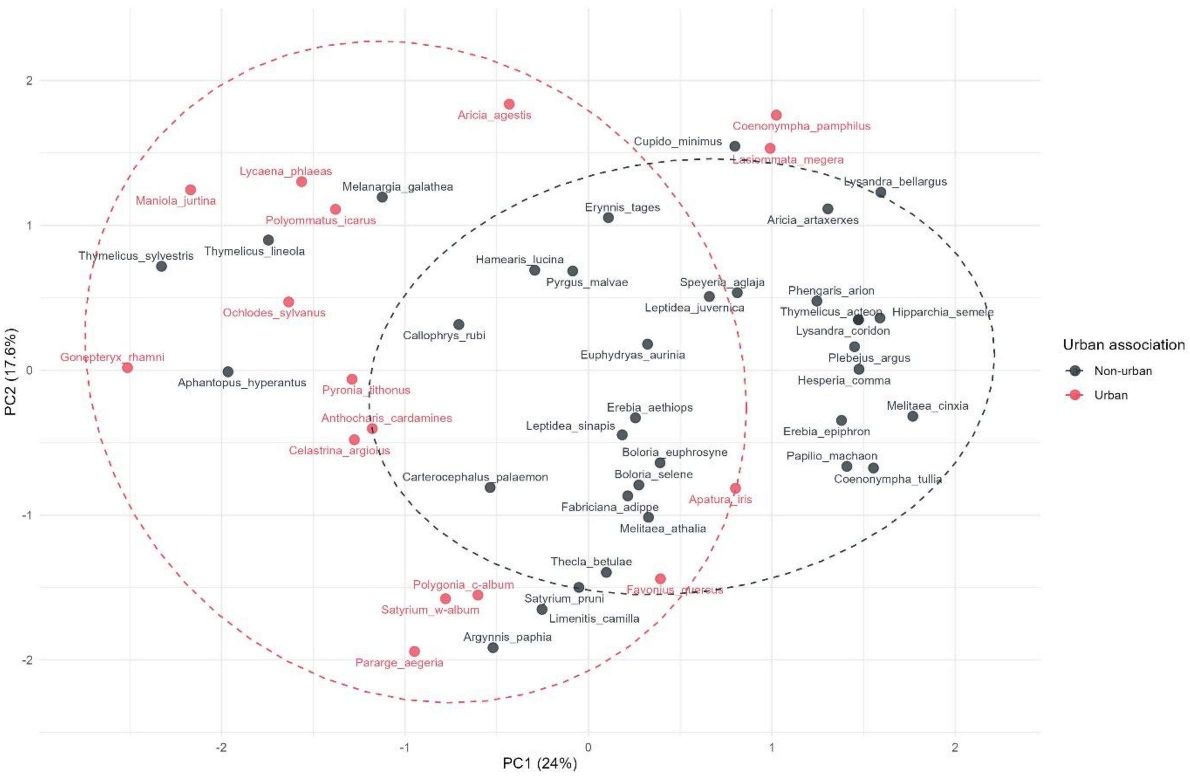

Figure Error! No text of specified style in document. **- PCA of all British butterfly species compared using habitat association traits with a 75% ellipse. The red ellipse and points shows urban association (1) black ellipse and points represent no urban association (0) according to the literature.**

Figure 2 shows that there are some species that can be considered urban by appearing outside of the 75% confidence ellipse and within the urban ellipse that are not discussed in the literature. Table 3 shows the species that have been determined as urban associated by observing the PCA in Figure 2. *Cupido minimus* and *Lysandra bellargus* are outliers, as they appear outside of both centroids. Therefore, due to the uncertainty, they are both not considered as urban-associated species for this analysis.

Table 2 – Additional urban-associated butterflies derived from the PCA including British Red List status.

Species	Common name	British Red List Status
Aphantopus hyperantus	Ringlet	Least concern
Argynnis paphia	Silver-Washed Fritillary	Least concern
Limentis camilla	White Admiral	**Vulnerable**
Melanargia galathea	Marbled White	Least concern
Thymelicus lineola	Essex Skipper	Least concern
Thymelicus sylvestris	Small Skipper	Least concern

A combination of the urban species in the literature combined with the species derived from the PCA comprise the completed list of urban butterflies is shown in Table 4. The table also shows habitat specialism as designated as reported by (JNCC, 2024) and Red List designations from Fox et al. (2022). The species in Table 3 are the species that are used in the analysis.

Table 3 - A completed list of all urban associated butterflies derived from literature combined with traits analysis.

Species	Common name	Family	British Red List Status	Habitat specialist
Aglais io	Peacock	Nymphalidae	Least concern	No
Aglais urticae	Small Tortoiseshell	Nymphalidae	Least concern	No
Anthocharis cardamines	Orange-tip	Pieridae	Least concern	No
Apatura iris	Purple Emperor	Nymphalidae	Least concern	**Yes**
Aphantopus hyperantus	Ringlet	Nymphalidae	Least concern	No
Argynnis paphia	Silver-Washed Fritillary	Nymphalidae	Least concern	**Yes**
Aricia agestis	Brown Argus	Lycaenidae	Least concern	No
Celastrina argiolus	Holly Blue	Lycaenidae	Least concern	No
Colias crocea	Clouded Yellow	Pieridae	Least concern	No
Favonius quercus	Purple Hairstreak	Lycaenidae	Least concern	No
Gonepteryx rhamni	Brimstone	Pieridae	Least concern	No
Lasiommata megera	Wall Brown	Nymphalidae	**Endangered**	No
Limentis camilla	White Admiral	Nymphalidae	**Vulnerable**	**Yes**
Lycaena phlaeas	Small Copper	Lycaenidae	Least concern	No
Maniola jurtina	Meadow Brown	Nymphalidae	Least concern	No

Melanargia galathea	Marbled White	Nymphalidae	Least concern	No
Ochlodes sylvanus	Large Skipper	Hesperiidae	Least concern	No
Pararge aegeria	Speckled Wood	Nymphalidae	Least concern	No
Pieris brassicae	Large White	Pieridae	Least concern	No
Pieris napi	Green-veined White	Pieridae	Least concern	No
Pieris rapae	Small White	Pieridae	Least concern	No
Polygonia c-album	Comma	Nymphalidae	Least concern	No
Polyommatus icarus	Common Blue	Lycaenidae	Least concern	No
Pyronia tithonus	Gatekeeper	Nymphalidae	Least concern	No
Satyrium w-album	White-letter Hairstreak	Lycaenidae	**Vulnerable**	No
Thymelicus lineola	Essex Skipper	Hesperiidae	Least concern	No
Thymelicus sylvestris	Small Skipper	Hesperiidae	Least concern	No
Thymelicus sylvestris	Small Skipper	Nymphalidae	Least concern	No
Vanessa atalanta	Red Admiral	Nymphalidae	Least concern	No
Vanessa cardui	Painted Lady	Nymphalidae	Least concern	No

Urban traits analysis

The traits database shows that 83% of urban butterflies lay their eggs on grasses, with grassland and woodland being the most common habitat associations. Species more closely linked to bracken, mountains, and wetlands are the least likely to inhabit urban areas. Urban butterfly communities typically comprise species from four of the six total butterfly families: Nymphalidae (15 species), Lycaenidae (7 species), Pieridae (7 species), and Hesperiidae (3 species). The two families not represented in these communities are Riodinidae and Papilionidae. In terms of life history traits, all butterfly species associated with urban settings can be observed between June and August. Their larval food plants are primarily herbaceous perennials (83%) and tall herbs exceeding 30 cm (74%). Urban butterflies include no monophagous species but do feature four oligophagous species restricted to one genus, 10 polyphagous species, and 17 oligophagous species associated with a single plant family. The most frequently utilised plant families are Poaceae (10 species), Fabaceae (6 species), Rosaceae (4 species), Brassicaceae (4 species), Cannabaceae (4 species), and Urticaceae (4 species). Over 90 species of Poaceae, 50 species of Fabaceae, and 42 species of Brassicaceae serve as food plants for urban butterflies.

Habitat preference

Fisher's exact test was conducted between the urban grouping and each habitat and life history trait to determine statistically significant relationships (Table 4). Of these traits, the most significant correlations are associations with gardens, field margins, set aside, road verges and various elements of woodland features and broad types of grassland.

Table 4 - Statistically significant Fisher's exact test associations with the urban butterfly group sorted by p value.

Habitat association	p
Garden	< 0.001
Field Margin	< 0.001
Set aside	< 0.001
Road verge	< 0.001
Woodland glade	< 0.001
Woodland canopy	< 0.001
Hedgerow	< 0.001
Woodland Rides	< 0.001
Dry grassland	< 0.001
Oak woodland	< 0.001
Deciduous woodland	< 0.001
Acid grassland	< 0.001
Disused railway	0.001
Vegetation on shingle	0.002
Woodland (General)	0.002
Coniferous woodland	0.002
Quarries	0.002
Woodland clearings	0.007
Cliffs	0.008
Post-industrial sites	0.01
Brownfield sites	0.02
Heathland	0.02
Sand dunes	0.03
Damp grassland	0.03
Woodland edge	0.04
Scrub	0.04

Life-history traits

Significant life history traits (Table 5) show that urban butterflies are associated with shrubs, trees and woody plants, flight in the cooler parts of the year (February and November), and multiple broods per year (multivoltine species).

Table 5 - Table of statistically significant Fisher's exact test results showing associations between different life-history traits and the urban associated group.

Life history trait	p
Flight month of November	< 0.001
Flight month of February	< 0.001
Multivoltine	< 0.001
Egg laying on bare ground or bare ground artefact	0.004
Adult roosting in the tree canopy	0.006
Flight month of October	0.007
Adult roosting on host plant	0.009
Egg laying on short turf and herbs	0.01
Flight month of March	0.01
Adults roosting on tree trunks or fences	0.02
Overwintering as adults	0.02
Adults feeding on minerals	0.03
Adults feeding on shrub or tree flowers	0.03

Statistical model

Several iterations of the model were possible in keeping with the assumptions of the GLM model. Since may variables correlated with each other, there are few combinations possible without breaching VIF or causing singular fits. Table 6 shows some notable models with associated AIC values.

Table 6 - Model selection using AIC with the selected model italicised.

Terms	AIC
Egg laying on short turf and herbs, Multivoltine, Hedgerow, Woodland Glade	*36.91*
Woodland Glade + Hedgerow + Pupation in the shrub layer + Multivoltine	37.07
Hedgerow, Woodland Glade + Multivoltine + Flight month: October + Egg laying on short turf and herbs	38.83
Egg laying on short turf and herbs, adult feeding on shrub/tree flowers, Multivoltine, Hedgerow, Woodland Glade	38.84
Multivoltine, Roadside verge, Woodland glade, Hedgerow	41.41
Multivoltine, Woodland glade, Hedgerow	42.77
Egg laying on short turf and herbs, adult feeding on shrub/tree flowers, Multivoltine, Hedgerow, Woodland Glade, Road Verge	43.36
Significant habitat associations only (Hedgerow, Woodland Glade, Road Verge)	44.04
Significant life history traits only (Egg laying on short turf and herbs, Multivoltine)	62.87

Model 3 had the lowest AIC only due to the removal of the non-significant term of adults feeding on tree/shrub flowers.

Table 7 - GLM showing the full combination of all life-history and habitat association traits (model 3).

Term	Estimate	Std. error	Statistic	p-value	Conf int.	VIF
(Intercept)	-0.39	1.07	-0.37	0.71	-2.68 , 1.81	-
EL on Short Turf / Herbs	-3.57	1.51	-2.36	***0.02***	-7.26, -0.99	1.64
Multivoltine	3.69	1.44	2.56	***0.01***	1.27, 7.28	1.93
Hedgerow	3.19	1.27	2.51	***0.01***	1.07, 6.50	1.62
Woodland glade	3.54	1.48	2.39	***0.02***	1.06, 7.23	1.15
Observations	59					
R^2 Tjur	0.70					

Table 7 shows the fitted model with a high R^2 Tjur of 0.70. Egg Laying on Short Turf / Herbs is negatively associated with the urban butterfly group, with multiple broods per year (multivoltine) and association with hedgerows and woodland glades showing strong positive correlations.

Discussion

This study has identified a distinct suite of UK urban butterflies and provides new insights into their life history and habitat association traits. Urban butterfly communities are comprised of 30 species, 51% of all resident British butterflies. These species are from four of the six butterfly families: Nymphalidae (15 species), Lycaenidae (6 species), Pieridae (7 species), and Hesperiidae (3 species). Of these, 3 are habitat specialists: *Argynnis paphia*, *Limentis camilla* and *Apatura iris*. The majority are classified as 'least concern' on the British Red List, except for *Lasiommata megera*, *Limenitis camilla*, and *Satyrium w-album* which are listed as Endangered or Vulnerable (Fox *et al.*, 2022). However, 31 of the 59 resident species in the United Kingdom are in long-term decline (Butterfly Conservation, 2025), and it’s therefore essential that we ensure that even our most common species remain abundant in the face of such rapid change.

Key habitat associations

Woodland glades and hedgerows key traits associated with urban butterflies. The significant association of woodland glades and road verges with urban butterflies underscores the importance of grassland and woody vegetation in cities (Klaus, 2013; Sehrt *et al.*, 2020). Urban areas typically include lots of grass, shrubs and trees together at high granularity which may explain these relationships. Species which require resources from these habitats where they are found close together likely simulates the conditions in a woodland glade; trees transitioning to shrubs to open grassland. Robertson, Clarke and Warren (1995) recognised woodlands as key butterfly habitat and the Fisher-test analysis reinforces this: woodland glades, canopy cover, and rides all show significant associations with urban butterflies, although did not form part of a suitable model. Model comparisons indicated that models based solely on habitat associations or life histories had poorer fit than those incorporating both, highlighting the importance of considering habitat association and life history in combination.

Woodland glades, with their open canopy, humid microclimate, abundant flowering herbs, and mosaic of grasses and shrubs, likely provide an array of nectar sources, host-plant diversity and sunny-but-sheltered environment that butterflies associated with both grasses and woody plants require. Variation among these features likely explains the relationship between species richness and diversity in structurally complex urban woodlands (Neal, Araya and Wheeler, 2024). Accordingly, conserving and enhancing woodland glades in urban woodlands through practices such as rotational ride management, selective coppicing to create and maintain clearings, and allowing understorey growth of tall grasses and herbaceous plants (Van Calster *et al.*, 2008; Jim, 2011) emerges as a priority for supporting urban butterflies.

Closure of the woodland canopy drives biodiversity decline (Kirby, Buckley and Mills, 2017), and therefore the relationship between urban butterflies and woodland glades shows the importance of well-documented woodland management techniques such as rotational coppice (Warren and Thomas, 1992; Broome *et al.*, 2011) are important for urban woodlands too. Notably, some species are specialists of woodland, one of which is *Limentis camilla* which has likely benefitted from canopy closure due to the preference for shade of its larval host plant *Lonicera periclymenum* (Pollard and Cooke, 1994). This dichotomy suggests that woodland management combined with urban woodland restoration and habitat creation are both necessary to provide a suitable mixture and quantity of habitat for the array of butterflies possible in urban areas.

Life history traits of urban butterflies

The model shows that two life history traits are strongly associated with urban butterflies: multivoltinism and oviposition on short turf and herbs.

Voltinism describes the number of generations a species produces in a year, and species which are multivoltine produce multiple generations per year, a trait common in butterflies (Aalberg Haugen, Berger and Gotthard, 2012). Having multiple broods per year is a trait typical of generalist species (Plazio and Nowicki, 2021). In this case, the butterflies that have this trait also have a wide breadth of larval host plants or are associated with plants which are widespread in urban areas, such as Poaceae. This combination of long flight periods, multiple broods and lots of suitable habitat likely explains a large part of why these species to thrive in urban areas. Evidently, urban butterflies are species with both larval food plants which occur widely, and the ability to have multiple broods per year allows them to colonise more suitable patches more quickly than a species with a single annual brood. This trait can be considered a reasonable indicator of dispersal capability (Sekar, 2012). These species can be supported by the urban landscape through the abundance of non-native nectar resources (Jain, Zeng and Webb, 2021) and provision of nectar resources when non-native species have ceased flowering (Rivest, Wolkovich and Kharouba, 2023). There is also a degree of thermal flexibility in this butterfly group as well, evident by their flight in the colder months of the year. Of the life history traits, the two strongest associations with urban butterflies are the flight month of November and February, extending beyond the typical March to October flight season. Excluding December and January where only 3 and 4 urban species flies, these are cold months of the year but still with a significant amount of butterfly activity. Urban butterflies are influenced by the urban heat island effect with populations emerge earlier and fly longer (Dennis *et al.*, 2017). This thermal flexibility is also a trait of habitat generalists and appears to be advantageous in urban environments. Callaghan, Bowler and Pereira (2021) found that in parts of Europe, urban butterflies were associated with tolerance of a wider range of temperatures. Although these terms did not fit into the model, it is clear there are associations between flight month and urban tolerance here.

Species which oviposit on short turf and herbs shows a negative correlation, suggesting that species with this trait and urban avoiders. This is likely due to intensive management typical of urban green spaces, where over-mowing leads to a both reduction in botanical diversity and destruction of any butterflies at the egg or larval stage (Klaus, 2013). Plant communities that result in short turf are also likely to be associated with animal grazing (Beck *et al.*, 2015); something that is not typical management for urban green spaces and perhaps not compatible with most urban areas outside of specific sites under conservation management plans. However, should this be achieved, it is possible that more species that are not considered urban-associated in this analysis may thrive in urban areas.

A mosaic of sword heights in grasslands can promote butterfly conservation (Joubert-van der Merwe, Pryke and Samways, 2019) but also road verges are beneficial to a wider range of butterflies and should be similarly managed for botanical diversity. Urban areas can often show high degrees of nitrogen deposition, and this nutrient enrichment can reduce plant species richness by competition from fast growing grasses (Bobbink *et al.*, 2010), and likely shading out the short turfs and herbs. Cut-and-collect method of mowing should be applied to remove nutrient load from the soil to encourage botanical diversity (Bowskill, Bhagwat and Gowing, 2023).

Importance of linear features and connective corridors

The model shows significant odds of an urban butterfly being associated with hedgerows, and the Fisher tests along with some weaker fitting models showed relationships with roadside verges. A roadside verge can be defined as strip of land which runs parallel to road or motorway, which can encompass a wide variety of habitat qualities. Verges can connect habitat patches together, but potentially also act as reproductive habitat for some species, where allowing road verges to grow can provide substantial value for butterflies (Priyadarshana *et al.*, 2025). The potential value of roadside verges for biodiversity has been widely recognised, with 2,579 km^3 of road verge habitats in the UK (Phillips *et al.*, 2021). Areas such as the A354 Weymouth Relief Road have been specific managed for floral diversity and have 30 species butterflies in 2019 (Butterfly Conservation, 2019), orchids and other species of national importance (Dorset Local Nature Partnership, 2020). However, in an urban context, most road verges are intensively managed grassy strips with some woody vegetation. In contrast to the woodlands, roadsides are often warm and sunny, but can have complex topography and aspect, which results in a mixture of microclimates (Fekete *et al.*, 2023). Most of the butterfly species that occur on road verges share association with annual plants, Poaceae, and overwintering in both tall and short grasses.

Hedgerows showed strong associations with the urban group and are considered important habitats for wildlife in both urban and countryside contexts (Gosling *et al.*, 2016). The UK has lost 189,900 km of hedgerows since 1950 due to agricultural intensification (Woodland Trust, 2013) which explains some countryside wildlife loss (Boatman *et al.*, 2007). Habitat required by hedgerow-associated species is abundant in urban areas and hedgerows are a common feature of urban parklands and gardens. However, this association is more complex when considering the specific ecology of hedgerow association. Hedgerows are often trees and shrubs grown in a border-wall style fashion to act as a perimeter to properties and to divide land. Of the 39 British butterfly species stated by Dover and Sparks (2000) as being associated with hedgerows, 26 of them use hedgerows as breeding habitat and many species use them as transport corridors for dispersal. They state that even though woodland and unimproved grassland are optimum habitats for butterflies, hedgerows can be so extensive that they are of critical importance to them. However, the species mixture matters in the context of habitat, where hedgerows provide best habitat for invertebrates when they use native vegetation, including drawing in forest specialist species when they were comprised of native trees (Lövei and Magura, 2017). Hedgerow biodiversity is further bolstered by structural diversity, which promotes pollinator community richness, increased pollination visits and more pollinator transfer (Kratschmer *et al.*, 2024). Non-native but commonly widespread urban hedge plants such as Cherry Laurel (*Prunus laurocerasus*) do not act as a larval host plant for any British butterfly (See list of larval host plants in (Eeles, 2019)), and therefore the hedgerow mixture itself likely plays a strong role in the context of habitat. This research then suggests that structurally diverse hedgerows comprised of native trees and shrubs will be greatly beneficial to urban butterflies. Larval hostplant richness is strongly associated with butterfly diversity in urban gardens, and therefore the same conclusions can likely be drawn for other urban areas (Gordon and Kerr, 2025).

Conclusion

This study demonstrates that UK urban butterfly communities are defined not only by their species composition but by a distinctive combination of habitat associations and life history traits that offer resilience in human-dominated landscapes. Urban butterflies are largely habitat generalists capable of exploiting the fine-grained mosaic of woodland glades, hedgerows, and road verges typical of cities, while multivoltinism and thermal flexibility allow them to persist and reproduce across extended seasons. At the same time, the vulnerability of species reliant on short turf or specific larval host plants highlights how common urban management practices can erode local diversity. The findings reinforce that biodiversity-friendly urban planning, such as prioritising structurally complex woodlands, botanically diverse grasslands, and well-connected linear habitats can transform cities into viable strongholds for butterflies. In an era of rapid urban expansion, safeguarding and enhancing these features is not merely desirable but essential if urban landscapes are to serve as both refuges and dispersal hubs for Britain's butterflies.

Statements and Declarations

There are no conflicts of interest declared by the authors.

This research was conducted as part of a PhD funded by the Central England NERC (Natural Environment Research Council) Training Alliance (CENTA) doctoral training partnership (Grant number: 2605099).

Acknowledgements

Some data for part of the analysis was from a database produced by Middleton-Welling et al. (2020) for the purposes of butterfly traits-based research. Data collected for this research is available at: https://doi.org/10.21954/ou.rd.28903757.v1.

References

Aalberg Haugen, I.M., Berger, D. and Gotthard, K. (2012) 'The evolution of alternative developmental pathways: footprints of selection on life-history traits in a butterfly', *Journal of Evolutionary Biology*, 25(7), pp. 1377–1388. Available at: https://doi.org/10.1111/J.1420-9101.2012.02525.X.

Aronson, M.F.J. *et al.* (2014) 'A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers', *Proceedings of the Royal Society B: Biological Sciences*, 281(1780). Available at: https://doi.org/10.1098/RSPB.2013.3330.

Asher, J. *et al.* (2001) *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford: Oxford University Press.

Beck, J.J. *et al.* (2015) 'Grazing maintains native plant diversity and promotes community stability in an annual grassland', *Ecological Applications*, 25(5), pp. 1259–1270. Available at: https://doi.org/10.1890/14-1093.1.

Boatman, N.D. *et al.* (2007) 'Impacts of Agricultural Change on Farmland Biodiversity in the UK', in *Issues in Environmental Science and Technology*. RSC Publishing. Available at: https://doi.org/https://doi.org/10.1039/9781847557650.

Bobbink, R. *et al.* (2010) 'Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis', *Ecological Applications*, 20(1), pp. 30–59. Available at: https://doi.org/10.1890/08-1140.1;WEBSITE:WEBSITE:ESAJOURNALS;WGROUP:STRING:PUBLICATION.

Botzat, A., Fischer, L.K. and Kowarik, I. (2016) 'Unexploited opportunities in understanding liveable and biodiverse cities. A review on urban biodiversity perception and valuation', *Global Environmental Change*, 39, pp. 220–233. Available at: https://doi.org/10.1016/J.GLOENVCHA.2016.04.008.

Bowskill, V., Bhagwat, S. and Gowing, D. (2023) 'Depleting soil nutrients through frequency and timing of hay cutting on floodplain meadows for habitat restoration and nutrient neutrality', *Biological Conservation*, 283, p. 110140. Available at: https://doi.org/10.1016/J.BIOCON.2023.110140.

Broome, A. *et al.* (2011) 'The effect of coppice management on moth assemblages in an English woodland', *Biodiversity and Conservation*, 20(4), pp. 729–749. Available at: https://doi.org/10.1007/s10531-010-9974-y.

Butler, C.W. *et al.* (2024) 'Connection for conservation: The impact of counting butterflies on nature connectedness and wellbeing in citizen scientists', *Biological Conservation*, 292, p. 110497. Available at: https://doi.org/10.1016/J.BIOCON.2024.110497.

Butterfly Conservation (2019) *Counting the butterflies on the A354 Weymouth Relief Road in Dorset | Butterfly Conservation*. Available at: https://butterfly-conservation.org/our-work/conservation-projects/building-sites-for-butterflies/counting-the-butterflies-on-the-a354 (Accessed: 15 March 2024).

Butterfly Conservation (2025) *Half of UK butterfly species in long-term decline, monitoring reveals | Butterfly Conservation*. Available at: https://butterfly-conservation.org/news-and-blog/half-of-uk-butterfly-species-in-long-term-decline-monitoring-reveals (Accessed: 17 April 2025).

Callaghan, C.T., Bowler, D.E. and Pereira, H.M. (2021) ‘Thermal flexibility and a generalist life history promote urban affinity in butterflies’, *Global change biology*, 27(15), pp. 3532–3546. Available at: https://doi.org/10.1111/GCB.15670.

Van Calster, H. *et al.* (2008) ‘Coppice management effects on experimentally established populations of three herbaceous layer woodland species’, *Biological Conservation*, 141(10), pp. 2641–2652. Available at: https://doi.org/10.1016/J.BIOCON.2008.08.001.

Chollet, S. *et al.* (2018) ‘From urban lawns to urban meadows: Reduction of mowing frequency increases plant taxonomic, functional and phylogenetic diversity’, *Landscape and Urban Planning*, 180, pp. 121–124. Available at: https://doi.org/10.1016/J.LANDURBPLAN.2018.08.009.

Dearborn, D.C. and Kark, S. (2010) ‘Motivations for Conserving Urban Biodiversity’, *Conservation Biology*, 24(2), pp. 432–440. Available at: https://doi.org/10.1111/j.1523-1739.2009.01328.x.

Dennis, E. *et al.* (2017) ‘Urban indicators for UK butterflies’, *Ecological Indicators*, 76, pp. 184–193. Available at: https://doi.org/10.1016/J.ECOLIND.2017.01.009.

Dorset Local Nature Partnership (2020) ‘Lead Partner: Natural England and Dorset County Council (project completed prior to local government reorganisations) Case Study: Dorset’s Natural Influence at its best Biodiversity Net Gains from the Weymouth Relief Road construction’. Available at: https://dorsetlnp.org.uk/wp-content/uploads/2020/06/LNP-Weymouth-Relief-Road-Case-Study.pdf (Accessed: 15 March 2024).

Dover, J. and Sparks, T. (2000) ‘A review of the ecology of butterflies in British hedgerows’, *Journal of Environmental Management*, 60(1), pp. 51–63. Available at: https://doi.org/10.1006/JEMA.2000.0361.

Eeles, P. (2019) *Life cyles of British & Irish Butterflies*. Pisces Publications.

Faeth, S.H., Bang, C. and Saari, S. (2011) ‘Urban biodiversity: patterns and mechanisms’, *Ann. N.Y. Acad. Sci* [Preprint]. Available at: https://doi.org/10.1111/j.1749-6632.2010.05925.x.

Fekete, R. *et al.* (2023) ‘North-facing roadside slopes: Anthropogenic climate microrefugia for orchids’, *Global Ecology and Conservation*, 47, p. e02642. Available at: https://doi.org/10.1016/J.GECCO.2023.E02642.

Fox, R. *et al.* (2006) *The state of butterflies in Britain and Ireland*. NatureBureau.

Fox, R. *et al.* (2022) ‘A revised Red List of British butterflies’, *Insect Conservation and Diversity*, 15(5), pp. 485–495. Available at: https://doi.org/10.1111/ICAD.12582.

Fox, R. *et al.* (2023) *The State of the UK’s Butterflies* . Available at: https://butterfly-conservation.org/sites/default/files/2023-01/State%20of%20UK%20Butterflies%202022%20Report.pdf (Accessed: 16 May 2023).

Gordon, S.C.C. and Kerr, J.T. (2025) ‘A comparative analysis of metacommunities reveals contrasting drivers of alpha and beta diversity in urban butterflies’, *Journal of Urban Ecology*, 11(1). Available at: https://doi.org/10.1093/JUE/JUAF006.

Gorton, A.J. and Shaw, A.K. (2023) ‘Using theoretical models to explore dispersal variation and fragmentation in urban environments’, *Population Ecology*, 65(1), pp. 17–24. Available at: https://doi.org/10.1002/1438-390X.12135.

Gosling, L. *et al.* (2016) ‘Differences between urban and rural hedges in England revealed by a citizen science project’, *BMC Ecology*, 16(1), pp. 45–55. Available at: https://doi.org/10.1186/S12898-016-0064-1/FIGURES/2.

Hair, J.F. *et al.* (2019) ‘When to use and how to report the results of PLS-SEM’, *European Business Review*. Emerald Group Publishing Ltd., pp. 2–24. Available at: https://doi.org/10.1108/EBR-11-2018-0203.

Ignatieva, M. *et al.* (2020) ‘Lawns in Cities: From a Globalised Urban Green Space Phenomenon to Sustainable Nature-Based Solutions’, *Land 2020, Vol. 9, Page 73*, 9(3), p. 73. Available at: https://doi.org/10.3390/LAND9030073.

Jain, A., Zeng, Y. and Webb, E.L. (2021) ‘Critical Dependence of Butterflies on a Non-native Host Plant in the Urban Tropics’, *Frontiers in Ecology and Evolution*, 9, p. 655012. Available at: https://doi.org/10.3389/FEVO.2021.655012/BIBTEX.

Jim, C.Y. (2011) ‘Holistic research agenda for sustainable management and conservation of urban woodlands’, *Landscape and Urban Planning*, 100, pp. 375–379. Available at: https://doi.org/10.1016/j.landurbplan.2011.01.006.

JNCC (2023) *UKBI - C6. Insects of the wider countryside | JNCC - Adviser to Government on Nature Conservation*. Available at: https://jncc.gov.uk/our-work/ukbi-c6-insects-of-the-wider-countryside/#habitat-specialists (Accessed: 23 May 2024).

JNCC (2024) *UK Biodiversity Indicators 2024. Insects of the wider countryside (butterflies) | JNCC Resource Hub*. Available at: https://hub.jncc.gov.uk/assets/612876cb-945a-41a1-a21c-cd49ecd3a051 (Accessed: 7 August 2025).

Johnson, R.K. *et al.* (2015) ‘Linking biodiversity, ecosystem functioning and services, and ecological resilience: towards an integrative framework for Improved Management’. Available at: https://doi.org/10.1016/bs.aecr.2015.09.004.

Joubert-van der Merwe, L., Pryke, J.S. and Samways, M.J. (2019) ‘Well-managed grassland heterogeneity promotes butterfly conservation in a corridor network’, *Journal of Environmental Management*, 238, pp. 382–395. Available at: https://doi.org/10.1016/J.JENVMAN.2019.03.021.

Kirby, K.J., Buckley, G.P. and Mills, J. (2017) ‘Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland’, *Folia Geobotanica*, 52(1), pp. 5–13. Available at: https://doi.org/10.1007/S12224-016-9252-1/TABLES/1.

Klaus, V.H. (2013) ‘Urban Grassland Restoration: A Neglected Opportunity for Biodiversity Conservation’, *Restoration Ecology*, 21(6), pp. 665–669. Available at: https://doi.org/10.1111/REC.12051.

Kratschmer, S. *et al.* (2024) ‘Hedgerow structural diversity is key to promoting biodiversity and ecosystem services: A systematic review of Central European studies’, *Basic and Applied Ecology*, 78, pp. 28–38. Available at: https://doi.org/10.1016/J.BAAE.2024.04.010.

Lele, S.R. and Keim, J.L. (2006) ‘Weighted distributions and estimation of resource selection probability functions’, *Ecology*, 87(12), pp. 3021–3028. Available at: https://doi.org/10.1890/0012-9658(2006)87[3021:WDAEOR]2.0.CO;2.

Lewington, R. and Thompson, K. (2019) *Guide to garden wildlife*. Second Edition. London: Bloomsbury Wildlife Guides.

Lövei, G.L. and Magura, T. (2017) ‘Ground beetle (Coleoptera: Carabidae) diversity is higher in narrow hedges composed of a native compared to non-native trees in a Danish agricultural landscape’, *Insect Conservation and Diversity*, 10(2), pp. 141–150. Available at: https://doi.org/10.1111/ICAD.12210;REQUESTEDJOURNAL:JOURNAL:17524598;JOURNAL:JOURNAL:17524598;WGROUP:STRING:PUBLICATION.

Middleton-Welling, J. *et al.* (2020) ‘A new comprehensive trait database of European and Maghreb butterflies, Papilionoidea’, *Scientific Data*, 7(1), pp. 1–10. Available at: https://doi.org/10.1038/s41597-020-00697-7.

Neal, W., Araya, Y. and Wheeler, P.M. (2024) ‘Influence of canopy structural complexity on urban woodland butterfly species richness’, *Journal of Insect Conservation*, pp. 1–12. Available at: https://doi.org/https://doi.org/10.1007/s10841-024-00594-z.

Newland, D. *et al.* (2020) *Britain’s Butterflies*. Fourth. Oxford: Princeton University Press.

Nilon, C.H. (2011) ‘Urban biodiversity and the importance of management and conservation’, *Landscape and Ecological Engineering*, 7(1), pp. 45–52. Available at: https://doi.org/10.1007/S11355-010-0146-8/FIGURES/3.

Oates, M. (2020) *His Imperial Majesty: A natural history of the Purple Emperor*. London: Bloomsbury Wildlife.

Olivier, T. *et al.* (2016) ‘Butterfly assemblages in residential gardens are driven by species’ habitat preference and mobility’, *Landscape Ecology*, 31(4), pp. 865–876. Available at: https://doi.org/10.1007/S10980-015-0299-9/FIGURES/2.

Phillips, B.B. *et al.* (2021) ‘Road verge extent and habitat composition across Great Britain’, *Landscape and Urban Planning*, 214, p. 104159. Available at: https://doi.org/10.1016/J.LANDURBPLAN.2021.104159.

Plazio, E. and Nowicki, P. (2021) ‘Inter-sexual and inter-generation differences in dispersal of a bivoltine butterfly’, *Scientific Reports 2021 11:1*, 11(1), pp. 1–10. Available at: https://doi.org/10.1038/s41598-021-90572-1.

Pollard, E. and Cooke, A.S. (1994) ‘Impact of muntjac deer Muntiacus reevesi on EGG-laying sites of the white admiral butterfly Ladoga camilla in a cambridgeshire wood’, *Biological Conservation*, 70(2), pp. 189–191. Available at: https://doi.org/10.1016/0006-3207(94)90287-9.

Priyadarshana, T.S. *et al.* (2025) ‘The direct and indirect effects of road verges and urban greening on butterflies in a tropical city-state’, *Landscape and Urban Planning*, 258, p. 105335. Available at: https://doi.org/10.1016/J.LANDURBPLAN.2025.105335.

Proske, A., Lokatis, S. and Rolff, J. (2022) ‘Impact of mowing frequency on arthropod abundance and diversity in urban habitats: A meta-analysis’, *Urban Forestry & Urban Greening*, 76, p. 127714. Available at: https://doi.org/10.1016/J.UFUG.2022.127714.

R Core Team (2022) ‘R: A language and environment for statistical computing.’ Vienna, Austria: R Foundation for Statistical Computing.

Ramalho, C.E. *et al.* (2014) ‘Complex effects of fragmentation on remnant woodland plant communities of a rapidly urbanizing biodiversity hotspot’, *Ecology*, 95(9), pp. 2466–2478. Available at: https://doi.org/10.1890/13-1239.1.

Rivest, S.A., Wolkovich, E.M. and Kharouba, H.M. (2023) 'Flowering phenology influences butterfly nectar foraging on non-native plants in an oak savanna', *Ecology*, 104(4), p. e4004. Available at: https://doi.org/10.1002/ECY.4004.

Robertson, P.A., Clarke, S.A. and Warren, M.S. (1995) 'Woodland management and butterfly diversity', *Ecology and Conservation of Butterflies*, pp. 113–122. Available at: https://doi.org/10.1007/978-94-011-1282-6_8.

Rudolph, M. *et al.* (2017) 'Patterns and potentials of plant species richness in high- and low-maintenance urban grasslands', *Applied Vegetation Science*, 20(1), pp. 18–27. Available at: https://doi.org/10.1111/AVSC.12267.

Sehrt, M. *et al.* (2020) 'Less is more! Rapid increase in plant species richness after reduced mowing in urban grasslands', *Basic and Applied Ecology*, 42, pp. 47–53. Available at: https://doi.org/10.1016/J.BAAE.2019.10.008.

Sekar, S. (2012) 'A meta-analysis of the traits affecting dispersal ability in butterflies: Can wingspan be used as a proxy?', *Journal of Animal Ecology*, 81(1), pp. 174–184. Available at: https://doi.org/10.1111/j.1365-2656.2011.01909.x.

Thomas, J. and Lewington, R. (2016) *The Butterflies of Britain and Ireland*. Revised Ed. London: Bloomsbury.

Thomas, J.A. (2005) 'Monitoring Change in the Abundance and Distribution of Insects Using Butterflies and Other Indicator Groups', *Philosophical Transactions: Biological Sciences*, 360(1454), pp. 339–357. Available at: https://about.jstor.org/terms (Accessed: 16 November 2021).

Warren, Martin. and Fox, Richard. (2001) *The millennium atlas of butterflies in Britain and Ireland*. Edited by Jim. Asher et al. Oxford University Press.

Warren, M.S. and Thomas, J.A. (1992) ‘Butterfly responses to coppicing’, *Ecology and Management of Coppice Woodlands*, pp. 249–270. Available at: https://doi.org/10.1007/978-94-011-2362-4_13.

Wood, B.C. and Pullin, A.S. (2002) ‘Persistence of species in a fragmented urban landscape: The importance of dispersal ability and habitat availability for grassland butterflies’, *Biodiversity and Conservation*, 11(8), pp. 1451–1468. Available at: https://doi.org/10.1023/A:1016223907962.

Woodland Trust (2013) *Position Statement Hedges and hedgerows Hedges and hedgerows*. Available at: https://www.woodlandtrust.org.uk/publications/2013/02/hedges-and-hedgerows-position-statement/ (Accessed: 15 March 2024).