



Influence of canopy structural complexity on urban woodland butterfly species richness

Willow Neal¹ · Yoseph Araya¹ · Philip M. Wheeler¹

Received: 28 September 2023 / Accepted: 7 May 2024
© The Author(s) 2024

Abstract

As urban land use expands, understanding the conservation of biodiversity in urban settings becomes increasingly important. Urban areas contain a wide range of remnant natural, semi-natural and anthropogenic woodlands but the biodiversity of these woodlands is not well studied. Urban woodlands are usually constrained in size and subject to management which may not be focused on promoting biodiversity. As a habitat of critical importance, the characteristics of urban woodlands need to be better understood to maximise their biodiversity within a limited footprint in the urban landscape. We used repeat line-transect surveys and rapid woodland structure habitat assessments to investigate the habitat associations of butterflies in ten woodland patches representing a range of sizes (between 1 and 40 ha), ages and woodland characteristics in the urban habitat matrix of Milton Keynes, UK. We found that ancient woodland sites supported every species detected, but the butterfly communities of amenity and roadside woodlands had similar species richness, diversity and abundance, regardless of size. Butterfly species richness was strongly associated with both woodland area and structural complexity at a site-scale, but only with structural complexity on a transect scale. Simpson diversity showed no correlation with any variable at the site scale, but strong correlation with structural complexity on transects. Abundance only correlated with area at the site scale. Our results suggest that management techniques that introduce structural complexity within urban woodlands may be an effective way to support butterfly richness and diversity in contexts where woodland areas cannot be increased.

Keywords Butterfly conservation · Urban ecology · Urban woodlands · Habitat structure

Impacts for insect conservation

Urban woodlands can provide valuable habitat for butterflies on a multitude of scales, but structure is key. There is significant value in large urban woodland patches, but similar value in smaller patches under a management regime that introduces structural complexity and thereby habitat heterogeneity. Conversely, even large woodland patches can be poor sites for butterflies if management does not lead to structural complexity. A network of structurally diverse, large and small woodland patches has the potential to support diverse woodland butterfly populations within urban landscapes, and urban ancient woodlands also present extremely valuable habitats for butterflies.

Introduction

Global biodiversity is declining (Montgomery et al. 2020; Wagner 2020), with human land-use intensification and habitat loss driving extinctions (Allan et al. 2015; Betts et al.

2017). This is particularly the case in insects, where changes in habitat have caused over 40% of species to become threatened with extinction, with habitat loss, conversion to intensive agriculture and urbanisation as the biggest drivers (Sánchez-Bayo and Wyckhuys 2019). Among the insects, Lepidoptera are one of the most impacted orders (Maes and Van Dyck 2001). The United Kingdom (UK) is one of the world's most nature-depleted countries (Hayhow et al. 2019), in the bottom 10% globally, and the least nature-rich in the G7 group of industrialised nations (Ashworth 2021). In 2019, nearly 83% of the UK population lived in urban

✉ Willow Neal
willow.neal@open.ac.uk

¹ School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, UK

areas (UK Government 2021b). In England, there is a huge demand for house building as populations expand, increasing demand for land for conversion to urban areas (Environment Agency 2023). Globally, urbanisation of the landscape has expanded at a rate twice as fast as population growth from the 1980s to the 2010s (Angelstam et al. 2004; Seto et al. 2012), and is having a dramatic negative impact on biodiversity (Bateman et al. 2013; Aronson et al. 2014; Haaland and van den Bosch 2015), and therefore ecosystem function (Seto et al. 2012). As urbanisation has driven multiple taxa into decline in abundance and diversity at local and landscape scales (Piano et al. 2020), examining how species persist in fragmented habitats within a hostile urban matrix is important (Baldock et al. 2019; Rivkin et al. 2019). There are also a wide range of ecosystem services that urban green spaces provide (Livesley et al. 2016) with positive effects on human health (Lee and Maheswaran 2011; Sandifer et al. 2015). This includes psychological wellbeing, decrease in feelings of depression, stress, with positive effects on mood and self-esteem (see Sandifer et al. (2015) for an extended table of effects). Positive effects on human psychology have been linked not just to nature exposure, but species richness and habitat diversity as well (Fuller et al. 2007; Hough 2014). Biodiversity also positively affects physical health such as chronic allergies and inflammatory diseases (Hanski et al. 2012).

Butterflies in the UK are on an unprecedented downward trend, with 80% of UK butterflies having declined in abundance or distribution since the 1970s (Fox et al. 2023). Previous work has shown that urbanisation negatively impacts butterfly populations (Blair 1999; Hardy and Dennis 1999; Bergerot et al. 2012; Soga and Koike 2015; Dennis et al. 2017), with declining habitat quality and reduction of overall habitat area among the largest contributing factors (Olivier et al. 2016). Butterflies are effective bioindicator species which can represent the diversity of other taxa in response to environmental change (Thomas 2005; Pe'er and Settele 2013), and therefore such a rapid decline is alarming as it may indicate wider species loss.

Woodlands are used by 67% of UK resident butterfly species (Clarke et al. 2011) where they commonly breed and find resources in the woodland edge, its rides, glades and the tree canopy, with about one third of these species using woodlands exclusively (Warren and Thomas 1992). While urban woodlands and their butterfly populations are not well studied, urban butterflies have been found to rely on habitat quality, habitat variation and patch area (Bergerot et al. 2011; Olivier et al. 2016). Habitat preferences and dynamics of butterflies within wooded habitats out of urban areas have also been discussed (Shreeve and Mason 1980; Robertson et al. 1995; Slamova et al. 2013; van Halder et al. 2015; Villemeijer et al. 2015). Management strategies such as coppicing

are beneficial for much woodland biodiversity, particularly butterflies, as most of the species associated with woodlands are found and breed in open, grassy herbaceous areas (Warren and Thomas 1992). Management techniques such as these move the state of ecological succession away from a closed canopy towards a semi-open canopy structure that has more primary production and is a key tool in supporting woodland restoration and improving biodiversity (Kirby et al. 2017a; Vanbeveren and Ceulemans 2019). In an urban context, canopy cover extent has been shown to correlate positively with biodiversity (Wang et al. 2019) but canopy closure decreases biodiversity (Gao et al. 2014).

Urban woodlands are threatened by development, but also recreation (Jim 2011), habitat fragmentation (Ramalho et al. 2014), pollution (Hargitai et al. 2016) and invasive non-native species (Vallet et al. 2010). However, urban woodlands can provide a wealth of biodiversity under the right conditions (de Andrade et al. 2019). The characteristics of urban woodlands which support diverse and abundant butterfly populations are not well studied, therefore, an understanding of associations between urban woodland characteristics and butterfly diversity and abundance can help inform woodland management and urban woodland biodiversity more broadly (Ramírez-Restrepo and MacGregor-Fors 2016). The principal question we address here is: what habitat characteristics best explain variation in butterfly species richness, abundance and diversity across urban woodland patches? This will help inform the best practices for urban woodland conservation for butterflies and the species they represent as a bioindicator species. While increasing woodland size should support greater species diversity (Schoener 1976; Lawton 1999), this may not be possible within urban landscapes where space is limited through competing land uses and the prohibitive cost of land.

Method

Study area

The study was conducted in Milton Keynes, Buckinghamshire, UK (52.0406° N, 0.7594° W), a rapidly growing city of over 280,000 people that covers an area of approximately 89 km². It is home to three large and several smaller patches of ancient woodland, recent amenity plantation and parkland which are connected by 'grid-road corridors' that serve as the city's main transport routes. Milton Keynes was a new town, built from the late 1960s and was once touted to be a "city of trees", with a deliberate focus on tree planting when it was established, therefore the verges of these road corridors are largely wooded, and range in size from a few individual trees to long, thin patches of semi-mature

woodland. Woodland within the urban area is predominantly broadleaved deciduous, with few coniferous species. Soils are mostly calcareous and clay-rich (Milton Keynes Council 2016) that support a wide array of native and non-native species of trees, shrubs and other types of vegetation. As a place with several large ancient woodland patches, there are also over 200 notable, veteran or ancient trees (Woodland Trust 2023).

Ten woodland sites were selected for study in Milton Keynes to encompass a range of woodland types and sizes across three categories (1) Ancient woodland, as designated by Natural England (2023), areas that have been continuously wooded since at least 1600 AD, (2) Amenity sites: typical parks or similarly wooded areas of recent planting for recreational use with a mixture of native and non-native species. (3) Roadside, areas for woody vegetation in typically long thin strips along the “grid roads”. Roadside sites were characterised by an often-dense mixture of native and ornamental trees and shrubs. Site area was mapped in and measured in ArcGIS pro (Esri 2023). Study woodlands were selected based on age, size and broad composition following discussion with the site managers The Parks Trust (<https://www.theparkstrust.com/>) which owns and manages over 2400 ha of green space in Milton Keynes. Site selection was constrained by the availability, size and distribution of all woodland categories. The number of ancient woodlands within the urban matrix is limited, with three large sites (between 25 and 40 ha) and two substantially smaller sites (2 ha). There are several amenity woodlands in MK, but most of these are relatively small and located in specific parts of the city. Roadside woodlands are widespread but limited in size with relatively few contiguous patches large enough for a single 500 m transect. All but one of the ancient woodlands are under active management, but all other sites visited have no specific management regime described.

Butterfly surveys

Twenty-one 500 m line transects were placed across the ten urban woodland sites to measure butterfly occurrence and abundance from June to September 2022, with each transect visited weekly. Transects were surveyed using Pollard walks (Pollard 1977) in accordance with the standard UKBMS (no date) recording method, which includes consideration for temperature and time of day. This method involves walking a transect in a single line at a slow and steady pace, recording any butterflies that occur either 5 m in front, above or 2.5 m either side of the transect path. Any individual outside of this range was ignored. For this reason, the Pollard Walk method does not reliably record arboreal species as there is a limit to the height of the survey area. Each of the 3 roadside sites and two smaller ancient woodlands had one

transect each, with the two larger amenity sites assigned two each. The remaining woodlands which were significantly larger had 3 or 4 transects each.

Surveys were partially randomised: sites were grouped into 5 groups of nearby sites so that all sites within a group could be surveyed on a single day. The order of survey for each group was then randomised to reduce sampling bias. Transects were designed to capture as much character of each site as possible to ensure that the variation present in each woodland was recorded. Prior to beginning surveys, each woodland area was walked through numerous times to understand the variation in its character from a simple visual assessment. Once completed, transects were designed to pass through as many of the woodland features as possible, ensuring the unique characteristics of each site were surveyed such as areas of shaded or sparse tree cover, or open florally dense areas. Additionally, transects were designed with accessibility in mind, where the recorder would be able to focus their attention on recording butterflies without having to concentrate on navigating complex or unsafe terrain. This necessity often prevented surveys in the densest parts of a woodland. Transects were visited up to ten times during the survey period, avoiding periods of rain or extreme heat. Because of the high number of repeat visits combined with relatively low species diversity we considered that surveys gave a complete picture of the butterfly community at each site, and therefore used simple species richness rather than rarefaction in our analysis. Butterfly species richness and Simpson diversity index were calculated in R using the Vegan package (Oksanen et al. 2022).

Woodland structure surveys

Habitat data were collected at 100 m intervals along each of the transects. 10 × 10 m quadrats were placed on alternating sides along the transect where possible – at some narrow sites, it was not possible to alternate the position of quadrats as it would result in data collection in the road. Habitat structure was assessed by recording the percentage cover of vegetation at 1–2 m, 2–5 m, 5–10 m and over 10 m height intervals. Canopy openness was measured on a 0–25-point scale using a canopy scope, designed and used following Brown et al. (2000). Percentage of ground covered by vegetation of any kind (< 1 m height), bare ground and leaf litter cover were estimated. Finally, maximum tree height within each quadrat was estimated to the nearest metre. The standard deviation of maximum canopy height was calculated to produce a proxy for canopy structural complexity per site and transect (Zenner 2000). In total, 105 quadrats were surveyed across the 10 sites. Site areas were log-transformed for statistical analysis, and all independent variables were standardised using the ‘scale’ function in R.

Statistical analysis

All statistical analysis and visualisation were conducted in R (2023.03.1 Build 446 “Cherry Blossom”: R Core Team 2022) with model parameters checked for compliance with model assumptions using the R package ‘performance’ (Lüdecke et al. 2021). Associations between butterfly data (species richness, abundance and diversity) and habitat structure variables were investigated separately at site and transect level using linear regression models and linear mixed models respectively. For site-level analyses, the mean of all transect values in each site were calculated for butterfly and habitat structure data and analysed using the `lm()` function in R. Since multiple transects were surveyed in several sites, leading to potential spatial non-independence, transect-level analyses were carried out using linear mixed models in the `lme4` package in R (Bates et al. 2015) with ‘site’ as a random factor.

Independent variables were tested using Pearson correlations with the butterfly data due to the low degrees of freedom in an exploratory phase, and significant terms were chosen for the model. When a suitably structured model was produced, variables were checked for multicollinearity for Variance Inflation Factor (VIF), where a VIF of > 2 and Condition Index > 30 were removed from the model (Belsey et al. 1980; Hair et al. 2019). Non-significant terms were retained if they improved model fit, which was determined by selecting the model with the highest adjusted R^2 value but were otherwise discarded. Separate analyses to assess the effect of woodland type on butterfly species data were conducted at both site and transect scales. In these models the woodland type was included as a factor in separate linear regression models, and an ANOVA test using the function `aov()` was conducted on each model to determine the statistical significance of type on richness, abundance and diversity.

Results

Habitat structure

The three woodland types varied in their habitat characteristics (Table 1). There were similarities between aspects of the woodland types, but no two types were consistently more similar to each other across all variables. Ancient woodland sites were the largest overall, had taller trees and a more complex canopy structure. There are significant correlations between ancient sites and structural complexity ($p=0.02$, $R^2=0.69$) as well as canopy height ($p=0.04$, $R^2=0.65$), but this is not the case with roadside or amenity sites. Canopy was more open at amenity sites despite these having the lowest structural complexity. Mid and under-storey canopy cover was most similar between ancient woodlands and roadside sites, but ground cover was most similar between amenity and ancient woodlands.

Butterfly abundance

Across all sites, a total of 1,111 individuals from 16 butterfly species were detected (Table 2). The most abundant species were *Pararge aegeria* (409 individuals), *Aphantopus hyperantus* (210 individuals) and *Pieris brassicae* (111 individuals). The largest most structurally complex site contained every species seen in the study, except *Melanargia galathea*, and had the highest total butterfly abundance. *P. aegeria* and *P. brassicae* were most widespread, occurring at every site, followed by *Maniola jurtina* that occurred at 9 sites. Mean butterfly richness was highest in ancient woodlands (11.8 species per site), followed by amenity (7 species) and roadsides (6 species). The single species that occurred at the amenity sites and not the roadside was *Vanessa atalanta*. Only *Argynnis paphia* occurred exclusively

Table 1 All habitat data summary by woodland type, presented with the range (minimum to maximum), mean, and standard deviation (S.d.). Highest mean values are highlighted in bold

Variable	Amenity			Ancient			Roadside		
	Range	Mean	S.d.	Range	Mean	S.d.	Range	Mean	S.d.
Mean Area (Ha)	5–10	7.3	3.8	2–40	20.1	17.3	0.5–1	0.7	0.2
Canopy Height (m)	9–12	10.6	1.5	10–14	11.5	0.6	7–8	7.5	0.8
Structural Complexity	1–4	2.7	2.1	4–6	4.4	1.6	3–3	3.1	0.3
Canopy Openness	10–15	12.5	3.9	4–13	8.8	3.9	6–16	9.3	6.5
Cover 10 m + (%)	5–27	16.2	15.8	18–46	33.9	11.0	0	0.0	0.0
Cover 5–10 m (%)	17–62	39.5	31.8	30–44	40.2	6.1	40–53	46.0	6.6
Cover 2–5 m (%)	13–30	21.3	11.7	36–72	49.1	14.4	48–80	59.3	17.9
Cover 1–2 m (%)	13–31	22.4	12.3	29–59	40.8	11.5	36–61	48.5	12.5
Ground Cover (%)	50–83	66.8	23.0	56–84	68.7	10.4	70–96	81.8	13.3
Leaf Litter (%)	24–47	35.7	16.2	18–69	39.0	19.5	31–48	41.3	8.8
Woodchip (%)	4–5	4.7	0.9	0–6	2.3	2.8	0–75	36.7	37.5
Bare Ground (%)	13–32	22.4	13.8	3–40	25.8	17.3	4–20	11.3	8.1
No. sites		2			5			3	

Table 2 Butterfly species occurrence (number of sites each species was recorded) and abundance across all 10 sites

Species	No. sites	Abundance
Speckled Wood (<i>Pararge aegeria</i>)	10	409
Large White (<i>Pieris brassicae</i>)	10	111
Meadow Brown (<i>Maniola jurtina</i>)	9	67
Gatekeeper (<i>Pyronia tithonus</i>)	8	83
Green-Veined White (<i>Pieris napi</i>)	8	33
Ringlet (<i>Aphantopus hyperantus</i>)	7	210
Peacock (<i>Aglais io</i>)	7	19
Small White (<i>Pieris rapae</i>)	6	14
Red Admiral (<i>Vanessa atalanta</i>)	5	13
Comma (<i>Polygonia c-album</i>)	4	27
Silver-washed Fritillary (<i>Argynnis paphia</i>)	3	60
Large Skipper (<i>Ochlodes sylvanus</i>)	3	26
Brimstone (<i>Gonepteryx rhamni</i>)	3	10
Common Blue (<i>Polyommatus icarus</i>)	3	9
Holly Blue (<i>Celastrina argiolus</i>)	3	7
Marbled White (<i>Melanargia galathea</i>)	2	13

at ancient woodland sites, of which were the three largest patches.

Associations with woodland type

At the site scale, ancient woodland sites had the highest species richness and abundance, but amenity woodlands had a higher Simpson's index value (Table 3). Amenity woodlands had higher species richness (7 versus 6 species per site) and Simpson's index (0.69 vs. 0.62) at the site level than the roadside sites. At the transect scale, ancient woodland had

the highest values for all three metrics. Species richness was similar between amenity and roadside sites (2.60 species transect⁻¹ vs. 2.27 species transect⁻¹ respectively) at this scale, but Simpson's index was notably higher at the amenity sites (0.47 vs. 0.36). Using type as a factor, an ANOVA test on six different linear regression models for the butterfly data (3 for each scale) show that there is no correlation between woodland type and species richness ($F = 4.36$, $p = 0.059$), abundance ($F = 2.76$, $p = 0.13$) or Simpson diversity ($F = 1.19$, $p = 0.35$) on the site scale. On the transect scale, woodland type positively correlates with richness ($F = 7.81$, $p = 0.003$) and abundance ($F = 6.52$, $p = 0.007$) but not Simpson diversity ($F = 0.80$, $p = 0.46$).

Site level butterfly analysis

The exploratory data analysis using significant Pearson correlations resulted in terms used for site-level models for butterfly richness, abundance and Simpson diversity including log site area, canopy height and structural complexity as independent variables (Table 4). Type was included in building these models, but the VIF exceeded the threshold for richness (8.1), abundance (2.5) and diversity (9.6) so these terms, along with other variables which exceeded this level, were removed from the model.

The richness and abundance models showed very good fit with high R^2 values, but not the model for Simpson diversity. Structural complexity and log site area showed significant positive associations with richness but not abundance.

Table 3 Summaries of diversity, abundance and Simpson's diversity index by woodland type at site and transect scale. Highest mean values per metric are in bold. Bracketed values represent the range (minimum – maximum)

Type	Site level			Transect level		
	Richness	Abundance	Simpson	Richness	Abundance	Simpson
Amenity	7 (6–8)	59 (57–61)	0.72 (0.65–0.78)	3 (3–3)	5 (6–4)	0.47 (0.46–0.47)
Ancient	12 (6–15)	177 (25–349)	0.70 (0.60–0.85)	5 (3–7)	13 (13–18)	0.60 (0.50–0.72)
Roadside	6 (5–8)	26 (16–38)	0.59 (0.51–72)	3 (2–3)	5 (8–3)	0.36 (0.29–0.42)

Table 4 Multiple regression model outputs of the relationship between butterfly species richness, Simpson diversity and abundance and habitat variables at site level. Confidence interval (CI) is presented in brackets underneath each estimate

Variable	Richness (Site)		Abundance (Site)		Simpson (Site)	
	Estimates	<i>p</i>	Estimates	<i>p</i>	Estimates	<i>p</i>
(Intercept)	9 (7.90–10.10)	< 0.001	108.5 (64.1–152)	< 0.001	0.68 (0.59–0.76)	< 0.001
Structural Complexity	1.73 (0.45–3.01)	0.01			0.07 (-0.02–0.17)	0.10
Log area	3.35 (1.8–4.8)	0.001	95.3 (48.5–142)	0.002	-0.04 (-0.14–0.07)	0.42
Canopy Height	-1.43 (-2.9–0.07)	0.06				
Canopy Openness					0.03 (-0.06–0.13)	0.38
Ground cover					-0.04 (-0.13–0.06)	0.38
Sites	10		10		10	
R^2 / Adj. R^2	0.90 / 0.85		0.73 / 0.70		0.50 / 0.01	

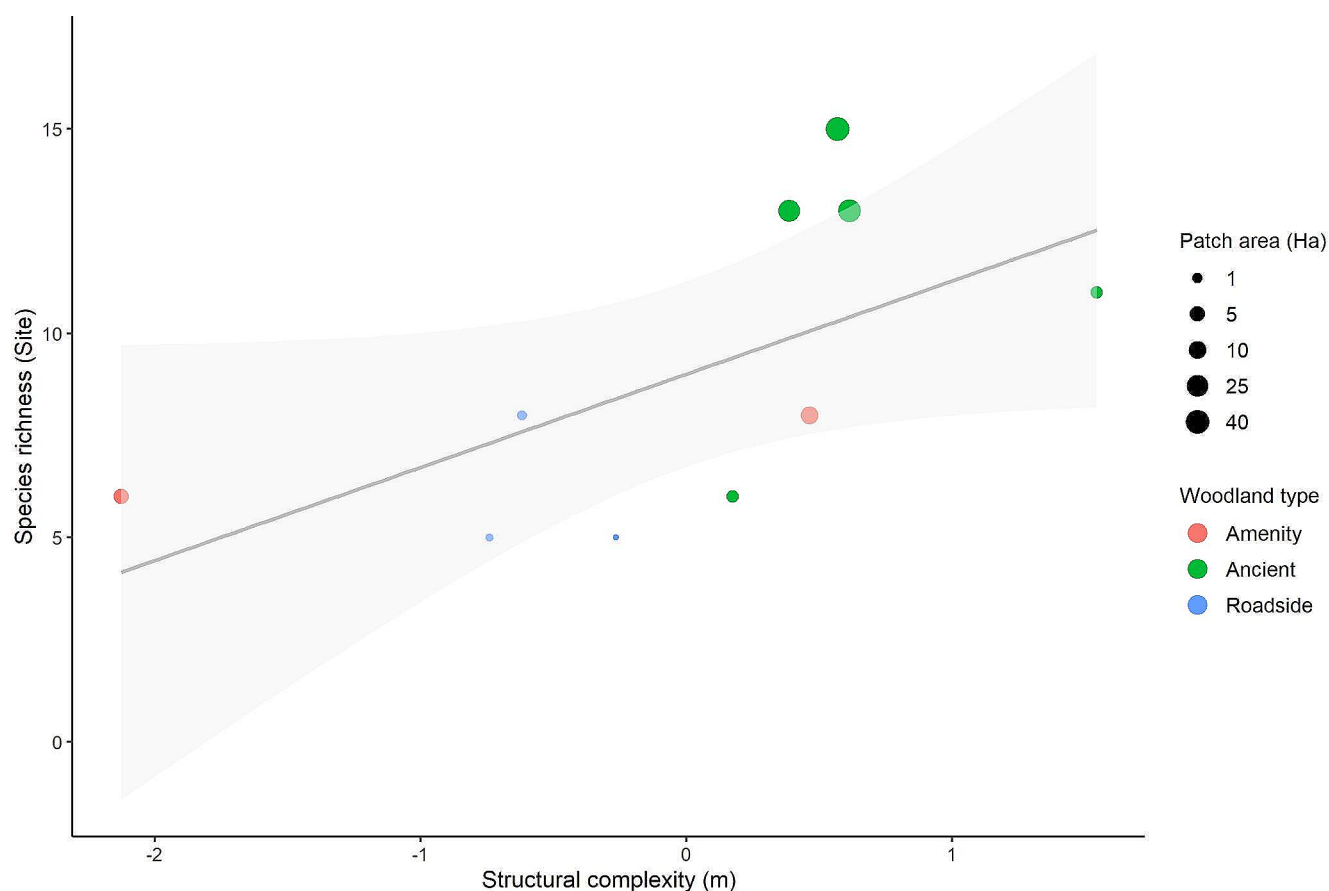


Fig. 1 Butterfly richness plotted against structural complexity at the site level, with the grey shading showing the confidence interval (95%). Transect level butterfly analysis

Table 5 – Mixed effect model outputs of the relationship between butterfly species richness, Simpson diversity and abundance and habitat variables at transect level, with site as a random effect. Confidence interval (CI) is presented in brackets underneath each estimate

Variable	Richness (Transect)		Abundance (Transect)		Simpson (Transect)	
	Estimates	<i>p</i>	Estimates	<i>p</i>	Estimates	<i>p</i>
(Intercept)	8.3 (7.0–9.5)	< 0.001	51.7 (35.3–68.1)	< 0.001	0.68 (0.63–0.74)	< 0.001
Structural Complexity	1.41 (0.09–2.7)	0.04			0.06 (0.01–0.12)	0.03
Log Area	1.26 (-0.18–2.6)	0.08	14.3 (-1.2–29.9)	0.07	-0.03 (-0.09–0.04)	0.40
Canopy Cover (1–2 m) (%)	-0.09 (-1.50–1.3)	0.9			-0.07 (-0.13 – -0.01)	0.03
Random Effects						
σ^2	5.8		700.8		0.01	
τ_{00}	0.36 _{site}		204.20 _{site}		0.00 _{site}	
ICC	0.06		0.23		0.11	
N	10 _{site}		10 _{site}		10 _{site}	
Transects	21		21		21	
R ² / Adj. R ²	0.46 / 0.42		0.37 / 0.10		0.40 / 0.32	

Log site area showed a positive correlation with abundance. No terms were significant in the Simpson diversity model.

Figure 1 shows the relationship between species richness and structural complexity at the site scale, with types and patch sizes included.

Transect level models were fitted with mixed effects, with site as a random effect to account for spatial

non-independence (Table 5). Type was included in building these models, but there was no significant fit, and the VIF exceeded the threshold for richness (8.2), abundance (5.4) and diversity (6.3) so these terms, along with other variables which exceeded the threshold, were removed from the model.

Structural complexity showed significant positive correlations with species richness and Simpson diversity but not abundance which has no significant terms. Log site area showed no correlation with richness, diversity, or abundance at the transect scale. Canopy Cover (1–2 m) (%) showed a negative correlation with Simpson diversity ($p=0.03$). Figure 2 shows the relationship between species richness and structural complexity at the transect scale.

Discussion

Woodland biodiversity is affected by many factors including age, size, structure and connectivity. Urban settings contain a mix of woodland formations that can support a range of diverse insect assemblages, and this study shows that urban woodlands can have significant value as habitat for butterflies. We found 16 butterfly species on our transects across the ten sites in our study. Since the survey method we deployed tends to miss canopy-dwelling species, it is likely that the actual species richness in these urban woodlands is somewhat higher. Purple Emperor (*Apatura iris*), Black Hairstreak (*Satyrium pruni*), Purple Hairstreak (*Favonius quercus*) and White Admiral (*Limenitis camilla*) have been

recorded in previous surveys of these sites by landowner the Parks Trust (The Parks Trust 2014, 2015, 2017b) and as part of ongoing biodiversity monitoring (The Parks Trust 2017a).

Across all our sites, ancient woodlands supported the highest richness and abundance of butterflies. Ancient woodlands have several characteristics that distinguish them from the other woodland types, such as more diverse and often unique and dispersal-limited ground flora (Ellis 2015), tree species richness, unique soil properties and longevity (Erenler et al. 2010; Alder et al. 2023). They are considered priority habitats for conservation of nature in the UK (Thomas et al. 1997) and receive additional protection in the planning system (UK Government 2021a).

Although the special characteristics of ancient woodlands undoubtedly underpin their species richness, this study demonstrates that patch area and structural complexity explain a substantial proportion of the variation in species richness, abundance and diversity across urban woodlands, independent of woodland type. This is best exemplified by the contrast between the two smallest ancient woodland sites, both of which are around 2 ha in area (Fig. 1). The less structurally diverse of these two had fewer species than three of the non-ancient woodlands. Conversely, the more structurally

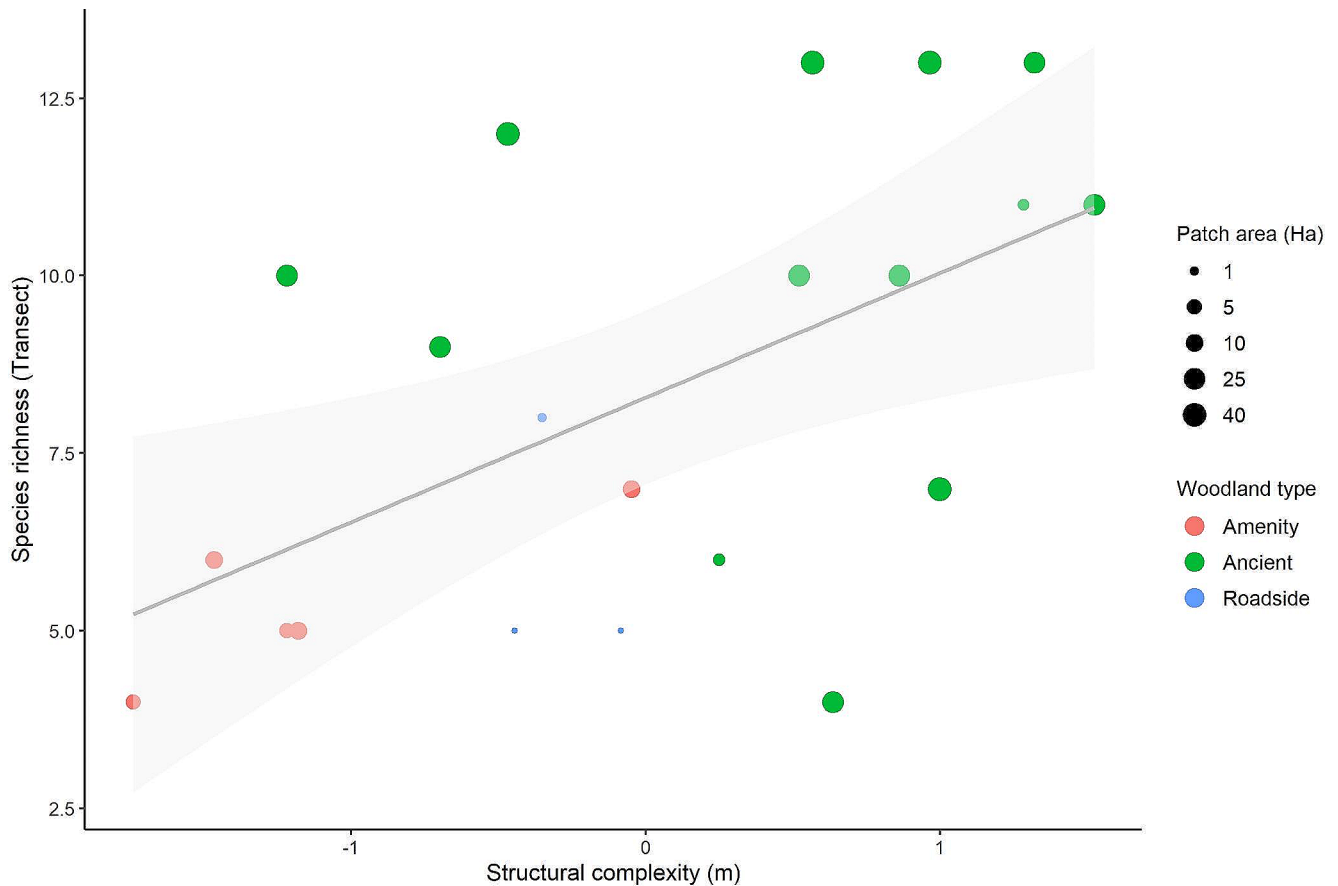


Fig. 2 - Butterfly richness plotted against structural complexity at the site level, with the grey shading showing the confidence interval (95%)

diverse of these two sites was more species rich than all but the three larger ancient woodlands. Our models could not be fitted with type as term that resulted in a significant correlation with the butterfly data that stayed within the VIF threshold.

At site scale, both structural complexity and site area were positively correlated with species richness, with area having the greatest effect overall. Simpson diversity showed no correlation with any variable at this scale, and abundance was strongly correlated with area only. At the transect scale, site area had no statistically significant correlation with butterfly species richness, abundance or diversity. Instead, structural complexity was the largest contributing factor to species richness and Simpson diversity, but not abundance. This suggests that more species rich and diverse transects are ones with a greater degree of structural complexity. Percentage ground cover also had a significant negative correlation with Simpson Diversity. The reasons for these patterns most likely relate to the size and management of these woodlands. As including type in the models at either scale causes a VIF to exceed the threshold or no significant correlation, this suggests these terms are capturing some of what is being summarised by the habitat type designation of ancient, as the ancient woodland type strongly correlates with structural complexity.

Species-area relationships are very widely reported across ecosystems, including woodlands (Shirley and Smith 2005; Beninde et al. 2015; Haddad et al. 2015; Rabelo et al. 2017; MacDonald et al. 2021). There are several potential reasons for this including greater habitat heterogeneity in large sites, lower extinction rates and higher colonisation rates (Franzén and Nilsson 2010; Fernández-Chacón et al. 2014). The fact that the area-richness relationship breaks down at transect level indicates that, in our study system, higher richness in large sites is because of greater heterogeneity within sites: large sites do not consistently have more species per transect than smaller ones. Instead, our results show that structural complexity is a key factor determining species richness and diversity in our urban woodlands.

Previous authors have identified stronger links between insect species richness and habitat complexity than habitat area (Thomas et al. 2001; Helden and Leather 2004), and the general importance of habitat heterogeneity for species richness (Báldi 2008; Kallimanis et al. 2008; Shen et al. 2009) including in urban areas (Beninde et al. 2015). Structural complexity is important as woodland butterfly species are adapted to a natural cycle of open canopy which closes over time (Merckx et al. 2012; Fartmann et al. 2013). Complexity may be a proxy for the combined effects of other variables that we were unable to measure in this study, such as floristic diversity, which accompanies this cycle. Ancient woodlands are typically associated unique Ancient Woodland Indicator

(AWI) species that are often dispersal limited (Panter and Dolman 2012). While varied, most butterflies in this study are not dispersal limited or woodland habitat specialists that do not rely on any larval foodplant uniquely associated with ancient woodlands. Similarly, they have also managed to pass the potentially challenging ecological filter that is the urban landscape itself (Wood and Pullin 2002) and therefore may not rely on the specific and unique features of an ancient woodland provides. This suggests that typical amenity woodlands in urban areas could be managed to improve their quality as butterfly habitat. Historical management in UK ancient woodlands involves coppicing (cutting at or near ground level) of species with the capacity for regeneration from the base of the stem. This practice mimics the natural cycle of canopy openness (Van Calster et al. 2008) and introduces canopy complexity but has declined since the 20th century, negatively impacting biodiversity (Kirby et al. 2017b) as unmanaged woodlands become more structurally homogeneous and lose their patchwork of successional states and therefore botanical diversity.

Management of urban woodlands

Our results indicate that effective management of urban woodland for butterflies should aim to introduce a diverse mosaic of structure. Neglecting commonplace traditional woodland management techniques and allowing woodlands to grow unmanaged can lead to a poor realisation of the potential value they hold for butterflies and other insects (Herrault et al. 2016). Thomas et al., (2001) called for a reprioritisation of habitat management for butterflies with a focus on habitat quality previously, and this study concurs. Using traditional coppicing techniques on urban woodlands, perhaps using ancient woodland management plans as a template, will positively impact butterfly populations as well as other species common in urban areas (Carr et al. 2020; Vymazalová et al. 2021). Rotational coppice management was evident at our ancient woodland sites, but not in the other sites we studied. The roadside sites were too young, small or species poor to allow for such management, and this may be a fundamental constraint on managing some urban woodlands for butterfly diversity. Underplanting with additional species (Moffatt et al. 2008) could accelerate this process, but establishing diverse and abundant woodland butterfly communities in urban woodlands will ultimately require space, resources and time: things which are currently in short supply.

Further research is required to determine how and whether the numerous small urban woodlands of different qualities that are found across urban landscapes operate as a network that supports functioning butterfly populations.

Conclusion

With woodlands becoming ever more fragmented, and the unique pressures faced by urban woodlands, a focus on how to best utilize the fragments we are left with is a key area of continued research. We find that urban woodlands hold significant value for butterflies, and even on a small scale can provide suitable habitat for a variety of species. Similarly, our results identify that, while patch area is important, structural complexity is a driver of species richness, with age undoubtedly underpinning the species richness as well. This is a key finding for urban settings where opportunities for expansion of individual sites may be limited, but establishing new sites and improving existing ones is possible. A lack of management leading to a homogenous canopy structure wastes the potentially high biodiversity value of an urban woodland. Incorporating traditional woodland management techniques should be considered as part of biodiversity management where the conditions allow.

Acknowledgements 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. The authors would like to thank Martin Kincaid and The Parks Trusts biodiversity officers Lewis Dickinson and Carla Boswell for being supportive and cooperative in allowing access to the land and discussing characteristics of the sites. Special thanks to Kate Hand for advice with checking the integrity of the models, James Neal for help supporting data collection, and Dr Blanca Huertas for proofreading the final manuscript.

Author contributions W.N. co-designed the study, collected and analysed the data, wrote the main manuscript text, prepared figures and tables. P.W. co-designed the study, assisted with data collection and analysis and contributed text to the manuscript. Y.A. reviewed earlier versions of the manuscript and contributed comments on structure, content and presentation.

Declarations

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Alder DC et al (2023) 'Irregular silviculture and stand structural effects on the plant community in an ancient semi-natural woodland', *Forest Ecology and Management*, 527, p. 120622. <https://doi.org/10.1016/J.FORECO.2022.120622>
- Allan E et al (2015) 'Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition', *Ecology Letters*, 18(8), pp. 834–843. <https://doi.org/10.1111/ele.12469>
- Angelstam P et al (2004) 'Habitat modeling as a tool for landscape-scale conservation - a review of parameters for focal forest birds', (May 2014). <https://doi.org/10.2307/20113327>
- Aronson MFJ 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). <https://doi.org/10.1098/RSPB.2013.3330>
- Ashworth J (2021) *Analysis warns global biodiversity is below 'safe limit' ahead of COP 15*. <https://www.nhm.ac.uk/discover/news/2021/october/analysis-warns-global-biodiversity-is-below-safe-limit.html> (Accessed: 25 October 2021)
- Báldi A (2008) 'Habitat heterogeneity overrides the species–area relationship', *Journal of Biogeography*, 35(4), pp. 675–681. <https://doi.org/10.1111/J.1365-2699.2007.01825.X>
- Baldock KCR et al (2019) 'A systems approach reveals urban pollinator hotspots and conservation opportunities', *Nature Ecology and Evolution*, 3(3), pp. 363–373. <https://doi.org/10.1038/s41559-018-0769-y>
- Bateman IJ et al (2013) 'Bringing ecosystem services into economic decision-making: Land use in the United Kingdom', *Science*, 341(6141), pp. 45–50. <https://doi.org/10.1126/SCIENCE.1234379>
- Bates D et al (2015) 'Fitting Linear Mixed-Effects Models Using lme4', *Journal of Statistical Software*, 67(1), pp. 1–48. <https://doi.org/10.18637/JSS.V067.I01>
- Belsley Da, Kuh E, Welsch RE (1980) *Identifying influential data and sources of collinearity*. New York: John Wiley & Sons. <https://doi.org/10.1002/0471725153>
- Beninde J, Veith M, Hochkirch A (2015) 'Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation', *Ecology Letters*, 18(6), pp. 581–592. <https://doi.org/10.1111/ele.12427>
- Bergerot B et al (2011) 'Landscape variables impact the structure and composition of butterfly assemblages along an urbanization gradient', *Landscape Ecol*, 26(1), pp. 83–94. <https://doi.org/10.1007/s10980-010-9537-3>
- Bergerot B et al (2012) 'Habitat fragmentation impacts mobility in a common and widespread woodland butterfly: do sexes respond differently?', *BMC Ecology*, 12(1), pp. 1–11. <https://doi.org/10.1186/1472-6785-12-5/FIGURES/5>
- Betts MG et al (2017) 'Global forest loss disproportionately erodes biodiversity in intact landscapes', *Nature*, 547(7664), pp. 441–444. <https://doi.org/10.1038/nature23285>
- Blair R (1999) 'Birds and Butterflies along an Urban Gradient: Surrogate Taxa for Assessing Biodiversity?', *Ecological Applications*, 9(1), p. 164. <https://doi.org/10.2307/2641176>
- Brown N et al (2000) 'An improved method for the rapid assessment of forest understorey light environments', *Journal of Applied Ecology*, 37(6), pp. 1044–1053. <https://doi.org/10.1046/J.1365-2664.2000.00573.X>
- Carr A, Weatherall A, Jones G (2020) 'The effects of thinning management on bats and their insect prey in temperate broadleaved woodland', *Forest Ecology and Management*, 457, p. 117682. <https://doi.org/10.1016/J.FORECO.2019.117682>

- Clarke S et al (2011) *Woodland management for butterflies and moths: a best practice guide* Butterfly Conservation. <https://butterfly-conservation.org/our-work/downloads-resources-reports/woodland-management-for-butterflies-and-moths> (Accessed: 21 June 2023)
- de Andrade AC, Medeiros W, Adams M (2019) 'Urban forest fragments as unexpected sanctuaries for the rare endemic ghost butterfly from the Atlantic forest', *Ecology and Evolution*, 9(18), pp. 10767–10776. <https://doi.org/10.1002/ECE3.5596>
- Dennis EB et al (2017) Urban indicators for UK butterflies. *Ecol Ind* 76:184–193. <https://doi.org/10.1016/J.ECOLIND.2017.01.009>. Available at:
- Ellis C.J. (2015) Ancient woodland indicators signal the climate change risk for dispersal-limited species. *Ecol Ind* 53:106–114. <https://doi.org/10.1016/J.ECOLIND.2015.01.028>. Available at:
- Environment Agency (2023) *The state of the environment: the urban environment - GOV.UK*. <https://www.gov.uk/government/publications/state-of-the-environment/the-state-of-the-environment-the-urban-environment> (Accessed: 30 May 2023)
- Erenler HE et al (2010) 'Factors determining species richness of soil seed banks in lowland ancient woodlands', *Biodiversity and Conservation*, 19(6), pp. 1631–1648. <https://doi.org/10.1007/S10531-010-9793-1/TABLES/5>
- Esri (2023) *2D, 3D & 4D GIS Mapping Software | ArcGIS Pro*. <https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview> (Accessed: 17 July 2023)
- Fartmann T, Müller C, Poniatowski D (2013) 'Effects of coppicing on butterfly communities of woodlands', *BIOLOGICAL CONSERVATION*, 159, pp. 396–404. <https://doi.org/10.1016/j.biocon.2012.11.024>
- Fernández-Chacón A et al (2014) 'Determinants of extinction-colonization dynamics in Mediterranean butterflies: the role of landscape, climate and local habitat features', *Journal of Animal Ecology*, 83(1), pp. 276–285. <https://doi.org/10.1111/1365-2656.12118>
- Fox R et al (2023) *The State of the UK's Butterflies*. [https://butterfly-conservation.org/sites/default/files/2023-01/State of UK Butterflies 2022 Report.pdf](https://butterfly-conservation.org/sites/default/files/2023-01/State%20of%20UK%20Butterflies%202022%20Report.pdf) (Accessed: 16 May 2023)
- Franzén M, Nilsson SG (2010) 'Both population size and patch quality affect local extinctions and colonizations', *Proceedings of the Royal Society B: Biological Sciences*, 277(1678), p. 79. <https://doi.org/10.1098/RSPB.2009.1584>
- Fuller RA et al (2007) 'Psychological benefits of greenspace increase with biodiversity', *Biology Letters*, 3(4), pp. 390–394. <https://doi.org/10.1098/RSBL.2007.0149>
- Gao T et al (2014) 'The role of forest stand structure as biodiversity indicator', *Forest Ecology and Management*, 330, pp. 82–93. <https://doi.org/10.1016/J.FORECO.2014.07.007>
- Haaland C, van den Bosch CK (2015) 'Challenges and strategies for urban green-space planning in cities undergoing densification: A review', *Urban Forestry and Urban Greening*, 14(4), pp. 760–771. <https://doi.org/10.1016/J.UFUG.2015.07.009>
- Haddad NM et al (2015) 'Habitat fragmentation and its lasting impact on Earth's ecosystems', *Science Advances*, 1(2), pp. 1–10. <https://doi.org/10.1126/sciadv.1500052>
- Hair JF 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. <https://doi.org/10.1108/EBR-11-2018-0203>
- Hanski I et al (2012) 'Environmental biodiversity, human microbiota, and allergy are interrelated', *Proceedings of the National Academy of Sciences of the United States of America*, 109(21), pp. 8334–8339. <https://doi.org/10.1073/PNAS.1205624109/-/DCSUPPLEMENTAL/SAPP.PDF>
- Hardy PB, Dennis RLH (1999) 'The impact of urban development on butterflies within a city region', *Biodiversity and Conservation*, 8(9), pp. 1261–1279. <https://doi.org/10.1023/A:1008984905413/METRICS>
- Hargitai R et al (2016) 'Effects of breeding habitat (woodland versus urban) and metal pollution on the egg characteristics of great tits (*Parus major*)', *Science of the Total Environment*, 544, pp. 31–38. <https://doi.org/10.1016/j.scitotenv.2015.11.116>
- Hayhow D et al (2019) *The State of Nature 2019*. Nottingham. <https://nbn.org.uk/wp-content/uploads/2019/09/State-of-Nature-2019-UK-full-report.pdf> (Accessed: 24 May 2023)
- Helden AJ, Leather SR (2004) 'Biodiversity on urban roundabouts-Hemiptera, management and the species-area relationship', *Basic and Applied Ecology*, 5(4), pp. 367–377. <https://doi.org/10.1016/j.baaec.2004.06.004>
- Herrault PA et al (2016) 'Combined effects of area, connectivity, history and structural heterogeneity of woodlands on the species richness of hoverflies (Diptera: Syrphidae)', *Landscape Ecology*, 31(4), pp. 877–893. <https://doi.org/10.1007/S10980-015-0304-3/FIGURES/6>
- Hough RL (2014) 'Biodiversity and human health: Evidence for causality?', *Biodiversity and Conservation*, 23(2), pp. 267–288. <https://doi.org/10.1007/S10531-013-0614-1/METRICS>
- Jim CY (2011) 'Holistic research agenda for sustainable management and conservation of urban woodlands', *Landscape and Urban Planning*, 100, pp. 375–379. <https://doi.org/10.1016/j.landurbplan.2011.01.006>
- Kallimanis AS et al (2008) 'How does habitat diversity affect the species-area relationship?', *Global Ecology and Biogeography*, 17(4), pp. 532–538. <https://doi.org/10.1111/J.1466-8238.2008.00393.X>
- Kirby KJ, Buckley GP, Mills J (2017a) 'Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland', *Folia Geobotanica*, 52(1), pp. 5–13. <https://doi.org/10.1007/S12224-016-9252-1/TABLES/1>
- Kirby KJ, Buckley GP, Mills J (2017b) 'Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland', *Folia Geobotanica*, 52(1), pp. 5–13. <https://doi.org/10.1007/S12224-016-9252-1/TABLES/1>
- Lawton JH (1999) 'Are There General Laws in Ecology?', *Oikos*, 84(2), p. 177. <https://doi.org/10.2307/3546712>
- Lee ACK, Maheswaran R (2011) 'The health benefits of urban green spaces: a review of the evidence', *Journal of Public Health*, 33(2), pp. 212–222. <https://doi.org/10.1093/PUBMED/FDQ068>
- Livesley SJ, Mcpherson EG, Calfapietra C (2016) 'The Urban Forest and Ecosystem Services: Impacts on Urban Water, Heat, and Pollution Cycles at the Tree, Street, and City Scale'. <https://doi.org/10.2134/jeq2015.11.0567>
- Lüdecke D et al (2021) 'performance: An R Package for Assessment, Comparison and Testing of Statistical Models', *Journal of Open Source Software*, 6(60), p. 3139. <https://doi.org/10.21105/JOSS.03139>
- MacDonald ZG et al (2021) 'Distinguishing effects of area per se and isolation from the sample-area effect for true islands and habitat fragments', *Ecography*, 44(7), pp. 1051–1066. <https://doi.org/10.1111/ecog.05563>
- Maes D, Van Dyck H (2001) 'Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario?', *Biological Conservation*, 99(3), pp. 263–276. [https://doi.org/10.1016/S0006-3207\(00\)00182-8](https://doi.org/10.1016/S0006-3207(00)00182-8)
- Merckx T et al (2012) 'Conserving threatened Lepidoptera: Towards an effective woodland management policy in landscapes under intense human land-use', *Biological Conservation*, 149(1), pp. 32–39. <https://doi.org/10.1016/J.BIOCON.2012.02.005>
- Milton Keynes Council (2016) 'Milton Keynes Landscape Character Assessment Milton Keynes Landscape Character Assessment'. Available at: www.gillespies.co.uk (Accessed: 21 December 2023)
- Moffatt C, Morton AJ, McNeill S (2008) 'Has Botanical Enhancement of Broad-Leaved Plantations in Milton Keynes, United Kingdom, Resulted in More Woodland-Like Insect

- Assemblages?', *Restoration Ecology*, 16(1), pp. 50–58. <https://doi.org/10.1111/J.1526-100X.2007.00261.X>
- Montgomery GA et al (2020) 'Is the insect apocalypse upon us? How to find out', *Biological Conservation*, 241(October 2019). <https://doi.org/10.1016/j.biocon.2019.108327>
- Natural England (2023) *Ancient Woodland (England) | Natural England Open Data Geoportal*. https://naturalengland-defra.opendata.arcgis.com/datasets/a14064ca50e242c4a92d020764a6d9df_0/explore (Accessed: 11 May 2023)
- Oksanen J et al (2022) 'vegan: Community Ecology Package' #8217
- 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. <https://doi.org/10.1007/s10980-015-0299-9>
- Panter CJ, Dolman PM (2012) 'Mammalian herbivores as potential seed dispersal vectors in ancient woodland fragments', *Wildlife Biology*, 18(3), pp. 292–303. <https://doi.org/10.2981/11-112>
- Pe'er G, Settele J (2013) 'Butterflies in and for conservation: Trends and Prospects', *Brill*, 54(1), pp. 7–17. <https://doi.org/10.1560/IJEE.54.1.7>
- Piano E et al (2020) 'Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales', *Global Change Biology*, 26(3), pp. 1196–1211. <https://doi.org/10.1111/gcb.14934>
- Pollard E (1977) 'A method for assessing changes in the abundance of butterflies', *Biological Conservation*, 12(2), pp. 115–134. [https://doi.org/10.1016/0006-3207\(77\)90065-9](https://doi.org/10.1016/0006-3207(77)90065-9)
- R Core Team (2022) R: a language and environment for statistical computing. Vienna. R Foundation for Statistical Computing, Austria
- Rabelo RM et al (2017) 'Are fluvial islands real islands for arboreal mammals? Uncovering the effect of patch size under the species–area relationship', *Journal of Biogeography*, 44(8), pp. 1802–1812. <https://doi.org/10.1111/jbi.13034>
- Ramalho CE et al (2014) 'Complex effects of fragmentation on remnant woodland plant communities of a rapidly urbanizing biodiversity hotspot', *Ecology*, 95(9), pp. 2466–2478. <https://doi.org/10.1890/13-1239.1>
- Ramírez-Restrepo L, MacGregor-Fors I (2016) 'Butterflies in the city: a review of urban diurnal Lepidoptera', *Urban Ecosystems* 2016 20:1, 20(1), pp. 171–182. <https://doi.org/10.1007/S11252-016-0579-4>
- Rivkin LR et al (2019) 'A roadmap for urban evolutionary ecology', *Evolutionary Applications*, 12(3), pp. 384–398. <https://doi.org/10.1111/eva.12734>
- Robertson PA, Clarke SA, Warren MS (1995) 'Woodland management and butterfly diversity', *Ecology and Conservation of Butterflies*, pp. 113–122. https://doi.org/10.1007/978-94-011-1282-6_8
- Sánchez-Bayo F, Wyckhuys KAG (2019) 'Worldwide decline of the entomofauna: A review of its drivers', *Biological Conservation*, 232, pp. 8–27. <https://doi.org/10.1016/J.BIOCON.2019.01.020>
- Sandifer PA, Sutton-Grier AE, Ward BP (2015) 'Exploring connections among nature, biodiversity, ecosystem services, and human health and well-being: Opportunities to enhance health and biodiversity conservation', *Ecosystem Services*, 12, pp. 1–15. <https://doi.org/10.1016/J.ECOSER.2014.12.007>
- Schoener TW (1976) 'The species-area relation within archipelagos: Models and evidence from island land birds', *16th International Ornithological Congress*, pp. 629–642. <https://cir.nii.ac.jp/crid/1572543024367922816> (Accessed: 8 January 2024)
- Seto KC, Güneralp B, Hutyra LR (2012) 'Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools', *Proceedings of the National Academy of Sciences of the United States of America*, 109(40), pp. 16083–16088. <https://doi.org/10.1073/pnas.1211658109>
- Shen G et al (2009) 'Species–area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity', *Ecology*, 90(11), pp. 3033–3041. <https://doi.org/10.1890/08-1646.1>
- Shirley SM, Smith JNM (2005) 'Bird community structure across riparian buffer strips of varying width in a coastal temperate forest', *Biological Conservation*, 125(4), pp. 475–489. <https://doi.org/10.1016/j.biocon.2005.04.011>
- Shreeve TG, Mason CF (1980) 'The number of butterfly species in woodlands', *Oecologia*, 45(3), pp. 414–418. <https://doi.org/10.1007/BF00540215/METRICS>
- Slamova I, Klecka J, Konvicka M (2013) 'Woodland and grassland mosaic from a butterfly perspective: habitat use by *Erebia aethiops* (Lepidoptera: Satyridae)', *Insect Conservation and Diversity*, 6(3), pp. 243–254. <https://doi.org/10.1111/J.1752-4598.2012.00212.X>
- Soga M, Koike S (2015) 'Life-history traits affect vulnerability of butterflies to habitat fragmentation in urban remnant forests', <http://dx.doi.org/10.2980/19-1-3455>, 19(1), pp. 11–20. <https://doi.org/10.2980/19-1-3455>
- The Parks Trust (2014) *Linford Wood Management Plan*. www.theparkstrust.com
- The Parks Trust (2017b) 'Shenley Wood Management Plan' #8217
- The Parks Trust (2015) 'Howe Park Wood Management Plan' #8217
- The Parks Trust (2017a) *Biodiversity Action Plan*
- Thomas JA (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. <https://about.jstor.org/terms> (Accessed: 16 November 2021)
- Thomas RC, Kirby KJ, Reid CM (1997) 'The conservation of a fragmented ecosystem within a cultural landscape—The case of ancient woodland in England', *Biological Conservation*, 82(3), pp. 243–252. [https://doi.org/10.1016/S0006-3207\(97\)00039-6](https://doi.org/10.1016/S0006-3207(97)00039-6)
- Thomas JA et al (2001) 'The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes.', *Proceedings of the Royal Society B: Biological Sciences*, 268(1478), p. 1791. <https://doi.org/10.1098/RSPB.2001.1693>
- UK Government (2021a) *National Planning Policy Framework - GOV.UK*. <https://www.gov.uk/government/publications/national-planning-policy-framework--2> (Accessed: 4 September 2023)
- UK Government (2021b) *Trend Deck 2021: Urbanisation - GOV.UK, Government Office for Science*. <https://www.gov.uk/government/publications/trend-deck-2021-urbanisation/trend-deck-2021-urbanisation> (Accessed: 24 May 2023)
- UK Butterfly Monitoring Scheme (2023) (no date) *Guidance & recording forms | UKBMS*. <https://ukbms.org/guidance-recording-forms> (Accessed: 11)
- Vallet J et al (2010) 'The effects of urban or rural landscape context and distance from the edge on native woodland plant communities', *Biodiversity and Conservation*, 19(12), pp. 3375–3392. <https://doi.org/10.1007/S10531-010-9901-2>
- 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. <https://doi.org/10.1016/J.BIOCON.2008.08.001>
- van Halder I et al (2015) 'Woodland habitat quality prevails over fragmentation for shaping butterfly diversity in deciduous forest remnants', *Forest Ecology and Management*, 357, pp. 171–180. <https://doi.org/10.1016/J.FORECO.2015.08.025>
- Vanbeveren SPP, Ceulemans R (2019) 'Biodiversity in short-rotation coppice', *Renewable and Sustainable Energy Reviews*, 111, pp. 34–43. <https://doi.org/10.1016/J.RSER.2019.05.012>
- Villemey A et al (2015) 'Mosaic of grasslands and woodlands is more effective than habitat connectivity to conserve butterflies in French farmland', *Biological Conservation*, 191, pp. 206–215. <https://doi.org/10.1016/J.BIOCON.2015.06.030>

- Vymazalová P et al (2021) 'Positive impact of traditional coppicing restoration on biodiversity of ground-dwelling spiders in a protected lowland forest', *Forest Ecology and Management*, 490, p. 119084. <https://doi.org/10.1016/J.FORECO.2021.119084>
- Wagner DL (2020) 'Insect declines in the anthropocene', *Annual Review of Entomology*, 65, pp. 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>
- Wang Y et al (2019) 'What makes urban greenspace unique – Relationships between citizens' perceptions on unique urban nature, biodiversity and environmental factors', *Urban Forestry & Urban Greening*, 42, pp. 1–9. <https://doi.org/10.1016/J.UFUG.2019.04.005>
- Warren MS, Thomas JA (1992) 'Butterfly responses to coppicing', *Ecology and Management of Coppice Woodlands*, pp. 249–270. https://doi.org/10.1007/978-94-011-2362-4_13
- Wood BC, Pullin AS (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. <https://doi.org/10.1023/A:1016223907962/METRICS>
- Woodland Trust (2023) *Tree Search - Ancient Tree Inventory*. <https://ati.woodlandtrust.org.uk/tree-search/?v=2421620&ml=map&z=12&nwLat=52.09199896318023&nwLng=-1.0004687108993693&seLat=51.982177414699265&seLng=-0.4758715429306193> (Accessed: 21 December 2023)
- Zenner EK (2000) 'Do residual trees increase structural complexity in Pacific Northwest coniferous forests?', *Ecological Applications*, 10(3), pp. 800–810. <https://doi.org/10.1890/1051-0761>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.