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Bat activity decreases as diversity increases in a transition from urban to rural habitats: implications for urbanisation

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Abstract. Bat activity estimated using bat passes along 12 km of a valley bottom in southern England, UK, confirmed the trend of lower species diversity (H′) in urban compared with rural habitats. *Pipistrellus pipistrellus* accounted for 57.48% of passes (n = 3,532), most of which were recorded in the urban part of the valley, confirming the urban fallout driven by dominance of this species. Where the valley bottom transitioned from urban to rural habitats, species diversity (H′) increased. However, overall bat activity decreased, driven by a dramatic decline in the number of passes of *P. pipistrellus* in rural areas. Conversely, activity of *Pipistrellus pygmaeus* and five other bat species/species groups, each of which accounted for less than 25% of passes, was higher in rural areas. This transition was interrupted at a small scale (250 m) by 'hotspots' of high bat activity associated with favourable habitats (e.g. a mill pond) and 'coolspots' (e.g. ground cleared of vegetation prior to housing construction). The results indicate that ongoing building works within the valley would affect the bat assemblage in different ways depending on the surrounding landscape. In rural areas, an increase in the extent of built structures and other hard surfaces could increase overall bat activity but decrease diversity (H′) as scarcer species undergo 'urban fallout'.

Keywords: bat activity, acoustic monitoring, urbanisation, species diversity, urban fallout.

INTRODUCTION

Bats account for one third of all land mammal species in the UK and occupy the full range of urban and rural habitats (Harris and Yalden 2008). As top predators of nocturnal insects, often with exacting roosting, commuting and foraging requirements, bats are especially sensitive to land use and other environmental changes, as reviewed by Jones *et al.* (2009). The pressures they face also affect many other species (Browning *et al.* 2021), which means bats should make robust indicators for the health of the wider environment (Russo *et al.* 2021). In the UK, bat populations are recovering after what are believed to have been major population declines during the 20th century (Harris and Yalden 2008; Barlow *et al.* 2015). The recovery is at least partly due to their legal protection under the UK's Wildlife and Countryside Act 1981 (as amended — UK Parliament 1981) and the Conservation of Habitats and Species Regulations 2017 (as amended — UK Government 2017), hereafter the 'Habitat Regulations'. There are now positive trends for 10 of the 11 species monitored in the UK (DEFRA 2021; Bat Conservation Trust 2025), which are congruent with similar trends in mainland Europe (e.g. van der Meij *et al.* 2015; Toffoli and Calvini 2021, and references therein).

The relative influences of variables determining where different bat species forage, including at the transition between rural and urban habitats, are poorly understood (Browning *et al.* 2021). Most wildlife avoids urban areas because the habitats there are isolated and fragmented, and noise, light, and aerial/water borne pollution levels are high (Hale *et al.* 2012). For bats, physical barriers, artificial light at night (ALAN) (Berthinussen and Altringham 2012; Hale *et al.* 2015; Mathews *et al.* 2015; Stone *et al.* 2015; Haddock *et al.* 2019; Voigt *et al.* 2020; Hooker *et al.* 2022) and traffic noise (Finch *et al.* 2020) in urban areas can be substantial deterrents. In general, in Europe, the number of bat species decreases as natural habitats are replaced by built-up areas; those that tolerate urban habitats tend to be open- and edge-hawking species that can exploit a wide range of roosting sites (Russo and Ancillotto 2015; Jung and Threlfall 2018; Moretto *et al.* 2022*a*). Therefore, as rural areas transition to urban ones, a comparatively low proportion of the regional bat assemblage is likely to be present, because species that are sensitive to disturbance tend to decline or disappear. This 'urban fallout' may allow more synanthropic bat species to increase.

The majority of UK bat species roost and feed in landscapes containing woodland and/or water (Vaughan *et al.* 1997). Their distribution and activity are thus influenced by the relative amounts of urban 'Greyspace' — such as roads, buildings and other hard surfaces, 'Greenspace' — such as fields, hedgerows and woodlands, and 'Bluespace' — such as canals, rivers and lakes (e.g. Lintott *et al.* 2015*a*). Treelines, hedgerows and rivers/canals are important for commuting and foraging bats (Verboom

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and Huitema 1997) but the extent to which bats are able to cross gaps in such linear features and/or forage in the open, can be influenced by light levels. For example, *Pipistrellus* species are relatively tolerant of, but still inhibited by, ALAN (Downs and Racey 2006; Hale *et al*. 2012), whereas *Myotis* and *Rhinolophus* species are much less tolerant, with *R. hipposideros* only foraging in open habitats when moonlight and ALAN levels are extremely low (Downs *et al*. 2016). These patterns mean that, in the UK, *Pipistrellus pipistrellus* is the most frequently encountered bat species in urban and peri-urban landscapes (Lintott *et al*. 2015*a*), whereas *Pipistrellus pygmaeus*, most *Myotis* species, *Plecotus auritus* and *Rhinolophus* species roost, commute and forage in Greenspace-dominated landscapes (Harris and Yalden 2008; Dietz *et al*. 2009). Small changes in habitat management can be important. For example, along hedgerows, bat species richness (also insect family richness and dipteran abundance) can increase with time since the hedgerow was cut (Froidevaux *et al*. 2019).

In this study, the distribution of bats was measured by recording their relative activity using bat detectors along a valley that transitioned from rural to urban habitats. We asked three questions in relation to the urban-to-rural transition: 1) Which bat species/species groups were present and how did richness and diversity vary spatially? 2) How did overall and species-specific bat activity vary spatially? and 3) What habitat variables were associated with spatial variations in bat assemblages? In the urban areas with a high proportion of Greyspace, relatively high activity of *P. pipistrellus* was expected (Lintott *et al*. 2015*a*) resulting in low bat species diversity. Conversely, in rural areas with a high proportion of Greenspace, we expected bat activity to remain high, but the species assemblage to be less dominated by *P. pipistrellus*, resulting in higher species diversity. The linear survey route thus provided an opportunity to identify and quantify habitat and other variables that may help to explain an expected 'urban fallout' of bat species. Based on the observed patterns, we then considered the potential impact of ongoing urbanisation and canal restoration on the bat species assemblage.

MATERIAL AND METHODS

Study site

The Stroud Valleys in the county of Gloucestershire, UK, are characterised by deeply incised valleys cutting through the Jurassic limestone of the Cotswold scarp. The valleys hold most of the major transport networks, settlements and associated industrial development, canals and rivers. Above the valleys and the scarp, the open Cotswold plateau supports grasslands and arable fields interspersed with woodlands and villages. Fifteen of the UK's 17 bat species have been recorded in the county, four of which are listed under Annex II of the Habitat Regulations, and so require special protection: *Barbastella barbastellus*, *Myotis bechsteinii*, *Rhinolophus ferrumequinum* and *R. hipposideros* (https://glosbats.org.uk/bats-in-gloucestershire/). There are notable breeding and hibernation sites of the latter two species within the Stroud Valleys.

The 12 km linear study site ran with minimal elevational change east to south-east from the town of Stroud along the valley bottom (51.7457°N, 2.2178°W) mostly following the towpath of the Thames and Severn Canal (Fig. 1). From Stroud, moving upstream (east), the valley bottom ran through a mosaic of Greyspace (e.g. buildings, roads) and Greenspace (e.g. grasslands and woodlands), to a landscape dominated by Greenspace, much of which was designated as Local Wildlife Sites and/or Sites of Special Scientific Interest (SSSIs). For the westernmost eight km of the linear study site, the canal and the west-flowing River Frome formed a linear feature in which at least one side was dominated by Greyspace. East of the village of Chalford (Fig. 1), where the canal was largely dry/disused and lined with woodland, the valley bottom ran through about 1 km of mostly grassland, followed by 3 km, where the whole valley was wooded.

We chose this valley for bat surveys for two reasons. First, it allowed comparison between the activity of bat species in contiguous urban and rural landscapes. Second, given housing development and proposed canal restoration, it provided a baseline from which to track the impact of an increasing proportion of Greyspace on bat species.

For ease of surveying, the linear study site was divided into four 3 km contiguous transects heading east: 1, 'Stroud', 2, 'Thrupp', 3, 'Chalford' and 4, 'Daneway' (Fig. 1). Each transect was further divided into 12 consecutive 250 m transect sections using QGIS, such that there were 48 transect sections in total (12 sections per transect × 4 transects). The .gpx files were transferred to the mobile application, ViewRanger (Augmenta Ltd., now Outdooractive) for use in the field. The decision to use 250 m transect sections was made to ensure comparability with the spatial scale used to assess bat-habitat interactions in other urban/suburban landscapes (Lintott *et al*. 2015*a*). A distance of 125 m was taken on either side of the linear canal to assess habitat types, making a band 250 m wide in total, and thus each transect section became a 250 m by 250 m square plot.

Habitat mapping and measurement

The habitats were mapped within each 250 m × 250 m transect section, coinciding with the bat calls recorded in that section, using satellite imagery. Five habitat types were recognised according to the Corine Land Cover Classes (Kosztra and Buttner 2019): Greyspace — divided into (1) Hard cover, where > 80% of the land surface is covered by impermeable features like buildings, roads and artificially surfaced areas, and (2) Discontinuous Urban Fabric (DUF) when urban structures are associated with 30–80% vegetated areas such as gardens, (3) Bluespace — Water (water courses and water

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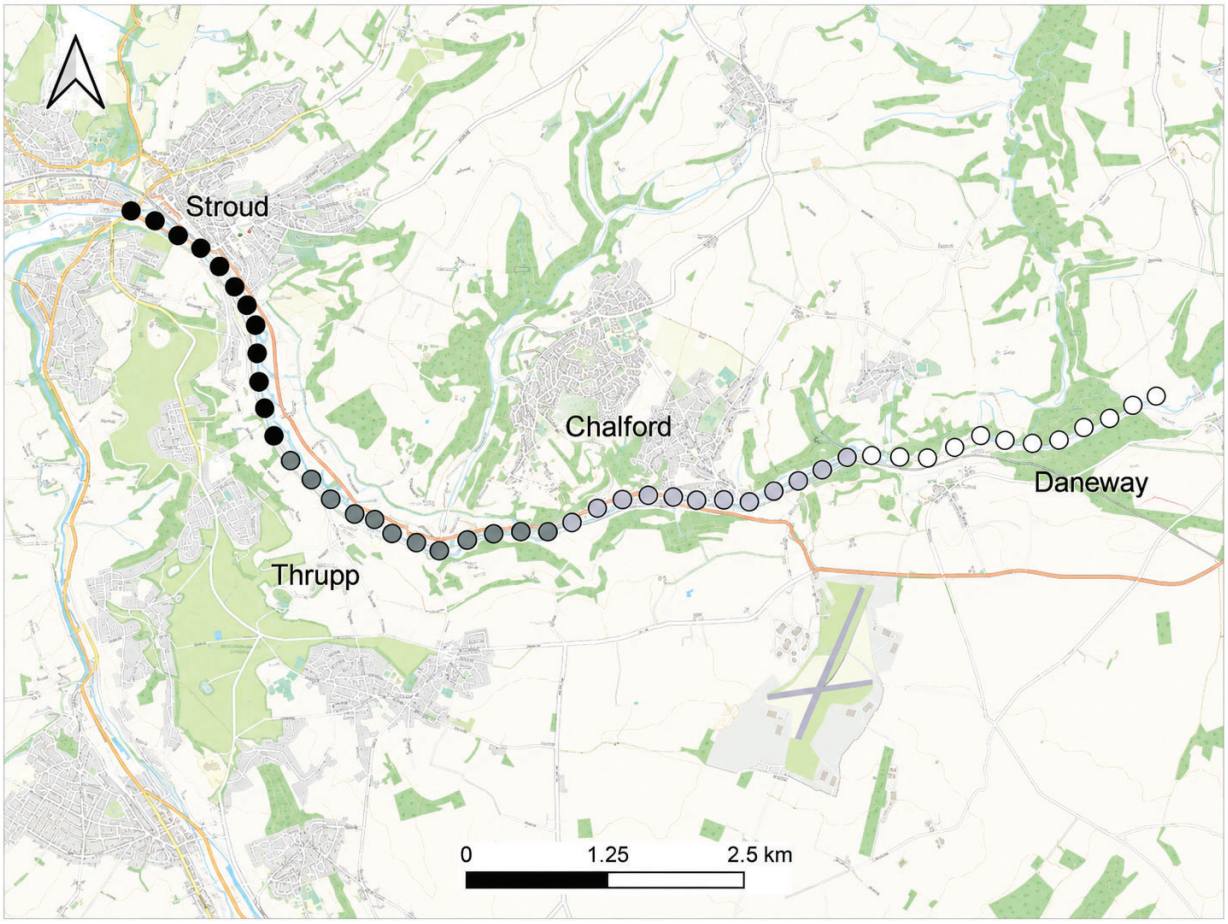

Figure 1. The 12 km survey route from Stroud to Daneway, along the Thames and Severn Canal with 48 × 250 m transect sections shown as coloured dots. Transects: Stroud (sections 1–12, black), Thrupp (transect sections 13–24, dark grey), Chalford (sections 25–36, light grey), Daneway (sections 37–48, white).

bodies), Greenspace, divided into (4) Trees/Scrub, and (5) Grass (Table 1). Habitats present within each 250 m × 250 m square were digitised within the open-source GIS software QGIS (https://qgis.org/en/site/). The area (in square metres) of each habitat type was recorded using QGIS. Data were exported to Excel for further analysis.

Light levels

As an estimate of relative light levels, radiance values, quantified using the Visible Infrared Imaging Radiometer Suite (VIIRS) satellite (https://nightblight.cpre.org.uk/), were assigned to each 250 m transect section.

Bat activity surveys

Bat activity surveys were conducted on foot along the canal towpath in the valley bottom between 25 May and 31 August 2020. These dates covered the periods when female bats were pregnant (up to mid-June), lactating (mid-June to early August), and post-lactating when summer maternity roosts were being vacated and mating behaviour occurred (middle to end of August). Juvenile bats were assumed to be flying from the first week of July.

Surveys commenced 20 minutes after sunset and were walked at c. 2.0 km per hour. Each of the four transects was walked six times (three times east-west and three times west-east) by two people (one surveyor plus a buddy for health and safety and cross-checking calls) across the survey season. As each transect took c. 1.5 h to survey, there were c. 9 h of bat data per transect (and 36 h of bat data overall). Use of six temporal replicates followed Scott and Altringham (2014), who found this was a representative sampling effort for species in UK woodlands; it was double that recommended by Collins (2023) for bat surveys in professional contexts in the UK.

Transects were walked on dry, warm (> 15°C) and calm (Beaufort < 3) evenings. As an index of foraging/commuting activity, bat echolocation pulses were recorded using an Echo Meter Touch 2 PRO (Wildlife Acoustics Inc.) bat detector from which the number of bat passes was quantified. One bat pass sequence was defined as a minimum of three pulses recorded from a single bat. Bat passes lasted up to 15 s, with a minimum interval of 1 s duration between passes.

Bat sound analysis

All sonograms were manually inspected using Kaleidoscope (Wildlife Acoustics Inc. Version 5.3.7) and

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Table 1. Habitat classifications generated in GIS using Corine land cover classes.

General description	Corine land cover classes	Abbreviated form
Greyspace	Continuous Urban Fabric: Hard cover > 80% of the land surface covered by impermeable features e.g. buildings, roads and artificially surfaced areas.	Hard cover
	Discontinuous Urban Fabric (buildings associated with 30–80% vegetated areas)	DUF
Bluespace	Water courses and water bodies (rivers, lakes)	Water
Greenspace	Forest and semi-natural areas (woodland; scrub; transitional woodland/scrub)	Trees/Scrub
	Agricultural areas (improved/amenity grassland, semi-improved grassland)	Grass

assigned using Russ (2012) to the following species: *Rhinolophus ferrumequinum*, *R. hipposideros*, *Pipistrellus pipistrellus*, *P. pygmaeus* and *Barbastella barbastellus*. In addition, we recorded two species groups: the genus *Myotis* (potentially including *M. alcathoe*, *M. bechsteinii*, *M. brandtii*, *M. daubentonii*, *M. mystacinus* and *M. nattereri*), and a combined *Eptesicus*/*Nyctalus* acoustic group, sometimes referred to as 'Nyctaloids' or colloquially as 'Big bat' (Collins 2023) covering three species with peak frequencies < 35 kHz: *Nyctalus noctula*, *N. leisleri* and *Eptesicus serotinus*. These two groups are commonly used within UK bat surveys because the species within each have very similar calls that are often impossible to reliably distinguish acoustically (Russ 2012; Walters *et al.* 2013; Collins 2023), such that this reduced taxonomic resolution is appropriate (Fraser 2018). A third group, 'Small bat', included all unidentified calls with peak frequencies at or above 40 kHz of possible *Plecotus* species and other calls at 40 kHz of *P. pipistrellus* or *P. nathusii*, plus ambiguous calls of *Pipistrellus* species between 49 kHz and 51 kHz. This was a way of assigning all bat calls to a group, but as this informal grouping encompassed species in several genera with potentially varying proportions depending on the sample, it was analysed only to a limited extent and not included in diversity metrics.

Data handling and statistical analysis

The relative frequency of each broad habitat type (Greyspace, Bluespace and Greenspace — defined in Table 1), in each transect was compared using a chi-square test for association.

To test for differences in species richness (number of species recorded; S) and diversity (Shannon–Wiener Index with log n; H') between the four transects, two Kruskal-Wallis tests were used. Data were pooled from each of the six surveys for each transect section within each transect, to give a data frame of 12 rows of data (transect sections) and four columns (four transects), providing the spatial replication required for the analysis. Analysis was done this way – collapsing temporal replicates and maintaining spatial replicates – since, for some of the subsequent analysis, transect sections became the unit of analysis. This meant that framework was consistent throughout, with temporal pooling of data per transect or transect section being done in the same way for all analyses. 'Small bat' was excluded from these analyses as species composition in this group may have varied along the survey route and over time. The Kruskal-Wallis framework was also used to test for differences in the activity of species/species groups based on the number of bat passes recorded. A critical significance value of 0.05 was used throughout.

The total number of bat passes per transect section was used to generate heatmaps using Jenks natural breaks (Foster 2019) by assigning colours of increasing shading intensity within QGIS to increasingly high values of activity. This allowed straightforward visual inspection of hotspots and coolspots of activity for all bats, and for bat species/species groups along the survey route.

Then, to test for differences in the bat assemblage between transects, (dis)Similarity Percentage (SIMPER) and Permutational Multivariable Analysis of Variance (PERMANOVA) analyses were used (Clarke 1993; Anderson 2006). SIMPER provided an intuitive way to assess dissimilarity, both overall and pairwise between transects, using Bray-Curtis scores (Bray and Curtis 1957), as well as quantifying the relative contributions of different species/species groups to observed dissimilarity. The data framework used all bats identified to species/species group level: the non-specific composite 'Small bat' variable was excluded. As per the Kruskal-Wallis tests, temporal data from the six surveys was pooled and data were arranged as transect sections (n = 12) within each transect (n = 4), such that the analysis took place at transect level with the transect sections essentially being the replicates needed for the test to be calculated (i.e., 12 values were entered per transect corresponding to each successive transect section as it was not possible for analysis to be conducted on a single value per transect). SIMPER was followed by PERMANOVA, again based on Bray-Curtis and using 9,999 permutations, to compare the metric centroid summarising the bat assemblage of each of the four transects to test for significance. Pairwise post-hoc tests were calculated between transect pairs; these were Bonferroni corrected to avoid family-wise error. SIMPER and PERMANOVA was calculated within R using the 'vegdist' package to create a distance matrix followed by 'simper' and 'adonis2' functions, respectively, all within the vegan package (Oksanen *et al.* 2007).

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To better understand causal mechanisms of the patterns observed, Nonmetric Multi-Dimensional Scaling (NMDS) was used. This allowed creation of a biplot based on two ordination axes summarising the bat assemblage. This was done for the 48 transect sections (48 datapoints) as habitat and light data were collected at that spatial scale. This meant that relationships between bats and habitat and abiotic variables could be considered in more detail, and at a finer spatial scale, than in the previous transect-level analysis. In addition to the five digitised habitat variables: Hard cover and Discontinuous Urban Fabric, DUF (previously combined into Greyspace), Water courses and water bodies (Bluespace), and Tree/scrub and Grass (previously combined into Greenspace), Light (in nanowatts, nW) was added as an abiotic factor. The six variables became environmental vectors in the NMDS analysis, all entered at transect section level, with angle and relative lengths of the Vector lines indicating the direction and strength each variable exerted on the bat assemblage. The 48 transect section-specific datapoints representing the bat data were shaded in relation to their respective transect ($n = 4$) to allow patterns to be visualised more clearly. Too few calls of *Rhinolophus* species and *Barbastella* were recorded for these taxa to be meaningfully analysed and they were thus excluded from the NMDS analysis, as was the non-specific composite of 'Small bat'. The NMDS analysis was performed in R using the function 'metaMDS' in the package vegan (Oksanen *et al.* 2007). Bray-Curtis was used as the ordination metric for consistency with the SIMPER and PERMANOVA approaches.

Data repository

The data and R code used for analysis are available from the University of Gloucestershire research repository via https://eprints.glos.ac.uk/15014/.

RESULTS

Habitat composition and light levels along the urban–rural gradient

There was a substantial and statistically significant difference in habitat composition between the four transects ($\chi^2 = 413{,}474$, $d.f. = 6$, $p < 0.001$; Fig. 2) driven by the proportion of Greyspace decreasing from transect 1–4 from c. 50% to < 5%, and Greenspace increasing from c. 45% to > 90%. Bluespace cover was low throughout (< 5%) but was highest in transect 1 and approximately equal for the remaining three transects. Along the survey route, ALAN, indexed by radiance values, ranged from 16 nW cm^{-2} sr^{-1} in the westernmost urban-dominated areas to < 0.5 nW cm^{-2} sr^{-1} in the easternmost rural areas.

Which bat species/species groups were present and how did richness and diversity vary spatially?

Of a total of 3,748 bat passes, 3,532 could be assigned to species/species groups. *Pipistrellus pipistrellus* was the most commonly recorded species (57.48% of assigned passes). Passes of all other species/species groups were much less frequent: 'Big bat' accounted for 20.78%, *P. pygmaeus* for 11.41%, *Myotis* species for 9.88%, *R. hipposideros* for 0.26%, *Barbastella* for 0.14% and *R. ferrumequinum* for 0.06%. The remaining 216 bat passes (5.76%) were classed as 'Small bat'. There were no indisputable records of *Plecotus* species, probably because their echolocation calls are so quiet (Russ 2012). In a random sample of five of the transect/dates in which 895 passes were assessed independently, only five (0.56%) were provisionally identified as *Plecotus* species (N. Smykatz-Kloss, personal communication).

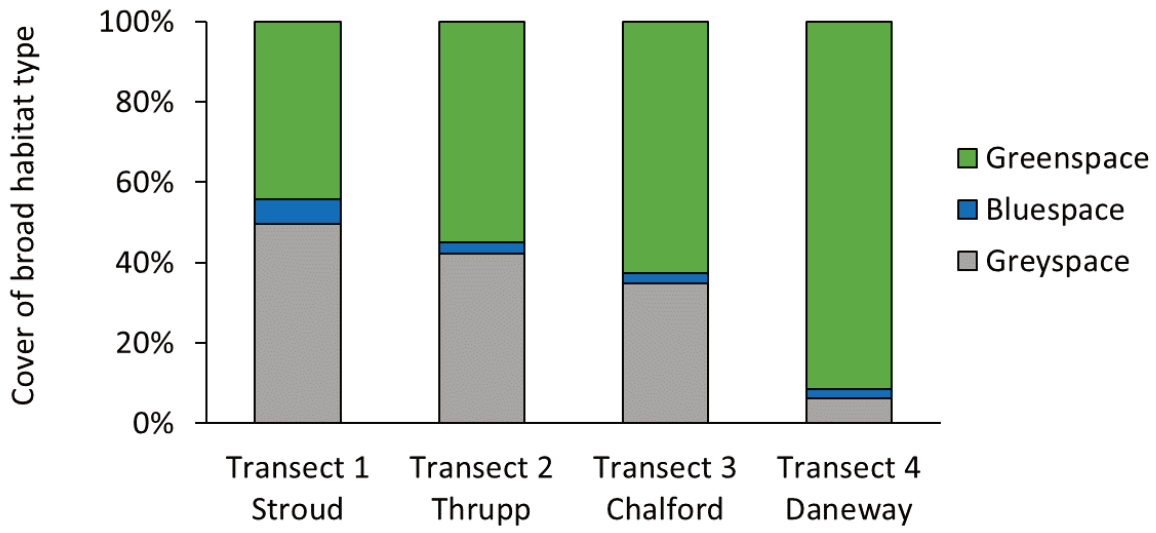

Figure 2. Percentage cover of Greyspace, Bluespace and Greenspace habitats, as defined in Table 1, across the four transects, heading from west to east along the linear study site.

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The number of species/species groups (richness, S) per transect increased from four (*P. pipistrellus*, *P. pygmaeus*, *Myotis* species and 'Big bat') in the Stroud transect (predominantly Greyspace) to six in the Daneway transect (predominantly Greenspace) due to the addition of *R. hipposideros* and *Barbastella* (Fig. 2). A few records of *Rhinolophus* in the intermediate transects (*R. ferrumequinum* and *R. hipposideros* in the Thrupp transect, *R. hipposideros* in the Chalford transect) gave S values of six and five, resulting in no significant difference in S between transects (Kruskal-Wallis $\chi^2 = 1.318$, *d.f.* = 3, $p = 0.725$). Diversity (H') was lowest in the Stroud and highest in the Daneway transect, with intermediate values in the Thrupp and Chalford transects (Fig. 3 and Table 2). This pattern was statistically significant (Kruskal-Wallis $\chi^2 = 17.778$, *d.f.* = 3, $p < 0.001$), driven primarily by differences in the evenness component of H' between the Stroud and Daneway transects.

How did overall and species-specific bat activity vary spatially?

The total number of bat passes differed significantly between the transects (Kruskal-Wallis $\chi^2 = 14.607$, *d.f.* = 3, $p = 0.002$; see also Fig. 4A), driven largely by a dramatic decline in *P. pipistrellus* passes from west (Stroud) to east (Daneway) ($\chi^2 = 33.481$, *d.f.* = 3, $p < 0.001$ — Fig. 4B). *Pipistrellus pygmaeus* passes were uncommon in the Stroud, Thrupp and Chalford transects and, although they accounted for more than 25% of passes in the Daneway transect (Fig. 4C), this difference was not significant ($\chi^2 = 1.085$, *d.f.* = 3, $p = 0.781$). Passes of *Myotis* species and 'Big bat' did not differ significantly between transects ($\chi^2 = 0.339$, *d.f.* = 3, $p = 0.953$; $\chi^2 = 3.866$, *d.f.* = 3, $p = 0.276$, respectively). Between 1% and 14% of passes per transect were recorded as 'Small bat' (Table 3). Any potential *Plecotus* passes recorded would have been entered in this category.

The species/species-group differences across the transects resulted in substantial assembly-level differences. A one-way PERMANOVA using Bray-Curtis showed that there was a significant difference in bat assemblage overall between the transects ($F_{3, 44} = 8.784$, $p < 0.001$), with significant post-hoc comparisons being recorded as the habitats changed from Greyspace-dominated transects to Greenspace-dominated transects (Fig. 2 gives relevant habitat values for each transect) with significance for Stroud vs Thrupp, Chalford vs Daneway, and Stroud

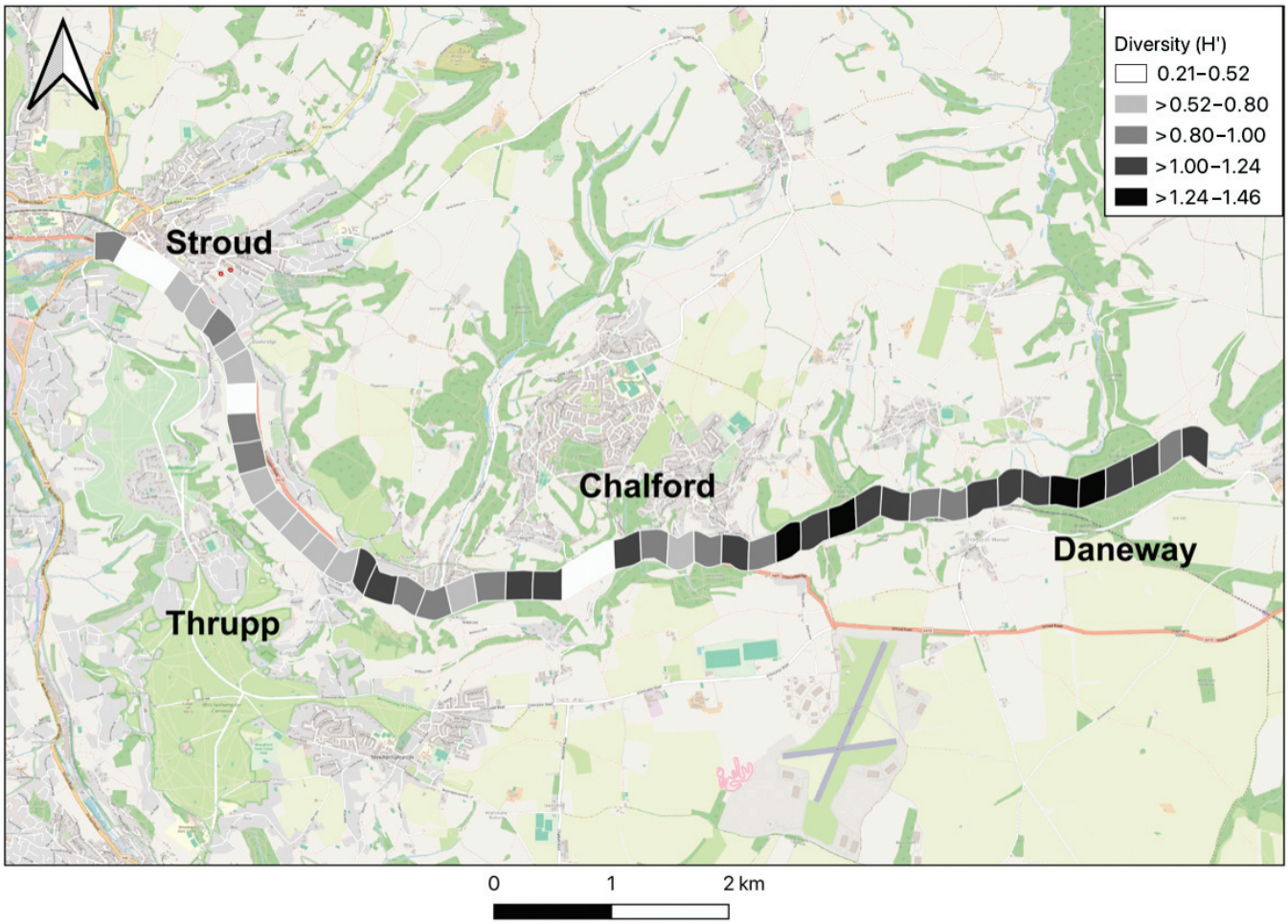

Figure 3. Increase in Diversity H' (Shannon–Wiener Index calculated using natural logarithms) for bat species/species groups from west to east along the 12 km of valley bottom.

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Table 2. Bat species/species group diversity H'.

Transect	Mean	Median	SE	SD
Stroud	0.675	0.699	0.062	0.215
Thrupp	0.925	0.901	0.054	0.188
Chalford	0.979	1.009	0.084	0.292
Daneway	1.128	1.129	0.052	0.181

vs Daneway (Fig. 5). The only pairwise comparison that was non-significant was between the two intermediate transects: Thrupp vs Chalford. A companion analysis using Bray-Curtis SIMPER indicated 53.7% dissimilarity between the transects overall. This also revealed that the high activity of *P. pipistrellus* in the Stroud and Thrupp transects was responsible for many of the observed assembly-level differences (Fig. 5). The high level of *P. pygmaeus* activity in the Daneway transect was an important contributor to the assembly-level differences when compared with the Chalford and Stroud transects, but not overall. As expected, given that the habitat differences were largest between Stroud and Daneway transects, this comparison returned the highest level of assembly dissimilarity and the most significant contrast (72.07% dissimilar; $p < 0.001$).

What habitat variables were associated with spatial variations in bat assemblages?

A biplot was created using NMDS, in which the activity of each bat species/species group in each of the 48 transect sections was entered, along with data for the six habitat and abiotic measurements, also recorded at transect section level. These were entered as environmental factors: Greyspace (Hard cover and Discontinuous Urban Fabric (DUF)), Bluespace (Water courses and water bodies) and Greenspace (Trees/Scrub and Grass), and Light. The biplot (Fig. 6) showed obvious grouping of transect section bat assemblage datapoints ($n = 48$) within transects ($n = 4$). Although there was some overlap, rather than discrete clusters being generated, 20 of the 24 datapoints relating to the western Stroud and Thrupp transects were located on the left side of the biplot (negative values on NMDS1); Stroud points generally positioned furthest to the left. Conversely, eight of the 12 datapoints relating to the eastern Chalford transect and all 12 datapoints relating to the Daneway transect were on the right of the biplot (positive values on NMDS1).

Heat maps showed the strong west-to-east gradient of decreasing bat activity. This was driven by a similar gradient of *P. pipistrellus* activity (Fig. 4B). Coolspots, where there were fewest overall bat passes, were associated with high Greyspace scores of which the most prominent were: transect sections 1–12 in the Stroud transect, section 14 (industrial units, roads, car parks and houses) and sections 21/22 (industrial units and a housing construction site) in the Thrupp transect, and section 25 within the Chalford transect (road and rail infrastructure). Greyspace and Light scores were low, and Greenspace scores were high, for most of the Chalford transect and the entirety of the Daneway transect; here, the total number of bat passes and those for *P. pipistrellus* were relatively low. *Myotis* species, 'Big bat' and *P. pygmaeus* showed no statistically significant trends in activity along the survey route. However, there was one hotspot for the latter, where the route passed a large pond (Fig. 4; sections 37–39 in the Daneway transect). For 'Big bat', the highest activity was recorded in the easternmost (Daneway) transect. The few records of *Rhinolophus* bats and *Barbastella* were wholly or largely recorded east of the Stroud transect and, for the latter, only in the Daneway transect.

DISCUSSION

Along the 12 km study area there was a west-to-east transition in habitat and abiotic parameters as the relative proportions of Greyspace decreased and

Table 3. Bat passes recorded along the survey route, shown as totals from six replicates of each transect and as percentages of each species or species group. For species groups, [1] — includes calls potentially attributable to *M. alcathoe*, *M. brandtii*, *M. bechsteinii*, *M. daubentonii*, *M. mystacinus*, and *M. nattereri*; [2] — includes *N. noctula*, *N. leisleri* and *E. serotinus*; and [3] — includes all unidentified passes with peak frequencies between 40 and 51 kHz.

Transect	Total bat passes	Percentage				
		P. pipistrellus	*P. pygmaeus*	*Myotis*[1]	Big bat[2]	Small bat[3]
Stroud	1399	79.0	4.7	5.6	9.7	4.3
Thrupp	926	62.9	9.5	11.2	13.6	5.7
Chalford	761	49.9	8.4	11.4	32.2	1.8
Daneway	662	12.7	27.8	12.1	34.0	13.4

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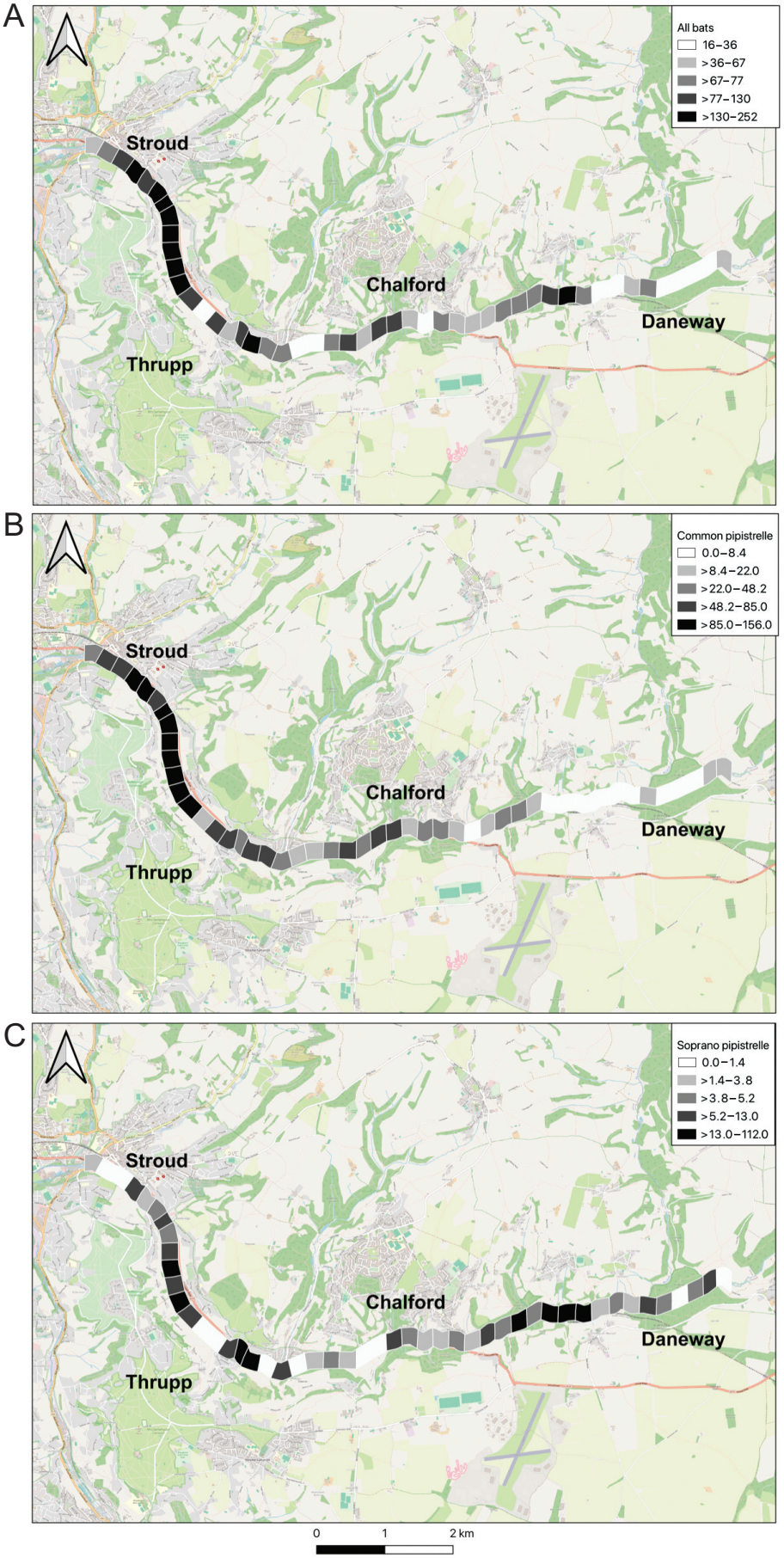

Figure 4. Total bat passes (A), *P. pipistrellus* passes (B) and *P. pygmaeus* passes (C) recorded in transect sections 1–48 from Stroud to Daneway.

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Greenspace increased (as per the values in Fig 2). Across the same gradient, Light, as measured by radiance, and open water associated with canal restoration progressively declined. The first two transects (Stroud and Thrupp) had relatively high Greyspace and high ALAN scores and, as such, were urban in character. In contrast, transect 4 (Daneway) was dominated by Greenspace and low ALAN scores was rural in character. transect 3 (Chalford) was intermediate in this respect. The profound differences in environment between transects 1–2 relative to transect 3 and especially transect 4 were associated with a substantial and significant changes in bat species richness, bat diversity, overall bat activity, and activity of specific bat species (and thus the bat assemblage structure).

Which bat species/species groups were present and how did richness and diversity vary spatially?

Overall, seven bat species/species groups were recorded with the majority of bat passes (58%) attributable to *P. pipistrellus*; records of other species/species groups were much less frequent. Dominance of *P. pipistrellus*, which is tolerant of anthropogenic landscapes (Lintott *et al.* 2015*a*, 2015*b*, 2016; Printz and Jung 2023; Starik *et al.* 2024), was anticipated in the urban areas, where there was substantial Greyspace confirming a general trend of 'urban fallout': decreasing bat diversity with increasing urbanisation and levels of disturbance (Russo and Ancillotto 2015; Moretto and Francis 2017; Medellín *et al.* 2000; Debata and Palita 2020). The findings further support the conclusion of Russo and Ancillotto (2015) that, in urban areas in which one or a few species dominate, activity per se is a relatively weak indicator of habitat suitability for local bat assemblages, and species diversity (H') can be more meaningful.

How did overall and species-specific bat activity vary spatially?

In the Greenspace-dominated transect 4 (Daneway), we expected bat activity to be similar to, or higher than, transects with more Greyspace, and for species richness

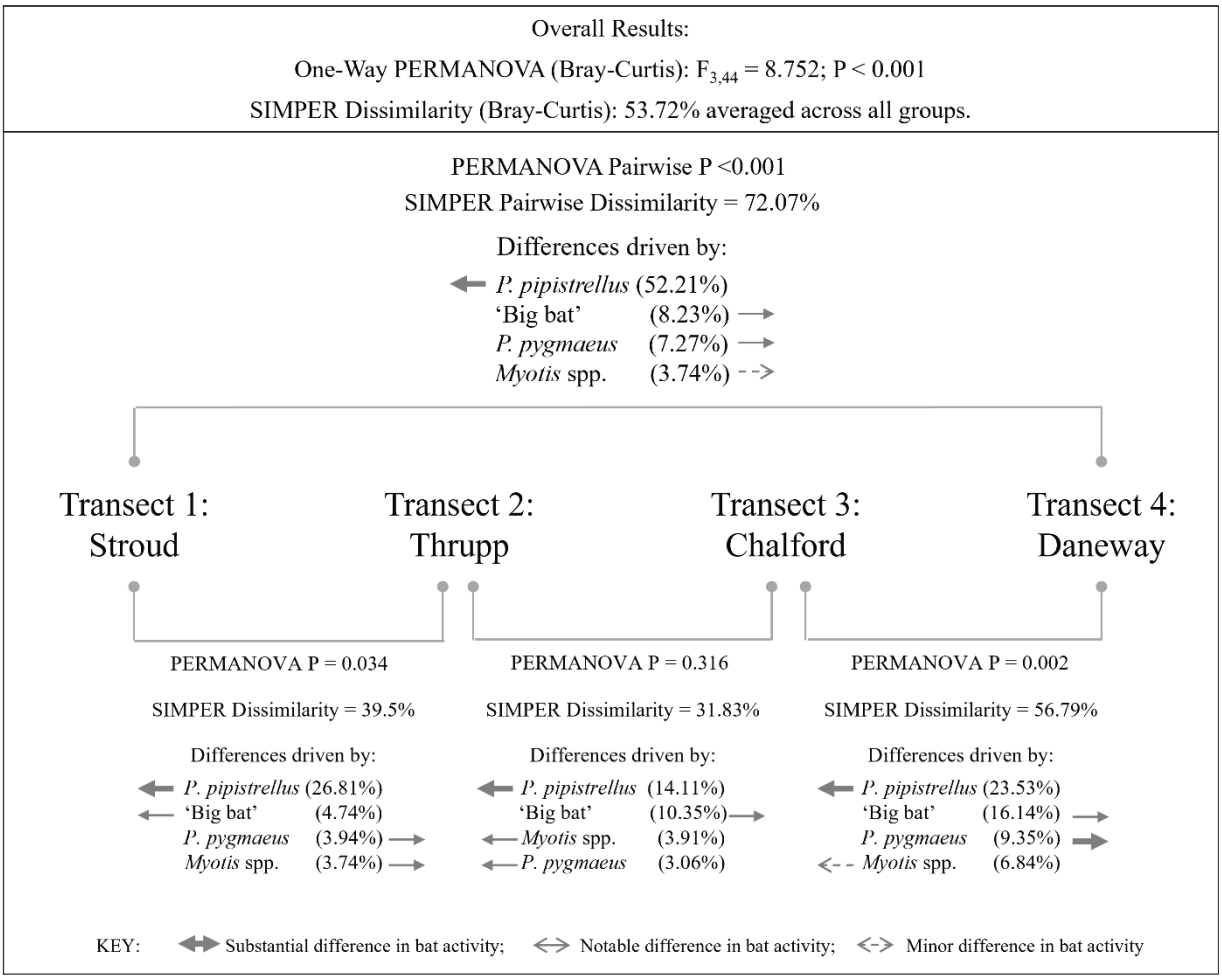

Figure 5. Comparison of bat assemblages among transects using SIMPER analysis and one-way PERMANOVA with Bray-Curtis dissimilarity as the distance measure. Arrows indicate which transects had a higher mean number of bat passes for that specific species or species group (arrows pointing left = increasingly more urban; arrows pointing right = increasingly less urban; thicker arrows = greater difference). *P*-values were Bonferroni-corrected to control the family-wise error rate.

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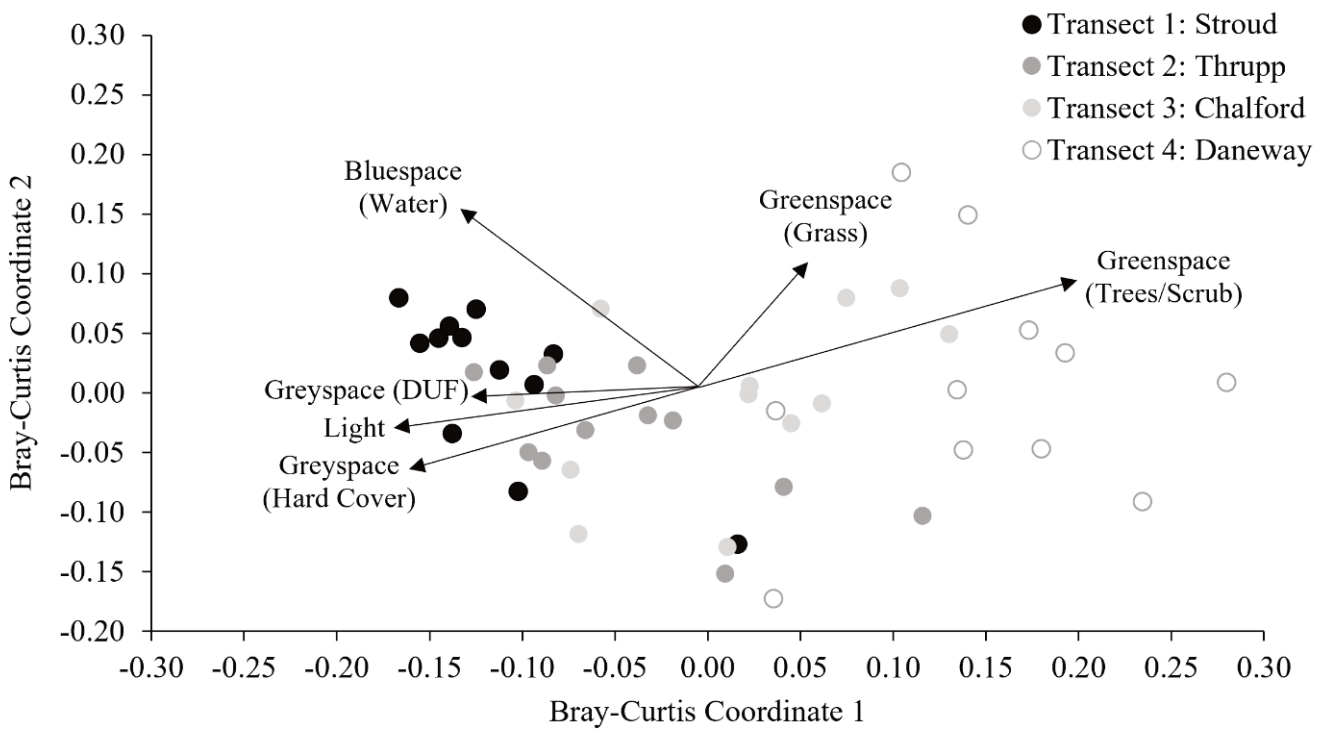

Figure 6. Non-metric multidimensional scaling (NMDS) biplot showing bat assemblage composition, with one data point per transect section, shaded according to transect ID. Habitat variables are shown as arrows, with arrow direction and relative length indicating the direction and strength of their association with assemblage composition. DUF = discontinuous urban fabric.

and diversity to be greater. However, there was a much lower level of bat activity than in urban-dominated transects (Fig. 4), which was seemingly driven by a decrease in the activity of *P. pipistrellus*. It is possible that this was partially a result of more species/species groups in this area with low energy calls that are harder to detect acoustically (e.g. *Myotis*). However, only three sections in transect 4 had high numbers of *Myotis* passes, and it seems more likely that the overall decrease in activity was a real ecological effect rather than a detectability artefact. More generally, as most of the UK's resident *Myotis* species (*bechsteinii*, *brandtii*, *daubentonii*, *mystacinus* and *nattereri*) have been recorded in the Stroud Valleys, the relative rarity of bats in this genus was surprising. The activity of *Myotis* bats was especially low in transects that ran through largely urban landscapes with associated high ALAN levels (Stroud, Thrupp and Chalford). In the Greenspace-dominated transect 4 (Daneway), *Myotis* bats may have been using woodland away from the survey route and beyond the range of detection.

The few records of the rarer woodland species *B. barbastellus* and *Rhinolophus* were largely confined to the Greenspace-dominated transect 4 (Daneway). The scarcity of *R. hipposideros* could have been due to one or more of the following: its general rarity (only one breeding roost was known within the linear study site); its selection of woodland for commuting and foraging (Bontadina *et al.* 2002); avoidance of competition with more light-tolerant *P. pipistrellus* (Arlettaz *et al.* 2000); and/or the difficulty of detecting its highly directional calls.

Most passes in the 'Big bat' group (84.88%) were believed to be *N. noctula*, with detected individuals usually flying high and fast, apparently using the valley for orientation while commuting rather than for feeding. *Plecotus auritus* is widespread and relatively common in the UK (Crawley *et al.* 2020) and so was likely to have been present. This species has low energy calls which would have been hard to detect acoustically. The proportion of passes in transect 4 (Daneway) assigned to 'Small bat' was relatively high, at 13.4%. Here, it is possible that *P. auritus*, which is strongly associated with wooded landscapes (Harris and Yalden 2008; Dietz *et al.* 2009), made up a higher proportion of the 'Small bat' species group than, for example, unidentified *Pipistrellus* species.

What habitat variables were associated with spatial variations in the bat assemblages?

The NMDS biplot of the bat assemblage (based on activity of each bat species/species group) in relation to the five habitat factors and Light revealed a clear urban–rural divide. The bat assemblage in the Stroud and Thrupp transects was strongly associated with the two Greyspace factors (Hard cover and DUF) and Light, while the bat assemblage in the Chalford and Daneway transects was strongly associated with the Greenspace factors (Grass and Trees/Scrub): this divide was reflected in NMDS1 (*x*-axis). The Bluespace variable was the main driver of NMDS2 (*y*-axis) but was also pulled towards the Stroud and Thrupp transects (i.e. negative

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NMDS1 values) where canal restoration had occurred. Taken together with the heatmaps, which revealed coolspots for all bat activity in 250 m transect sections with high Greyspace scores and high levels of ALAN (more prevalent in the Stroud and Thrupp transects), this suggests that human infrastructure likely presented barriers to bat movement except for high flying individuals in the 'Big bat' species group (Collins 2023). Reducing light and noise pollution could increase bat use of coolspots (Hale *et al*. 2012, 2015).

Open water in urban areas, especially where associated with riparian vegetation and low ALAN, supports relatively high bat activity (Moretto *et al*. 2022*b*). Interestingly, *P. pygmaeus*, which routinely forages over and near water (Barlow 1997; Davidson-Watts and Jones 2006; Nicholls and Racey 2006; Lintott *et al*. 2016), was not particularly associated with the recently cleared, open water stretches of the canal used by *P. pipistrellus*. In contrast, higher *P. pygmaeus* activity in the Chalford and Daneway transects, associated with Greenspace and especially 'Trees/Scrub', tended to occur in areas where *P. pipistrellus* was unexpectedly uncommon. The heatmaps also revealed an association between *P. pygmaeus* and larger static water bodies. A former mill pond in transect 4 (Daneway; transect sections 37–39) with > 0.5 ha of open water and a woodland edge, was a hotspot. *Pipistrellus pygmaeus* selects maternity roost sites within 2 km of open water bodies with woodland edges (Oakeley and Jones 1998). As such, the mill pond and its woodland edge should be regarded as of conservation significance for this Priority Species (Natural Environment and Rural Communities Act 2006 — UK Parliament 2006). Taken together, these findings suggest that, although the two *Pipistrellus* species can and do co-occur (Presetnik *et al*. 2001; Lintott *et al*. 2016), high *P. pipistrellus* activity was associated with open Bluespace. In contrast, *P. pygmaeus* activity was highest in areas of woodland, including Bluespace within woodland, where its higher peak frequency call and presumably greater ability to negotiate clutter may offer a competitive edge over *P. pipistrellus* (Lintott *et al*. 2015*a*).

Implications and recommendations

Urbanisation has a profound impact on bat assemblages (Bellamy *et al*. 2013; Lintott *et al*. 2015*a*; Russo and Ancillotto 2015; Korine *et al*. 2022; Moretto *et al*. 2022*b*). High levels of noise, ALAN and chemical pollution are likely to be tolerated by synanthropic species, especially *P. pipistrellus*, and have a negative impact on tree roosting bats such as *B. barbastellus* and *Myotis* species (Carr *et al*. 2020; Gili *et al*. 2020). Bats are indicators of biodiversity (DEFRA 2021) but the number of species *per se* does not accurately portray where there has been 'urban fallout' in which a small number of species dominate activity (Russo and Ancillotto 2015). As such, species diversity would be a better metric for tracking the impact of urbanisation than overall bat activity. To ensure that bats continue to commute between their roosts and feeding sites in landscapes that become fragmented by urbanisation, maintaining or creating connecting treelines and hedgerows and reducing ALAN levels should be promoted (Gili *et al*. 2020; Sutherland *et al*. 2021; Hooker *et al*. 2022). More research is needed on the impact of mitigations such as enhanced green and blue infrastructure and low–light areas on assemblages of bats and their roosts in urban and peri-urban areas (Patriquin *et al*. 2022). In the present study, minimum intervention is required to maintain the high bat species richness found along the valley bottom in the rural east of the survey route. Proposed restoration of the canal to a navigable state there is likely to be incompatible with a desire to protect the widest range of bat species and their insect prey.

AUTHOR CONTRIBUTIONS

DJB: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing, critical revision, and final approval of the article; GOD: collection and/or assembly of data, data analysis and interpretation, writing, critical revision, and final approval of the article; JES: collection and/or assembly of data, writing, critical revision, and final approval of the article; AEG: data analysis and interpretation, writing, critical revision, and final approval of the article.

COMPETING INTERESTS

The authors have no relevant financial or non-financial interests to disclose.

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