Can patterns of urban biodiversity be predicted using simple measures of green infrastructure?

Keywords: Birmingham; multi-taxa; remote sensing; tree canopy height; vegetation cover.

Highlights:

- Simple measures of vegetation cover can explain urban biodiversity variation
- Higher urban vegetation cover is associated with higher species richness for multiple taxa
- Bee and hoverfly richness and bat activity were negatively correlated with tree cover
- Bird richness and bat activity were positively correlated with diversity in tree canopy height
- Built surface cover is a poor correlate of tree canopy cover and height variability

Abstract

Urban species and habitats provide important ecosystem services such as summertime cooling, recreation, and pollination at a variety of scales. Many studies have assessed how biodiversity responds to urbanization, but little work has been done to try and create recommendations that can be easily applied to urban planning, design and management practice. Urban planning often operates at broad spatial scales, typically using relatively simplistic targets for land cover mix to influence biodiversity and ecosystem service provision. Would more complicated, but still easily created, prescriptions for urban vegetation be beneficial? Here we assess the importance of vegetation measures (percentage vegetation cover, tree canopy cover and variation in canopy height) across four taxonomic groups (bats, bees, hoverflies and birds) at multiple spatial scales (100, 250, 500, 1000m) within a major urban area (Birmingham, the United Kingdom). We found that small-scale (100-250m radius) measures of vegetation were important predictors for hoverflies and bees, and that bats were sensitive to vegetation at a medium spatial-scale (250-500m). In contrast, birds responded to vegetation characteristics at both a small (100m) and large (1000m) scale. Vegetation cover, tree cover and variation in canopy height were expected to decrease with built surface cover. However, only vegetation height showed the expected pattern. The results indicate the importance of vegetation cover for supporting urban biodiversity, and show that relatively simple measures of vegetation character can be useful predictors of species richness/activity density. They also highlight the danger of relying upon percentage built surface cover as an indicator of urban biodiversity potential.

Introduction

To describe patterns in urban biodiversity and understand their causes, researchers have employed varying measures of urban context (Sadler et al., 2010). Population density and distance to the urban center have facilitated coarse comparisons between studies; however, these measures do not always translate easily into urban management practice (McDonnell and Hahs, 2013). Other measures, such as built surface cover can be collected from digital data (maps and remote sensing) in a standardized manner, and are potentially more useful for translating into urban planning practice. Selecting the most appropriate measure of urban context is often seen as central to decision making around land-use planning, architecture and urban design (Boyko and Cooper, 2011). Many measures of urban context co-vary with other variables along rural-urban gradients (Andersson et al., 2009; Hale et al., 2013), so it is often not clear whether observed ecological responses are driven by the measure of urban context used, or by correlates with the gradient. Small-scale variability in urban habitat availability and character (e.g. availability and quality of nesting sites or feeding areas) can also strongly influence local biodiversity patterns (McDonnell and Hahs, 2013). However, at small scales, urban habitat character and availability can demonstrate high spatio-temporal variability, making the collection of accurate habitat measurements both difficult and time consuming. As a suite of ecosystem services are thought to be related to biodiversity (Niemelä et al., 2010), the pragmatic challenge is therefore to identify landscape predictors of urban biodiversity patterns that reflect important ecological processes, which are easily generated, available, and understandable by practitioners.

Given the ecological importance of vegetation and the increasing availability of spatial vegetation data for urban areas, it is sensible to explore the use of these data for predictive modelling of urban biodiversity. Simple measures of urban vegetation have been used to assess patterns in biodiversity with some success (e.g., Chong et al., 2014; Ferenc et al., 2014) and

approaches have been developed towards effective evaluation of structural urban habitat diversity (Young and Jarvis, 2001). However, new vegetation measures provide the opportunity to explore whether they provide additional value within ecological studies. Near Infrared imagery from satellites and aerial photographic surveys can be used to generate 2D maps of vegetation cover; a third dimension can be added using structural data derived from remote sensing techniques such as Light Detection And Ranging (LiDAR), providing fine-scale vegetation canopy height information (Lefsky et al., 2002). Stereophotogrammetry using aerial photography is an alternative source of data on canopy height, is simpler to collect than LiDAR and often cheaper and spatially more extensive. These techniques produce standardized high-resolution information on the structural complexity of vegetation over large spatial extents much more easily than traditional ground-based vegetation survey approaches.

Measuring environmental variables at multiple scales is recommended for ecological studies (Bellehumeur and Legendre, 1998) and may be particularly important in urban areas, where land-cover and land-use can be highly variable in composition and structure over small distances (Luck and Wu, 2002). Taxa are known to respond to urban form at different spatial scales (Goddard et al., 2010; Sattler et al., 2010), with some species responding to environmental variation at a very local level, and others responding to the urban form over much wider areas (Sadler et al., 2006). Some may move large distances because they require habitat resources at different times (e.g. nesting, foraging, etc.) that are sparsely distributed within the urban landscape (Ricketts, 2001), or because they possess traits that facilitate high mobility (e.g. flight), which give greater access to disparate resources. However, it is not clear at what spatial scales taxonomic groups respond most strongly to urban vegetation. The response of different species of urban birds to vegetation and tree cover have been found to vary (50–1000m) (Pennington and Blair, 2011), while less mobile species such as

ground-dwelling spiders in urban areas can respond to micro-climatic variables at a smaller scale (< 10m) (Sattler et al., 2010).

Policy frameworks surrounding the management and provision of urban green space are heavily geographically contextualized. Therefore, generalizations that have widespread planning and management applicability are not easily formulated (Sadler et al., 2010). In urban areas land-use parcels are often small, heterogeneous and managed by a diverse set of stakeholders, and planning input is usually sporadic and associated with early site development (Borgström et al., 2006; Ernstson et al., 2010; Sadler et al., 2010). Therefore, although broad-scale planning and management of urban green space is preferable, and can be enacted through a variety of planning approaches (e.g. Sadler et al., 2010), it is made difficult in practice because of the small-scale and site-specific management of privately owned property (Borgström et al., 2006; Ernstson et al., 2010). This fragmented management of urban green spaces might therefore mismatch with the appropriate scale of management for highly mobile species. Identifying the scale(s) at which the biodiversity of particular taxa are most sensitive to landscape composition, and creating a set of easily derived environmental metrics that encapsulate landscape:biodiversity relationships, are important ecological research goals to help inform effective urban planning, design and management.

Numerous studies have investigated the distribution and habitat preferences of single species or taxonomic groups (e.g., Ahrné et al., 2009; Bates et al., 2014; Goertzen and Suhling, 2014; Hale et al., 2012; Martinson and Raupp, 2013), and meta-analyses of links between urban biodiversity patterns and urban structure are beginning to emerge (Beninde et al., 2015). Nonetheless, the responses of different taxonomic groups to simple as well as more structurally complex characteristics of urban vegetation remain unclear, partly due to the lack of standardized descriptions of the urban context between studies (McDonnell and Hahs, 2008).

This paper assesses the extent to which simple landscape vegetation measures can reflect broad patterns in biodiversity across taxonomic groups using existing survey data from a well-studied urban area (Birmingham, UK). The landscape vegetation measures used here can be extracted with relative ease for many urban areas.

We address the following research questions: 1) How much of the variation in species richness of birds (Aves), bees (Apoidea), hoverflies (Syrphidae) and activity density in bats (Chiroptera) is linked to measures of vegetation cover, tree cover and diversity of tree canopy height? 2) At which spatial scales does each taxa most strongly respond to these vegetation measures? 3) What is the nature of the relationships between vegetation and species richness/activity density? 4) To what extend does the proportion of built surface correlate with these vegetation metrics, and do these patterns vary with spatial scale?

Methods and Materials

Study area

Birmingham in the West Midlands is one of the largest cities in the United Kingdom with a population of ~1 million people. Approximately 50% of the city area (135 out of 268km^2) is vegetated and 11% of the city area is covered by tree canopy (>4m). For each taxonomic group (birds, bees, hoverflies and bats) the study sites were selected to cover the variation in vegetation cover along the urban-rural gradient (for details see Bates et al., 2011; Hale et al., 2012; Rosenfeld, 2012)

Species data

Bees and hoverflies were sampled in 2010 using pan traps and sweep netting within 24 cemeteries and churchyards (as these provided relatively well replicated habitats along the urban-rural gradient) (Bates et al., 2011). Bat activity data were collected in 2009 using bat detectors along transects and at fixed points at 30 ponds (Hale et al., 2012). Bird presence was recorded from sightings or calls heard along transects in 2008-2011 within 68 urban green spaces (Rosenfeld, 2012) (Fig. 1). All data collection was performed in suitable weather and seasons for the target taxa. The recorded species richness varied by taxa, with hoverflies less species rich (3-20), birds most species rich (15-35), and bees with intermediate species richness (8-28) (Appendix S1). Bat activity, indicated by the count of bat calls during a night ranged from 6 to 1143. These taxonomic groups were expected to differ in the way they used the habitats within which they were surveyed. Bees and hoverflies were likely to be mostly foraging within the survey areas, but some would also be 'nesting'/ovipositing and travelling through the survey areas. Birds were probably present in an area because they used it for a mixture of foraging and nesting, whereas bats were recorded feeding at ponds, but also commuting via the adjacent vegetation to other feeding areas.

Vegetation data

Vegetation data covering the entire West Midlands were derived from 2007 aerial near-infrared and colour photography (Bluesky International Limited, Leicestershire, UK), using supervised classification within ArcGIS 10.3 (ESRI, Redlands, California, USA) (Hale et al., 2012). The resulting 2m pixel resolution binary raster layer represented broad vegetation, including both ground vegetation and tree canopies (even if they were overhanging roads and other built surfaces).

Digital elevation models (DEM) and digital surface models (DSM) for the whole of the West Midlands were also sourced from Bluesky International Limited, which had been generated by applying stereophotogrammetric techniques to overlapping aerial plane photographs captured in 2007 (https://www.bluesky-world.com/standard-height-data)). These height data had a horizontal pixel resolution of 2m and a vertical resolution of 1m. By differencing the two models, we created a raster that represented the height above the ground of large objects such as buildings and trees.

The vegetation and height data were combined to create additional layers representing tree canopy cover and tree canopy height using the Raster Calculator tool within ArcGIS. First, the vegetation layer was attributed with height values. Then, vegetation cover within 4m of buildings was excluded, using a building mask generated from Ordnance Survey MasterMap Data (2008). This processing step reduced the potential for small errors in georeferencing to cause buildings to be interpreted as vegetation. Next, cells with height values < 4m were converted to NoData, which helped to exclude built structures or other objects within vegetated areas (cars, sheds, etc.), that could have been interpreted as small trees or shrubs. The resulting raster represented the height of all tree cover ≥ 4m, which was then simplified to generate a binary raster representing all tree cover ≥ 4m in height.

Previously, LiDAR data have been used to compare vegetation and animal data (Vierling et al., 2008), and LiDAR was therefore considered as an alternative source of height data, but dismissed

because it was only available for approximately half of the study area (The Geoinformation Group, Cambridge, UK). Photogrammetry provides less accurate height data than LiDAR (Lefsky et al., 2002), but the data were more spatially extensive, allowing the capture of more of the urban gradient within the study area. For survey locations where both LiDAR and photogrammetry derived height data were available, we used these data to generate and compare estimates of tree canopy cover, median canopy height and standard deviation in canopy height (Appendix S2). These correlations were strong, indicating that despite its lower accuracy, photogrammetry derived data are a practical alternative in the absence of LiDAR for measuring canopy height.

Explanatory vegetation variables

To determine if the response variables for each taxonomic group were sensitive to the structural complexity of urban vegetation, a range of explanatory variables were generated for each sample location: %vegetation cover, %tree canopy cover, median tree canopy height and variation in tree canopy height (standard deviation (STD)). Median tree canopy height and STD tree canopy height were intended to reflect structural complexity and these measures (including vegetation cover and tree canopy cover) have previously been used to explain biodiversity patterns in several studies (e.g. Vierling et al., 2011; Zellweger et al., 2013).

These variables were calculated using circular buffer zones around survey locations of multiple radii ranging from small (100m buffer), over medium (250 and 500m buffers) to large (1000m), to test for environment-taxa responses at different spatial scales (Sattler et al., 2010). Calculations were performed in ArcGIS using the *Buffer* and *Zonal Statistics as Table* tools. We accounted for overlapping polygons by sequentially calculating *Zonal Statistics* on subsets of non-overlapping polygons.

Although it seems intuitive that broad vegetation cover decreases with increasing built surface cover, this may not always be the case. Agricultural fields on the urban fringe have no built surface

cover, yet at some times of the year they may also be devoid of vegetation. Conversely, built surfaces such as roads and civic squares may also have high levels of overhanging tree cover. Other measures of urban vegetation, like tree cover and diversity of tree canopy height, may have an even less predictable response to this urbanization gradient. To explore and compare the spatial structuring of the vegetation measures within a larger case study landscape, we extracted additional landscape GIS summary data covering the entire West Midlands region using a 1km grid of sample points, each buffered by 100, 250, 500 and 1000m. The resulting circular polygons were used to extract summaries both of built surface cover (Ordnance Survey Mastermap 2008) and our vegetation layers, using the isectpolyrst tool in the software Geospatial Modelling Environment (version 0.7.3.0) (Beyer, 2009-2012). This then allowed the variability in urban vegetation measures to be plotted against a gradient of built surface cover at different scales. We applied Generalized Additive Models (GAMs) to illustrate the potentially nonlinear relationship between urban vegetation measures and built surface cover.

Analyses

Data exploration was applied following Zuur et al. (2010). Outliers were detected using Cleveland dotplots (only one outlier was found for one of the hoverfly models), Cook's distances and hat-values. Explanatory variables were square root or log transformed if a few particularly high values were detected (%tree canopy cover was square root transformed for all buffer sizes for the bird data and bee data at 250, 500 and 1000m whereas %tree canopy cover was log transformed for hoverfly data at 250 and 1000m). Collinearity was assessed using Variance Inflation Factors (VIF) disregarding variables showing VIF values >3 from the VIF calculations (Zuur et al., 2010). Median tree canopy height was found to be collinear in models for bats (median canopy height 100m and variation in tree canopy height 250m were collinear) and for hoverflies (median canopy height 250m and tree cover 250m were collinear). When excluding median tree canopy height VIF

values for the remaining variables were < 3 and we therefore excluded median tree canopy height from the bat and hoverfly models. Linear models were selected if initial inspection of the relationship between response and explanatory variable using multi-panel scatterplots indicated a linear relationship. We created multi-variable models for all combinations of taxonomic group, variables and buffer sizes using GLM with Poisson error distribution using the log link function (one, two, three and four variables in a model = 624 combinations of variables for each taxonomic group). We used species richness as the response variable for bees, hoverflies and birds. The number of echolocation calls was used as a response variable for bats, as a broad indicator of bat activity. This measure was used because some species are not possible to differentiate reliably based upon their calls (Hale et al., 2012). The 'best' models were selected using Akaike's Information Criterion corrected for small sample sizes (AICc) (Johnson and Omland, 2004), selecting the best set of models with ΔAICc < 2, where ΔAICc is the AICc of a model minus the lowest AICc in the model sets (Burnham and Anderson, 2002). AICc was calculated in R using the MuMIn package (Barton, 2015). Because many of the lower-ranked models contained uninformative variables (sensu Arnold, 2010), which when present did not contribute sufficient explanatory power to offset the penalty of their inclusion, we applied occam's razor and selected the simpler model of the suites. For birds, season of observation was retained in the parsimonious model despite the lack of evidence of season as a variable in itself having a substantial effect.

Model validation was applied on the best models to verify the underlying assumptions as follows: If over dispersion was detected we used GLM with Negative Binomial error distribution instead of Poisson error distribution (Hilbe, 2011). Residuals versus fitted values were plotted to assess homogeneity of variance, and residuals versus each covariate to investigate model misfit. If non-linear patterns were detected in the residuals, polynomials were added to the GLM model. Non-linear patterns in residuals were detected for bat models at 500m and 1000m (GLM with tree

canopy cover^2 was used). Residuals were checked for spatial autocorrelation by visual inspection (Appendix S3). Modelling was performed in R version 3.2.0 (R Core team, 2015) using the mgvc (Wood, 2006) packages. To assess the model fit we compared deviance explained for the best model with deviance explained for a null model (intercept only) in the following way: Overall deviance explained for the best model was estimated by:

$$\frac{\text{deviance (null model)} - \text{deviance (best model)}}{\text{deviance (null model)}}$$

Likewise, partial deviance explained by each variable in the best model was estimated by:

$$\frac{\text{deviance (alternative model without the target variable)} - \text{deviance (best model)}}{\text{deviance (null model)}}$$

For each response variable in Negative Binomial GLM models we used the smoothing parameter (theta) from the best model throughout the set of models used to calculate the deviance explained. Summed partial %deviance explained for individual variables did not always add up to the total %deviance explained, for example, because of overlap in the variance explained by different variables within the same model.

To visualize the effect of vegetation cover, tree canopy cover, variation in canopy height and median canopy height on species richness we created a grid of points at 10m intervals covering a focal area within the case study city. This area included a broad variety of green infrastructure and built surfaces. For each of the resulting ~ 90,000 points we calculated the %vegetation, %tree cover and variation in tree canopy height (STD height) within a distance corresponding to the buffer size (100m, 250m or 500m) in the model with lowest AIC for bees and bats. For each of the points, we then predicted the species richness/bat activity based upon the GLM model. Please note, these visualizations were created for a sub-set of models and for a small focal area of the city to illustrate the contrasting habitat potential for different groups within the same location, and also to demonstrate the possible use of these maps for green infrastructure planning.

Results

Final models

Bat activity increased with greater vegetation cover within a 500m radius but decreased with increasing tree cover at the same scale while variation in tree canopy height had only a small effect (Fig.2a, Table 1). Bird species richness increased with greater variation in tree canopy height (STD) at a large spatial extent (1000m) and increased with tree cover at small scale (100m) with very limited effect of vegetation cover and median canopy height at all scales (Fig. 2b, Table 1). In contrast, bees and hoverflies responded more strongly to vegetation metrics at smaller spatial scales. For hoverfly species richness we found a positive effect of vegetation cover and a negative effect of tree canopy cover at this same relatively small spatial scale (250m) and very small effects of variation in tree canopy height at larger scale (500-1000m) (Fig. 2c, Table 1). The best model set for bee species richness was similar to that for hoverflies, a positive effect of vegetation cover and a negative effect of tree canopy cover, but this time at the smallest spatial scale measured (100m), with a small effect of variation in tree canopy height (100m) and median canopy height (1000m) (Fig 2d, Table 1). There was no indication of spatial autocorrelation (Appendix S3).

Overall, the correlation between vegetation metrics and richness/activity density varied with taxonomic group. For bats, bees and hoverflies the deviance explained due to variation in large scale vegetation was considerable (41.99-68.57%, Table 1). For birds these variables provided much less explanatory power (19.12-21.33%, Table 1).

Vegetation metrics along gradients of built surface cover

Within the West Midlands we found a strong negative relationship between built surface cover and vegetation cover across all scales. In contrast, tree canopy peaked at low to intermediate levels of built surface cover, before declining towards the most urban end of each gradient (Fig. 3,

Appendix S4). There was no obvious patterning of the variability in tree canopy height along any of the gradients in built surface cover.

Illustrating habitat suitability for bees and bats

The visualizations (Fig. 4) of the best habitat suitability models for bees and bats demonstrate the contrasting responses of different taxa to vegetation structure and spatial scale. Bee species richness was predicted to be high in open habitats (e.g. point X, Fig. 4, row C) and low in areas with dense tree cover (point Y, Fig. 4, row C). It was also found to be sensitive to changes in vegetation cover at a fine spatial scale, which can be seen by the sharp change in predicted bee species richness between points X and Y within Fig. 4 (row C). In contrast, bat call activity was predicted to be very similar at points X and Y (Fig. 4 row D), as the landscape surrounding these locations was found to be very similar when measured at the coarser scales used in the best model (250 - 500m).

Discussion

In this study we considered vegetation metrics that: 1) varied in their level of detail and 2) were measured at a range of spatial scales. Our results reveal that for hoverflies, bees, bats, and to a lesser extent birds, simple vegetation measures derived from remote sensing data explain appreciable amounts of variation in species richness and activity-density (Table 1). In general, vegetation cover at a small scale (100-250m radius) was most important for bees and hoverflies. The response of bats was strongest at an intermediate scale (250-500m), whilst birds responded to vegetation at both a small (100m) and large (1000m) scale. As the data used in this study are limited spatiotemporally and to only some taxonomic groups, the results need to be applied carefully. Nonetheless, because of our use of simple and spatially explicit vegetation metrics, the relationships we have identified between urban vegetation and biodiversity could be directly translated into recommendations for urban planning, design and management (see section *Planning, design and management implications*).

Vegetation cover and structure

Whilst our results cannot be used to better understand the ecology of the studied taxa, some broad observations can be made on their associations with vegetation cover and structure. Bat, bee and hoverfly assemblages were strongly and positively associated with vegetation cover - the simplest metric measured in this study. Such a result was expected, given the direct dependency of many invertebrates upon vegetation, and the insectivorous nature of UK bat species. Vegetation cover, or its coarse negative correlate, built surface cover, have been shown by several authors to be important variables explaining diversity of bee assemblages (e.g. Fortel et al., 2014; Hülsmann et al., 2015); and both vegetation cover (Chong et al., 2014) and tree cover (Ferenc et al., 2014) have been found to correlate with the species richness of birds. The negative effect of tree canopy cover on bees and hoverflies may be related to their broad preference for non-shaded areas in temperate

climates, despite the association of some species with woodlands (Branquart and Hemptinne, 2000). A higher degree of taxon-specific responses may have been anticipated because of different dispersal modes and resource requirements. For example, different responses to landscape characteristics have been found for bees and hoverflies in agricultural landscapes (Jauker et al., 2009).

Overall, the amount of explained deviation by the best models ranged from 19.12% - 68.57% indicating that these easy-to-measure vegetation variables are particularly useful predictors for some groups (hoverflies, bees and bats) while other taxonomic groups (birds) may be more sensitive to patch quality, broader landscape scales or other variables not measured in this study such as structural connectivity (LaPoint et al., 2015). There was some evidence for a positive effect of variation of tree height (within 1000m) on bird species richness. Whilst the mechanism(s) behind this relationship are unclear, this may reflect a higher number of nesting (Zellweger et al., 2013) and foraging (Laiolo, 2002) opportunities as a result of a greater mix of tree ages and species.

Urban gradients and vegetation

Since the gradient paradigm was suggested for studying ecological changes in urban areas (McDonnell and Pickett, 1990) it has been used by many researchers to quantify the degree to which the anthropogenic intensity of human settlements impact organisms (McDonnell and Hahs, 2008). Although patterns vary by taxonomic group, scale and study (McDonnell and Hahs, 2008), species richness is generally lowest in the most heavily urbanized areas (e.g. urban cores) whereas abundance often peaks at low to intermediate levels of urbanization (McKinney, 2008). Urban gradient studies typically use demographic variables, landcover/landuse variables or landscape structure metrics to define the gradient, but rarely assess what the gradient represents in terms of available habitat for biodiversity (but see Berland, 2012; Hahs and McDonnell, 2006). Although the use of built landcover/density gradients might facilitate the translation of results into planning

practice, there is the danger that a low level of built surface cover ends up being adopted as an indicator of high habitat suitability for all species groups. Vegetation cover, tree cover and diversity of tree canopy height exhibited highly contrasting patterns when compared along gradients of built surface cover, and all patterns were independent of the scale at which the proportion of built surface cover was measured. Our results serve to illustrate that, as one might expect, it is reasonable to use broad built surface cover as a negative linear proxy for vegetation cover in urban areas. However, we demonstrate that built surface cover is likely to be a relatively poor indicator of tree canopy cover and variability in canopy height. Trees are commonly planted within built civic spaces and frequently overhang roads; these trees clearly have some ecological value, which is missed by simple metrics such as the percentage of built surface cover (derived from cartography).

Planning, design and management implications

We believe that the simple approach presented in this paper using readily available data on vegetation in cities is a valuable means of generating a replicable analytical approach that can translate into urban planning practice. The results presented support the idea that strategic landscape-scale planning for urban bird communities should take direct advantage of canopy height mapping to identify locations with diverse tree heights that could be protected. Such planning should also seek to enhance canopy variability through strategic planting (e.g. species, variety, rootstock) and management (e.g. pruning) of trees (Hale et al., 2015).

Our results also support the retention and enhancement of even relatively small habitat patches within cities as bee and hoverfly assemblages responded to vegetation at a small scale (100-250m). Increased total vegetation cover within 250-500m of a particular location will likely enhance bat activity. Should urban planning policy seek to specifically provide habitats for ground foraging pollinators within development sites, more emphasis should be put on the retention and creation of low-growing vegetation than on enhancing tree cover, but it should be recognized that pollinators

363 also forage on tree blossoms, particularly in the spring. Similarly, sites intended to support high bat
364 activity should place greater emphasis on semi-open areas, with high variability in tree canopy
365 height.

366 Nature conservation and planning practitioners are clearly interested in encouraging
367 developments that maximize the percentage vegetated area, as well as the abundance of more
368 specific ecological features (Kruuse, 2010). Our study helps to improve the empirical basis for the
369 development of relatively straightforward guidance on vegetation provision/retention in urban
370 planning and to clarify the most appropriate spatial scale and location at which vegetation should be
371 clustered within development sites (Table 2). The visualization approach employed in Fig. 4 might
372 be particularly useful in this respect. For example, if there is a desire to increase pollinator diversity
373 in a particular part of the city, any new areas of gardens, amenity grassland or other short vegetation
374 should be located as close to each other as possible, and also close to existing patches of short
375 vegetation that are just outside the boundary of the development site. In contrast, proposals for new
376 bat habitats should carefully consider whether there is sufficient vegetation cover (that includes
377 scattered trees of varying heights) within 250 - 500m of the site. Again, we would like to emphasize
378 that these vegetation models should be used as an indication of biodiversity *potential* - other factors
379 such as patch quality or functional connectivity also need to be addressed within planning and
380 management practice. However, it is important not to overlook the need to specify the minimum
381 levels of ground vegetation and tree cover, as basic requirements for supporting particular taxa.

382 *Future research directions*

383 Based on our results, we recommend that analyses of the broad ecological potential of urban
384 areas should be based upon readily available high-resolution vegetation data for the whole
385 landscape. The variables used in this study can easily be calculated for other urban areas where
386 basic land use mapping and remotely sensed data have been produced, and can be used for future

research comparisons across other cities. However, as each city has a unique landscape character and associated fauna and flora, it is still necessary to test our models more widely. In addition, cities and urban developments are by no means static and the history of the built environment may play an important role in shaping ecological communities (e.g. changes in land use, species dispersal, evolution and extinction, regional species pools, geographical isolation) as has been found in more natural areas (Collins et al., 2000; Faeth et al., 2011).

Although simple two-dimensional vegetation measures are often considered sufficient from a management perspective (McDonnell and Hahs, 2013), the use of variables reflecting the three-dimensional vegetation structure has proved useful in this study. More sophisticated measures such as LiDAR-derived % penetration, or vegetation heights from multiple returns, may therefore prove to be even more valuable (Hancock et al., 2015). As LiDAR data becomes more readily available it would be interesting to explore whether this provides additional explanatory power when modeling ecological patterns in urban areas.

Most of our results indicated the importance of small-medium scale management for enhancing the species richness or activity of various taxonomic groups. Despite the preference for top-down, broad-scale planning and management of urban green space (Sadler et al., 2010) and its associated difficulties, our results provide grounds for optimism, indicating that local-scale vegetation management can be beneficial for urban biodiversity.

Appendix S1

Species richness and number of calls (bats) for each taxonomic group within sites.

Appendix S2

Correlations between explanatory variables derived from the LiDAR data set (X-axes) and the photogrammetry data set (Y-axes).

Appendix S3

Bubble plots of residuals from final models for each taxonomic group against the X/Y coordinates.

Appendix S4

Ranges of vegetation metrics varying in complexity from vegetation cover, tree canopy cover, mean, median and maximum canopy height to standard deviation of tree canopy height reflecting variation in tree canopy height. The metrics are derived from photogrammetry data for each buffer size (100, 250, 500, 1000m).

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Tables

Table 1 Model results for the set of best final models (ΔAICc<2) for each taxonomic group: bats (number of calls), bird (species richness), hoverfly (species richness) and bee (species richness). Explanatory variables were %vegetation cover (Veg. Cover), %tree canopy cover (Tree Cover), standard deviation of tree canopy height (STD height), and season (for birds only). Log and square root transformation of explanatory variables are indicated where relevant. Total %deviance explained for the final models, partial %deviance explained for significant explanatory variables, intercept, variable slope estimates (β-estimates), standard errors (Std. Error), AICc and N are given. N varies within taxonomic group due to the removal of outliers.

Response	Total deviation explained (%)	Partial deviation explained (%)	Intercept	β-estimates	Std. Error	AICc	N
Bats (no. calls); NB GLM, log link	45.50	Veg. Cover_500 (41.85), STD_250 (31.57), Tree cover_500 (21.09)	2.34	Veg. Cover_500 (0.04), STD_250 (0.56), Tree cover_500 (-0.06)	Veg. Cover_500 (0.01), STD_250 (0.12), Tree cover_500 (0.02)	395.19	29
Bats (no. calls)	48.96	Veg. Cover_500 (43.94), STD_250 (27.00), Tree cover_500 + Tree cover_500^2 (24.55)	1.82	Veg. Cover_500 (0.04), STD_250 (0.52), Tree cover_500 (0.01), TreeCover_500^2 (-0.002)	Veg. Cover_500 (0.01), STD_250 (0.12), Tree cover_500 (0.06), TreeCover_500^2 (0.001)	396.39	29
Bats (no. calls)	41.99	Veg. Cover_250 (38.33), STD_250 (24.86), Tree cover_500 (19.51)	2.81	Veg. cover_250 (0.03), STD_250 (0.46), Tree cover_500 (-0.06)	Veg. Cover_250 (0.01), STD_250 (0.12), Tree cover_500 (0.02)	397.09	29
Bird (species richness); Poisson GLM, log link	19.12	STD_1000 (11.78), sqrt (Tree cover_100) (5.53), season (0.29)	2.43	STD_1000 (0.11), sqrt (Tree cover_100) (0.02), season (0.02)	intercept (0.15), STD_1000 (0.04), sqrt (Tree cover_100) (0.01), season (0.04)	663.25	124

Bird (species richness)	21.33	STD_1000 (11.94), sqrt (Tree cover_100) (7.71), Veg. cover_250 (2.22), season (0.29)	2.48	STD_1000 (0.11), sqrt (Tree cover_100) (0.03), Veg. cover_250 (-0.001), season (0.02)	intercept (0.15), STD_1000 (0.04), sqrt (Tree cover_100) (0.01), Veg. cover_250 (0.001), season (0.04)	663.67	124
Bird (species richness)	20.32	STD_1000 (11.58), sqrt (Tree cover_100) (6.65), Veg. cover_100 (1.21), season (0.29)	2.46	STD_1000 (0.11), sqrt (Tree cover_100) (0.03), Veg. cover_100 (-0.001), season (0.02)	STD_1000 (0.04), intercept (0.15), sqrt (Tree cover_100) (0.01), Veg. cover_100 (0.001), season (0.04)	664.47	124
Bird (species richness)	20.00	STD_1000 (12.35), sqrt (Tree cover_100) (6.42), Veg. cover_500 (0.89), season (0.29)	2.46	STD_1000 (0.11), sqrt (Tree cover_100) (0.02), Veg. cover_500 (-0.001), season (0.02)	intercept (0.15), STD_1000 (0.04), sqrt (Tree cover_100) (0.01), Veg. cover_500 (0.001), season (0.04)	664.72	124
Bird (species richness)	19.47	STD_1000 (11.98), sqrt (Tree cover_100) (4.01), Median_100 (0.35), season (0.29)	2.45	STD_1000 (0.11), sqrt (Tree cover_100) (0.03), Median_100 (-0.01), season (0.02)	intercept (0.15), STD_1000 (0.04), sqrt (Tree cover_100) (0.01), Median_100 (0.01), season (0.04)	665.14	124
Bird (species richness)	19.40	STD_1000 (12.07), sqrt (Tree cover_100) (5.79), Veg. cover_1000 (0.28), season (0.29)	2.45	STD_1000 (0.11), sqrt (Tree cover_100) (0.02), Veg. cover_1000 (-0.001), season (0.02)	intercept (0.15), STD_1000 (0.04), sqrt (Tree cover_100) (0.01), Veg. cover_1000 (0.001), season (0.04)	665.20	124
Hoverfly (Species richness); Poisson GLM, log link	66.09	Veg. Cover_250 (62.68), log10(Tree cover_250) (39.46)	2.28	Veg. Cover_250 (0.02), log10(Tree cover_250) (-1.34)	intercept (0.27), Veg. Cover_250 (0.003), log10(Tree cover_250) (0.31)	113.16	24
Hoverfly (Species richness)	63.17	Veg. Cover_100 (59.77), log10(Tree cover_250) (37.50)	2.10	Veg. Cover_100 (0.02), log10(Tree cover_250) (-1.28)	intercept (0.27), Veg. Cover_100 (0.003), log10(Tree cover_250) (0.30)	114.62	24
Hoverfly (Species richness)	68.57	Veg. Cover_250 (65.14), log10(Tree cover_250) (33.39), STD_500 (2.48)	2.62	Veg. Cover_250 (0.02), log10(Tree cover_250) (-1.28), STD_500 (-0.12)	intercept (0.41), Veg. Cover_250 (0.004), log10(Tree cover_250) (0.32), STD_500 (0.11)	114.89	24

Hoverfly (Species richness)	68.14	Veg. Cover_250 (63.83), log10(Tree cover_250) (38.65), STD_1000 (2.05)	2.61	Veg. Cover_250 (0.02), log10(Tree cover_250) (-1.33), STD_1000 (-0.10)	intercept (0.42), Veg. Cover_250 (0.004), log10(Tree cover_250) (0.31), STD_1000 (0.10)	115.10	23
Bee (species richness); Poisson GLM, log link	48.40	Veg. Cover_100 (40.83), Tree cover_100 (30.20)	2.50	Veg. Cover_100 (0.01), Tree cover_100 (-0.02)	intercept (0.15), Veg. Cover_100 (0.003), Tree cover_100 (0.005)	134.90	24
Bee (species richness)	51.12	Veg. Cover_100 (42.25), Tree cover_100 (29.16), STD_100 (2.72)	2.35	Veg. Cover_100 (0.01), Tree cover_100 (-0.02), STD_100 (0.06)	intercept (0.21), Veg. Cover_100 (0.003), Tree cover_100 (0.007), STD_100 (0.06)	136.83	24
Bee (species richness)	51.47	Tree cover_100 (26.75), Veg. Cover_100 (17.45), log(Median_1000) (3.07)	1.84	Tree cover_100 (-0.02), Veg. Cover_100 (0.01), log(Median_1000) (0.82)	intercept (0.65), Tree cover_100 (0.005), Veg. Cover_100 (0.003), log(Median 1000) (0.78)	136.71	24

550 **Table 2** Translation of model results of model with lowest AICc for each taxonomic group into implications for conservation planning
551 practice. The *importance* category is derived from the partial deviation scores listed in Table 1. Low importance is an indication that the
552 presence of vegetation, trees, or trees of different heights might be less important than other site or context based variables (e.g. habitat
553 quality, disturbance or ecological connectivity).

Taxa	Important variable(s)	Most relevant scale	Direction	Implications	Importance
Bats	% vegetation cover	500m	Positive	A greater amount of vegetation at this spatial scale is associated with higher bat activity. We found increasing vegetation cover from 50% to 80% was associated with a tripling in bat activity. These results support the retention, creation and enhancement of even relatively small habitat patches within urban areas. Plausible causes include greater availability of their insect prey, more roosting sites or greater cover/darker areas to help avoid predators.	High
	Variation in tree canopy height	250m	Positive	Greater structural diversity potentially provides a broader variety of potential roosting and feeding habitats. The significance of this variable indicates the need for the retention of mature trees over medium spatial scales, as well as ensuring a diversity of tree size/age classes.	Medium
	% tree canopy cover (trees > 4m)	500m	Negative	Too dense/extensive tree cover may reduce habitat available for bat species which feed and commute along tree lines and forest edges.	Medium
Birds	Variation in tree canopy height	1000m	Positive	Greater structural diversity is known to provide a broader variety of potential territories, nesting and feeding habitats. This result indicates the need for the retention of mature trees over large spatial scales, as well as ensuring a diversity of size/age classes.	Low
	% tree canopy cover (trees > 4m)	100m	Positive	The greater potential for high bird species richness in areas with more trees at a local level may be due to higher availability of nesting and foraging sites.	Low
	% vegetation cover	250m	Negative	Minor contribution to the model – no obvious implications	Subsidiary
	Median canopy height	100m	Negative	Minor contribution to the model – no obvious implications	Subsidiary

Hoverflies	% vegetation cover	250m	Positive	We found a greater potential for high hoverfly species richness in areas of high vegetation cover. This could be due to higher availability of food resources (flowers and larval food sources). Increasing vegetation cover from 40% to 80% doubled hoverfly species richness. The results support the creation, retention and enhancement of even relatively small habitat patches within urban areas, but habitat quality should still be an important focus.	High
	% tree canopy cover (trees > 4m)	250m	Negative	Some hoverfly species prefer sunny patches and may be less abundant in areas shaded with high levels of tree canopy cover. The results support the need to be cautious about dense tree planting in areas where high pollinator diversity is desired.	High
	Variation in tree canopy height	500m	Negative	Minor contribution to the model – no obvious implications	Subsidiary
Bees	% vegetation cover	100m	Positive	We found a greater potential for high bee species richness in areas of high vegetation cover. This could be due to higher availability of food resources (flowers). Increasing small scale vegetation cover from 20% to 80% was associated with a doubling of bee species richness. The results support the creation, retention and enhancement of even relatively small habitat patches, but habitat quality should not be ignored.	High
	% tree canopy cover (trees > 4m)	100m	Negative	Most bee species prefer sunny/warm patches and as expected we found less species richness in areas of high tree cover. Increasing tree cover from 5% to 45% was associated with a reduction in bee species richness of 50%. Be cautious about dense tree planting where high pollinator diversity is desired.	Medium
	Variation in tree canopy height	100m	Positive	Minor contribution to the model – no obvious implications	Subsidiary
	Median canopy height	1000m	Positive	Minor contribution to the model – no obvious implications	Subsidiary

554

Figure legends

Fig. 1. Map of study sites for the four taxonomic groups (birds (n=68), bees (n=24), hoverflies (n=24) and bats (n=30)). The administrative boundaries for Birmingham and the West Midland are shown. Inset illustrates the approximate position of the West Midlands within the UK.

Fig. 2. Relationships between the best explanatory variables and species richness. Partial plots for the best model from each set of best models (Table 1) after accounting for uninformative variables as determined by AICc for each taxonomic group: a) bats, b) birds, c) bees and d) hoverflies) are depicted. As season did not have a substantial effect in the birds model both seasons are depicted with one line. The explanatory variables are vegetation cover (veg. cover, %), tree cover (%) and standard deviation of canopy height (STD) for the stated buffer sizes. Each row represents a model; points indicate raw values and dotted lines show 95 % credible intervals for the mean.

Fig. 3. Changes in a) %vegetation cover, b) %tree canopy cover and c) standard deviation (STD) of tree canopy height along gradients of built surface cover (according to Ordnance Survey Mastermap Data). The data were extracted at four different spatial scales (100, 250, 500 and 1000m radius buffers) using a 1km grid of points covering the West Midlands. Lines represent fitted Generalized Additive Models.

Fig. 4. Habitat suitability for bees and bats in the Selly Park neighborhood of Birmingham, UK. The varying vegetation cover and tree occurrence within the urban landscape affect the predicted bee species richness and bat activity. Right panel is an inset of the black box within the left panel. Row A) Aerial photograph of the Selly Park neighborhood, B) Variation in vegetation height. C) Predicted bee species richness based on the Poisson GLM model with lowest AICc (see Table 1). D) Predicted bat activity based on the Negative Binomial GLM with lowest AICc (see Table 1). To

577 illustrate the difference between the bee and bat models, we draw attention to a vegetated patch of
578 gardens with few trees (X) and an adjacent public green space with high levels of tree cover (Y).