



# Contrasting patterns in species richness of birds, butterflies and plants along riparian corridors in an urban landscape

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## ABSTRACT

**Aim** Urbanization is a major driver of global land-use change, substantially modifying patterns of biodiversity. Managing these impacts has become a conservation priority. The creation and maintenance of greenways, such as river corridors, is frequently promoted as a strategy for mitigating habitat fragmentation in urban areas by bringing semi-natural habitat cover into city centres. However, there is little evidence to support this assertion. Here, we examine whether riparian zones maintain semi-natural habitat cover in urban areas and how species richness varies along such zones.

**Location** Sheffield, Northern England.

**Methods** Multiple taxonomic groups (birds, butterflies, plants) were surveyed at 105 sites spanning seven riparian corridors that transect the study system. For all groups, we model the relationships between species richness and environmental variables pertinent to an urban system. To test whether riparian zones can act to maintain semi-natural habitats within a city, we modelled the proportion of semi-natural land cover within 250 m grid squares that do, and do not, contain a river.

**Results** Species richness varied markedly in relation to distance from the urban core. Trends differed both between taxonomic groups and between rivers, reflecting the complex patterns of environmental variation associated with cities. This suggests that biodiversity surveys that focus on a single group or transect cannot reliably be used as surrogates even within the same city. Nonetheless, there were common environmental predictors of species richness. Plant, avian and butterfly richness all responded positively to Habitat Diversity and the latter two declined with increases in sealed surface.

**Main conclusions** Multiple transects and taxonomic groups are required to describe species richness responses to urbanization as no single pattern is evident. Although riparian zones are an important component of the mosaic of urban habitats, we find that river corridors do not disproportionately support tree and Natural Surface Cover when compared to non-riverine urban areas.

## Keywords

Catchment, greenways, land-use change, rural–urban gradient, urban ecology, urbanization.

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## INTRODUCTION

Urbanization results in the most profound changes to the natural landscape of any human-driven land conversion (Marzluff & Ewing, 2001; Kareiva *et al.*, 2007). Even where semi-natural habitats remain within the urban matrix, their

structure, function and biodiversity value are altered by surrounding land-uses (Blair, 2004; McKinney, 2006, 2008; Shochat *et al.*, 2006). As a greater proportion of the world's population comes to live in cities (United Nations 2008), there is a growing interest in how existing land-uses can best be managed to ameliorate the urban environment. Greenspaces

have a key role to play, as they support biodiversity and a broad range of ecosystem services (Tratalos *et al.*, 2007; Tzoulas *et al.*, 2007; James *et al.*, 2009).

Rivers can be severely affected by urbanization. In many cases, they have been instrumental in the growth of cities because of the transport, food, power and waste removal services that they provide (Naiman & Decamps, 1997; Groffman *et al.*, 2003). Where vegetation is present, riparian zones can play a number of important roles, both for the rivers themselves (e.g. regulating water temperatures, providing woody debris) and as urban greenspaces. Many riparian zones are foci for recreational use (Groffman *et al.*, 2003) and support biodiversity (Pennington *et al.*, 2008), even allowing some species to persist that otherwise would not survive in the surrounding matrix (Naiman *et al.*, 1993; Oneal & Rotenberry, 2008). However, non-native species can be common because of additional nutrient availability (Moffatt *et al.*, 2004) and a high input of propagules from the surrounding landscape (Burton *et al.*, 2005; Loewenstein & Loewenstein, 2005).

Urban planning often recognizes the importance of riparian zones, and their associated greenspaces can be maintained as cities develop (e.g. Oneal & Rotenberry, 2008). The reduced likelihood of development could mean that riparian zones provide a disproportionate contribution to the greenspace provision in urbanized areas. Riparian zones (and other 'greenways') are assumed to mitigate the effects of habitat fragmentation by enhancing connectivity between otherwise isolated habitat patches, such as domestic gardens, parks and remnant woodlots (Bryant, 2006) and, therefore, allow continuity of semi-natural habitats into city centres. Such connectivity can facilitate wildlife movement and gene flow between populations and ultimately leads to improved habitat quality and biodiversity (Botkin & Beveridge, 1997; Savard *et al.*, 2000). However, edge effects associated with a linear habitat features (Martin *et al.*, 2006) may decrease the likelihood of species persistence in riparian zones. Species richness in these areas is also vulnerable to land-use changes associated with urbanization (Porter *et al.*, 2001; Groffman *et al.*, 2003; Moffatt *et al.*, 2004; Burton *et al.*, 2005; Oneal & Rotenberry, 2008, 2009; Pennington *et al.*, 2010).

Urban gradient analyses often assume a single urban–rural transition, with a highly developed core surrounded by areas of less intensive land-use (Chace & Walsh, 2006; McKinney, 2008). However, this pattern is a simplification of a complex mosaic, especially when considering river corridors, and we anticipate the response of species richness to urbanization will vary markedly between different riparian zones even across a single city. Here, using seven riparian corridors representing multiple rural–urban transects through the same city, we examine land cover trends and patterns of species richness from several taxa. We answer the following questions: (1) are there associations between species richness and distance from the centre of a city along river corridors, and to what extent are patterns the same across multiple taxa and river corridors? (2) What characteristics of the urban environment are associated with the observed patterns in species richness in riparian

zones? Finally, (3) do riparian zones disproportionately support higher amounts of semi-natural habitat than other urban land-uses?

## METHODS

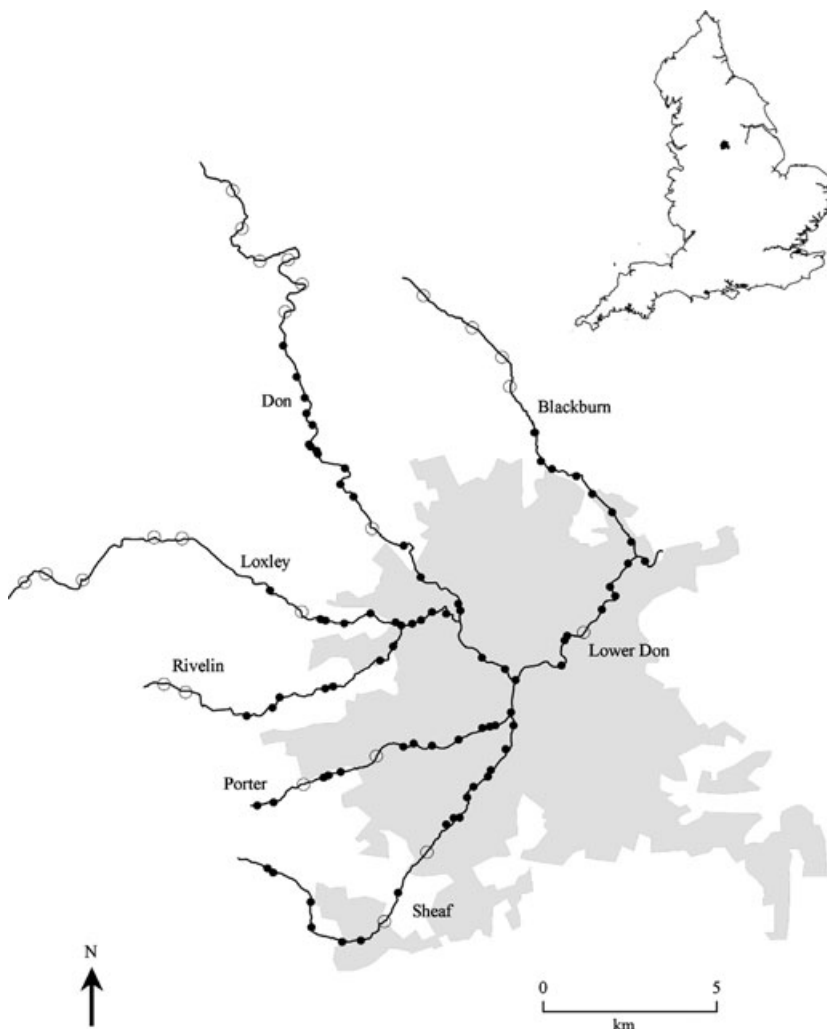
### Study area

Sheffield (53°22'N, 1°20'W), in the county of South Yorkshire, is a typical large city in England with respect to greenspace provision (Dallimer *et al.*, 2011) and, at the last census in 2001, had a human population of 513,234 at a density of 13.9 people per ha (ONS 2001). The city is bordered to the east by neighbouring urban centres, to the south, west and north by agricultural production. Hence, like the majority of cities worldwide, Sheffield is largely surrounded by human-managed landscapes with a mosaic of semi-natural habitats. The findings of this study are, therefore, likely to generalize widely. Sheffield lies at the confluence of five rivers, the Loxley, Rivelin, Porter, Sheaf and Don. A sixth, the Blackburn, enters the city on its Eastern fringes where it joins the Don (Fig. 1). The rivers have a long history of human exploitation and their physical properties have been critical in determining the development of Sheffield (Crossley & Cass, 1989). Water and water power were important drivers of the industrial development that took place during the 19th century. Industrial output and the human population peaked in the 1950s and both contracted rapidly through the latter half of the 20th century, resulting in large areas of vacant former industrial land by the mid-1980s, and a 10.4% fall in population between 1971 and 2001 (Hey, 2005). Pollution and environmental degradation followed the rapid urbanization, and despite the early recognition of the importance of greenspaces associated with rivers (Abercrombie, 1924), the Don remained one of the most polluted rivers in Europe through to the 1980s (Firth, 1997).

Across Sheffield, urbanization and industrialization has left watercourses heavily modified, with altered hydrology and extensive canalization. Weirs are common, and large sections of the Porter and Sheaf in the city centre are culverted. The Lower Don (the stretch of the Don downstream of its confluence with the Sheaf, when it flows away from central Sheffield; Fig. 1) is still dominated by large-scale industrial and commercial use. In contrast, long-established public parks are located along the Porter, Rivelin and Sheaf that pass through residential areas of south and west Sheffield.

### Species richness surveys

Species richness in urban areas responds to a variety of variables, such as habitat heterogeneity and the level of urbanization. However, crucially, the form of such relationships can depend on taxonomic group (Chace & Walsh, 2006; McKinney, 2008). We selected birds, butterflies and plants as three terrestrial taxa which, for this region, have a sufficiently high number of species for there to be variation across the study system.



**Figure 1** The urban area of Sheffield (shaded), showing the major rivers running through the city (solid lines) and survey points (filled circles butterfly, plant and birds were all surveyed, open circles plant and bird surveys only). The inset shows location of the study area in England.

To ensure that our sampling adequately covered the environmental variation in the study area, we followed Gradsect survey design principles by characterizing Sheffield according to land cover type and river features at a 250 m grid square resolution (Appendix S1 in Supporting Information; Austin & Heyligers, 1989). This provided 80 survey sites in the urban area and immediate rural surroundings (Fig. 1). To extend the transects, an additional 26 survey sites were placed along rivers at increasing distances from the urban centre, giving 106 sites (Appendix S1). A single site had access restrictions imposed during the field season, resulting in a final total of 105 (79 using the Gradsect survey design).

Bird surveys were carried out at the 105 sites on two separate visits between 29 March and 26 June 2009 to coincide with the breeding season, with the second visit at least 6 weeks after the first. To ensure that the maximum number of species was encountered, visits began between 1 and 3 h after sunrise (the time of highest bird activity) and were only carried out in suitable weather conditions (low wind, no rain or mist). For each visit, a single observer (MD) recorded the identity of each bird that was seen or heard from the survey point over a 5-min period, excluding individuals that were flying over the site. Any birds that flushed as the observer approached the survey

location were also recorded as being present. A list of all species encountered during both visits was collated. Previous research in Sheffield (Fuller *et al.*, 2009) indicated that bird detectability is unaffected by site characteristics, allowing us to compare species richness estimates directly between sites.

Butterflies were surveyed at 79 sites, with each location visited three times (late May/early June, July and August). The additional survey visits required for butterflies precluded us from using the full set of 105 sites. Surveys took place between 10.30 and 15.30, in suitable weather conditions (mostly sunny with low wind). Centred on the avian point count location, a 40 m by 10 m area (long axis parallel to the river) was searched for butterflies for a fixed 15-min time period. An active search method was chosen in preference to standard transects (Pollard, 1977) as, in many cases, difficult access prevented transects being walked. Pilot studies indicated that, even in the densest vegetation found in the study sites, the full area could be searched. This reduces the possibility that our results would be confounded by detectability differences between sites and enables non-biased comparisons of butterfly richness between sites. All butterflies within the survey area and time period were noted, and a list of species encountered across three visits compiled. Whites (*Pieris*) were recorded to genus level only

because of difficulties with consistently identifying individuals in the field.

Plants were surveyed at 99 of the 105 sites (access restrictions prevented surveys at six sites). A 40 m by 10 m area (the same as the butterfly survey area) was exhaustively searched. The presence of all forbs and woody plant species was recorded to produce a species list. This was further subdivided into four assemblages indicating the origin of each species (native, archaeophyte, neophyte, uncertain; Preston *et al.*, 2002). For all taxa, the number of species observed was used directly as the measure of species richness. To allow a common scale to be used across multiple taxa for which different numbers of species were recorded, richness for each was standardized with a mean of zero and a variance of one.

### Associations between distance to the city centre, richness and land-use

Species richness is likely to vary with proximity to the centre of a city (Chace & Walsh, 2006; McKinney, 2008). Therefore, for each taxonomic group, we tested for the presence of a bivariate relationship between richness and distance from central Sheffield (here defined as the confluence of the rivers Sheaf and Don; Fig. 1), using Akaike's Information Criterion (AICc corrected for small sample sizes) to choose the most parsimonious representation between competing model forms along each river transect (no relationship, linear or quadratic).

If riparian zones do bring natural habitat into city centres and, therefore, have the potential to function as ecological corridors, we predict that the coverage by semi-natural habitat should be higher closer to the city centre where a river is present compared to where it is not. To test this hypothesis, we used land cover in the 250 m grid squares to model the proportion of each square covered by Natural Surfaces and trees against increasing proximity to central Sheffield for riparian (squares containing a watercourse) and non-riparian (squares without a watercourse) zones.

### Environmental characterization of the survey points

We characterized the environmental variation across the riparian zones and carried out multiple regression to determine which variables were most strongly related to species richness. Variables used included measures of land cover (Water Bodies and Tree Cover), aspects of topography (altitude, distance from source), proxies for urbanization (sealed surface, human population density) and Habitat Diversity, all of which vary spatially across the landscape and could be related to species richness patterns.

Land cover characteristics were determined in a 50 m radius around each survey point in a GIS, based on the classification of surface cover polygons by Ordnance Survey within the MasterMap digital cartographic dataset (Murray & Shiell, 2003). This distance was chosen to represent adequately the immediate local surroundings of the survey point. The MasterMap classifications were grouped into three categories

– Natural Surface, Water Bodies and sealed surfaces. Natural Surface included all land covers that were defined as green-space (e.g. domestic gardens, woodlots, public parks), while sealed surfaces comprised all buildings and hard surfaces. Water Bodies included the rivers themselves, plus ponds, reservoirs and lakes. Tree Cover was mapped in a GIS by manually tracing around each tree or group of trees shown in aerial photographs (Davies *et al.*, 2008). Human population density was calculated within a 50 m radius of each survey point based on a human population density surface created using the Surface Builder tool (Martin, 1989) and 2001 census data for Sheffield. Distance from source was quantified in a GIS by measuring the distance along the river channel from the survey site to the Source of the river, that is, the furthest point upstream where the river is still marked on the GIS. Altitude was measured in the field using a hand-held GPS. Finally, Habitat Diversity at each site was calculated using the Shannon diversity index based on the percentage cover of broad habitat types recorded in the field across the same 40 m by 10 m search area that was surveyed for butterflies and plants (for a description of the possible habitat types see Appendix S2).

### Data analysis

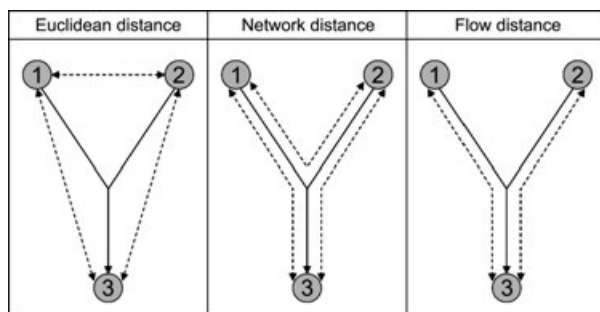
Multiple regression models were constructed using standardized species richness as response variables and were carried out using R version 2.10.0 (R Development Core Team 2009). For many taxonomic groups, the general form of the relationships between richness and different metrics of urbanization (here sealed surface and human population density) is for richness to peak at intermediate levels (Chace & Walsh, 2006; McKinney, 2008), a pattern that can often be simply described by including quadratic predictor terms in a linear regression. However, including such terms for all variables could lead to over specified models. To avoid this, we only included quadratic terms for environmental variables that exhibited bivariate quadratic relationships with a given measure of species richness. For each response variable (avian, butterfly, total plant, native plant and neophyte plant richness), we tested for the presence of bivariate quadratic relationships with the explanatory variables. Where models containing the quadratic term were most parsimonious (lowest AICc), these terms were included in the modelled set of explanatory variables, otherwise a linear relationship was assumed.

We tested the collinearity of the explanatory variables and discarded any with a variance inflation factor (VIF) that was  $> 3$  (Zuur *et al.*, 2010). Both distance from source and Natural Surface Cover had VIFs greater than this threshold value so were not considered further, resulting in a final set of six environmental variables. We constructed all possible model combinations of these, using AICc comparisons to identify the most parsimonious model and also a subset of models offering parsimonious explanations for variations in the data. This subset includes those with an AICc score within two of the minimum (Burnham & Anderson, 2002). We calculated the model-averaged parameter estimates for this model set using

model weights. Further, we examined the relative importance of each variable in explaining species richness by calculating  $w_i$ , the Akaike weight, for each predictor variable.

We also expect that the patterns of species richness might show a strong spatial structure. Spatial autocorrelation does not cause problems for linear regression when both the extrinsic causes of the spatial patterning are accounted for by the spatial structure of the measured explanatory variables, and where there is no intrinsic cause of spatial autocorrelation in the response variable, such as patterns driven by dispersal (Beale *et al.*, 2010). Although we cannot dismiss the latter possibility, instead of explicitly including the spatial patterning in the modelling process, we assessed the form and significance of spatial autocorrelation remaining in the residuals of the most parsimonious models using the global Moran's  $I$  test in SPDEP v0.4-54 (Bivand, 2009).

When testing for spatial structure in riparian systems, a standard Euclidean distance matrix may not be ecologically meaningful, as it fails to represent the spatial configuration, connectivity and directionality of river networks (Peterson *et al.*, 2007). All sites in a given riparian network are physically connected in two additional ways (Fig. 2). First, terrestrial taxa in riparian zones may, to a greater or lesser extent, be restricted to them. Hence, the relationship between sites may be influenced by the distance between them when following the riparian network (Network distance). Second, water flow may influence the passive dispersal of plant propagules, especially for invasive species (Säumel & Kowarik, 2010). Therefore, for 'Flow Distance', only sites that are joined by water flow are connected by distances. We assigned identical distances in both directions for sites that are connected by water flow. Although downstream sites do not affect upstream sites, the conditions at the downstream site could be influenced by the upstream



**Figure 2** Distance classes that are relevant to a network of riparian zones. The riparian network is represented by solid lines, with the direction of water flow indicated by the arrow, while distance measurements are represented by dotted lines. For the Euclidean distance, all sites are connected to one another by the shortest straight line distance. With the Network distance, all sites are connected, but the line follows the riparian network. For the Flow Distance, only sites that are joined by flow are connected by distances. In this example, sites 1 and 2 are connected to site 3, but they themselves are not connected as to get from site 1 to site 2 would require a movement against the direction of flow (after Peterson *et al.*, 2007).

site, and hence, there is a symmetric correlation between them (Peterson *et al.*, 2007).

## RESULTS

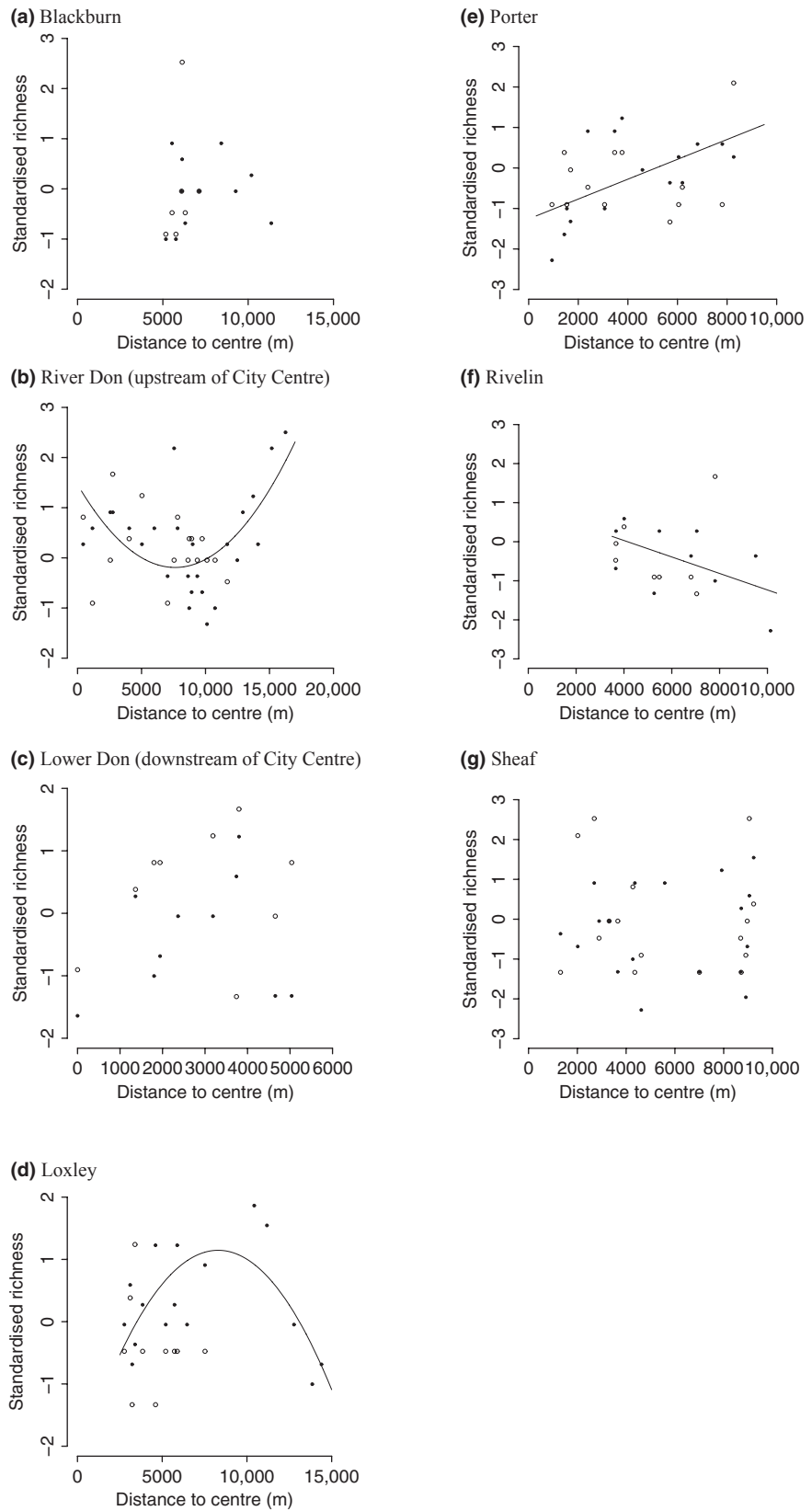
A total of 74 bird (median 11, range 4–19 per site), 21 butterfly (median 3, range 0–9) and 363 plant species (median 43, range 9–95) were observed across the riparian corridors in and around Sheffield (Appendix S3). The 74 bird species observed during the surveys comprise about 88% of the 84 species which occur regularly within Sheffield (Hornbuckle & Herringshaw, 1985). The butterfly species encountered represent 75% of the 28 species recorded in South Yorkshire (Sorby Natural History Society, 2003). The regional species pool for plants, however, is much larger, and only around 18% of the more than 2000 species found within South Yorkshire (Wilmore *et al.*, 2011) were recorded.

Of the plant species, 226 (62%) were native, 103 (28%) were neophytes, 28 (8%) were archaeophytes, and six (2%) were of uncertain origin. Because of a limited number of archaeophytes and species of uncertain origin, only native and neophyte plant richness were used as response variables in subsequent analyses. Native plant richness varied from 6 to 69 species per site (median 36), while neophyte plant richness ranged from 0 to 19 (median 5), with three sites consisting solely of native plants. Butterfly richness was positively correlated with avian (Spearman's rank correlation,  $r_s = 0.305$ ,  $n = 79$ ,  $P = 0.006$ ) and total plant richness ( $r_s = 0.230$ ,  $n = 79$ ,  $P = 0.037$ ), but no correlation existed between avian and plant richness ( $r_s = 0.141$ ,  $n = 99$ ,  $P = 0.158$ ).

The most ubiquitous species of bird were the wren (*Troglodytes troglodytes*), blackbird (*Turdus merula*) and woodpigeon (*Columba palumbus*), occurring at 100 (95%), 80 (76%) and 80 sites, respectively. Twenty-five species were recorded from a single site. Only three non-native species were encountered (feral pigeon *Columba livia*, pheasant *Phasianus colchicus* and ring-necked parakeet *Psittacula krameri*). Excluding whites (observed at 62 sites, 78%), the most widespread butterfly species was the speckled wood (*Pararge aegeria*; 51 sites, 65%). Ten species were recorded on fewer than five sites, including two species, the white-letter hairstreak (*Satyrrium w-album*) and the dark green fritillary (*Argynnis aglaja*) which were only observed at single sites. The most frequently encountered plant species were bramble (*Rubus fruticosus*) and dandelion (*Taraxacum agg.*) occurring at 85 (85%) sites. Sycamore (*Acer pseudoplatanus*; 82 sites; 82%) and Indian balsam (*Impatiens glandulifera*; 59 sites, 59%) were the most widely distributed neophytes. Only one of the 20 most widespread plant species was non-native (the sycamore). A total of 113 (49 neophytes) plant species occurred at single sites.

Associations between richness and distance from the city centre varied across taxa and rivers, and the environmental variables associated with these transects also differed between the taxonomic groups. For avian richness, no one form of relationship was consistently observed across individual rivers (Fig. 3). Instead, a full range of patterns with distance from the





**Figure 3** Urban-rural gradients along riparian zones in Sheffield. Patterns of avian (solid circle) and butterfly (open circle) species richness (standardized with a mean of 0 and variance of 1), with increasing distance from central Sheffield for sites surveyed along seven major riparian corridors. Solid lines show relationships for avian richness. Where no line is drawn, the null model was more parsimonious (lower AICc). No relationships are present for butterfly richness. AICc, Akaike's Information Criterion.

urban core was observed, including no relationship (Fig. 3a,c), a decline (Fig. 3f), an increase (Fig. 3e), a peak (Fig. 3d) and a trough (Fig. 3b). When considering the environmental drivers

that might be responsible for these patterns, we did not find humped relationships with either of the measures of urbanization used here (sealed surface or human population). Avian

richness did, however, respond negatively to sealed surface and increased with Habitat Diversity (Table 1; Appendix S4).

Butterfly richness did not change with increasing proximity to the urban core along any riparian corridor (Fig. 3). When considering the environmental drivers, butterfly richness responded differently to two measures of urbanization; peaking at intermediate levels of human population density, but declining with increasing sealed surface cover. Richness was positively related to Habitat Diversity and declined with altitude. However, the strongest relationship was for richness to increase with declining Tree Cover (Table 1; Appendix S4).

Patterns in total plant richness were undoubtedly influenced by conflicting drivers for the native and neophyte assemblages. Along individual rivers, native richness tended to show no trend (Fig. 4) although richness peaked at intermediate distances in one instance (Fig. 4d) and was highest closer to the city centre for the river Sheaf (Fig. 4g). In contrast, neophyte richness increased closer to the urban core along all rivers (Fig. 4) with the single exception of the Lower Don riparian corridor (Fig. 4c). Here, the trend in neophyte richness was reversed and increased with distance from the city centre. However, the Lower Don flows out from the urban core, effectively meaning that, in all cases, neophyte richness increased in the direction of the flow of each river. Native richness did not respond to either measure of urbanization examined but was positively related to coverage by water and Habitat Diversity. Nevertheless, the explanatory power of the models remained poor. Neophyte richness was positively related to both metrics of urbanization, while declining with Tree Cover and Habitat Diversity (Table 1; Appendix S4).

There was no evidence for the presence of spatial autocorrelation in the residuals of any environmental models (Table 2) regardless of the autocorrelation matrix used. The strongest (although still non-significant) spatial signal was in the residuals of neophyte richness when tested against Flow Distances. However, when these spatial relationships were explicitly included in the modelling process, there were no substantive changes in the parameter estimates of the environmental variables of the most parsimonious model. Conclusions based solely on the non-spatial regression models were, therefore, considered to be robust and are reported here.

Land-use at the 250 m grid square level was highly variable at all distances from the urban core (Fig. 5). However, the

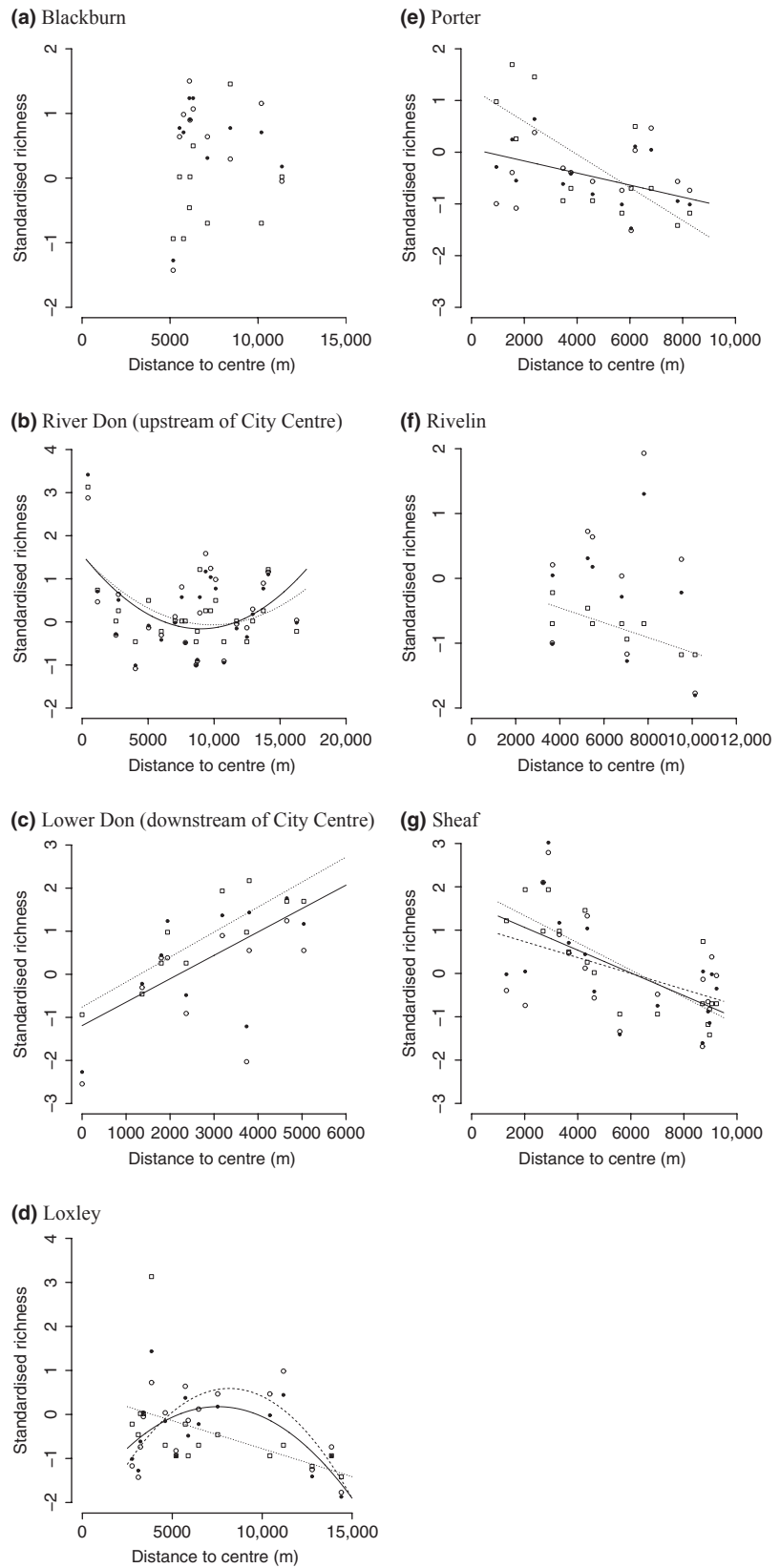
general trends were that Natural Surface Cover was low in central Sheffield, rising to 100% at greater distances. In contrast, Tree Cover was lowest at greater distances from the centre, reflecting the lack of trees in the agricultural and upland landscapes surrounding Sheffield. Tree Cover peaked at intermediate distances of 5–6 km from the city centre, before declining again towards the urban core. Riparian grid squares did have significantly more Tree Cover (0.149 compared to 0.092) and Natural Surface Cover (0.039 compared to 0.003) than non-riparian squares (Wilcoxon rank sum test,  $W = 2,496,603$ ,  $P < 0.001$ ; and  $W = 5,200,132$ ,  $P < 0.001$ , respectively). However, there was no substantive difference between the relationships for grid squares that did or did not contain rivers in relation to distance from the centre (Fig. 5).

## DISCUSSION

Anthropogenic habitat loss and fragmentation, leading to small isolated habitat patches that do not support viable populations (Soulé, 1987; Fahrig, 2003), is as detrimental to the persistence of species in urban areas as it is in the wider countryside. To overcome these processes, enhanced habitat connectivity is commonly promoted as a way to sustain biodiversity by facilitating movements between populations that may otherwise be isolated. Whether this is best achieved via corridors remains uncertain (Hobbs, 1992; Simberloff *et al.*, 1992; Beier & Noss, 1998; Bennett, 1999; Haddad & Tewksbury, 2005). Nevertheless, the importance of retaining vegetation cover in urban landscapes is well recognized as it promotes species persistence and provides other ecosystem services such as microclimate regulation, control of pollution, carbon storage, recreational opportunities and health benefits (Tratalos *et al.*, 2007; Tzoulas *et al.*, 2007; James *et al.*, 2009). Vegetation cover is often negatively correlated with measures of urbanization, such as housing density and sealed surface cover (for Sheffield, Davies *et al.*, 2008), a pattern that is repeated in riparian zones (e.g. survey site level Natural Surface Cover was negatively correlated with both sealed surface  $r = -0.743$ ,  $n = 105$ ,  $P < 0.001$  and human population density  $r = -0.324$ ,  $n = 105$ ,  $P < 0.001$ ). Vegetation cover and structure are key determinants of urban biodiversity (Fernandez-Juricic, 2004; Oneal & Rotenberry, 2009). Hence, without these

**Table 1** For those variables that appear in the  $\Delta AIC < 2$  model set, the relationship (+ve, -ve, those that appear in the most parsimonious are in bold) between species richness for five taxonomic groups and environmental variables along the riparian zones of Sheffield. n.a. indicates that square terms were not included in the multiple regression modelling process. Where no symbol is given, variables did not appear in the  $\Delta AIC < 2$  model set.

Response	Sealed surface	Water	Tree	Tree <sup>2</sup>	Habitat diversity	Human population	Human population <sup>2</sup>	Altitude	Altitude <sup>2</sup>	R <sup>2</sup>
Avian	-ve		-ve	-ve	<b>+ve</b>		-ve	<b>+ve</b>	<b>-ve</b>	0.28
Butterfly	<b>-ve</b>		<b>-ve</b>	n.a.	<b>+ve</b>	<b>+ve</b>	<b>-ve</b>	-ve	n.a.	0.24
Total plant	<b>+ve</b>	<b>+ve</b>	<b>-ve</b>	n.a.	<b>+ve</b>	-ve	n.a.	<b>-ve</b>	n.a.	0.17
Native plant	<b>+ve</b>	<b>+ve</b>	<b>+ve</b>	-ve	<b>+ve</b>	-ve	n.a.	-ve	n.a.	0.08
Neophyte plant	<b>+ve</b>	<b>+ve</b>	<b>-ve</b>	n.a.	-ve	<b>+ve</b>	n.a.	<b>-ve</b>	n.a.	0.38



**Figure 4** Urban-rural gradients along riparian zones in Sheffield. Patterns of total (solid circles), native (open circle) and neophyte (open square) richness (standardized with a mean of 0 and variance of 1) with increasing distance from central Sheffield for sites surveyed along seven major riparian corridors. Lines show relationships (solid- total, dashed – native, dotted - neophyte). Where no line is drawn, the null model was more parsimonious (lower AICc). AICc, Akaike’s Information Criterion.

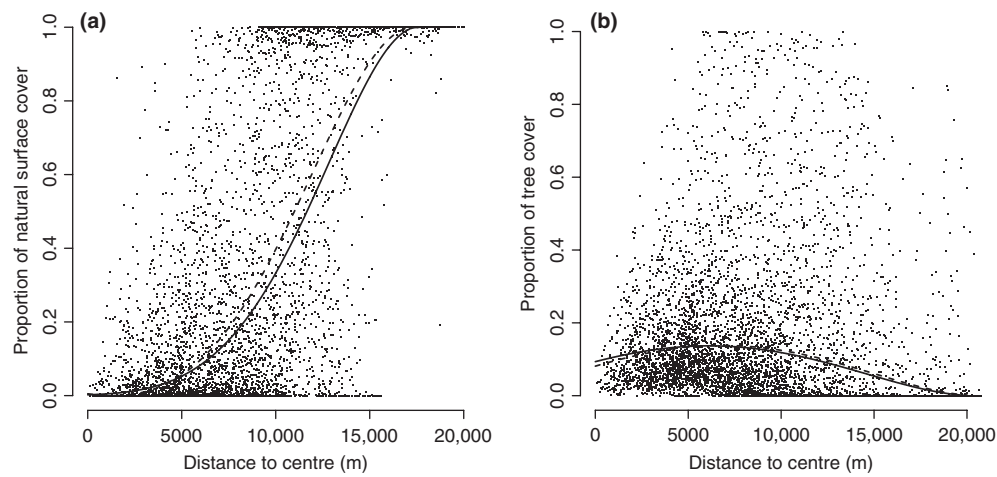
structural components of habitat, it is unlikely that biodiversity would be able to persist in riparian corridors in the urban core of the city.

Here, we found non-uniform responses to increasing distance from the city centre both between taxonomic groups (Chace & Walsh, 2006; McKinney, 2008) and within individual



**Table 2** Spatial autocorrelation in the residuals for environmental models of species richness in riparian zones of Sheffield. (multiple tests Bonferroni corrected threshold significance level 0.0167).

	Euclidean		Network		Flow	
	Moran's <i>I</i>	<i>P</i> -value	Moran's <i>I</i>	<i>P</i> -value	Moran's <i>I</i>	<i>P</i> -value
Avian	-0.010	0.828	-0.009	0.675	0.004	0.440
Butterfly	-0.011	0.427	-0.013	0.883	-0.014	0.950
Total plant	-0.010	0.492	-0.012	0.568	0.003	0.483
Native plant	-0.010	0.655	-0.010	0.979	0.018	0.121
Neophyte	-0.011	0.993	-0.012	0.425	0.025	0.056

**Figure 5** Proportion of 250 m grid squares covered by (a) Natural Surface and (b) trees with increasing distance from central Sheffield. Lines represent the relationships between cover and distance for squares that do not (solid) and do (dashed) contain a river.

groups for different riparian corridors, re-enforcing our expectation that urbanization does not exert common impacts across taxa (cf. Blair, 1999; Bräuniger *et al.*, 2010). Avian richness exhibited a range of relationships (increasing, decreasing or humped) with distance from the urban core. Although neophyte richness behaved relatively consistently, increasing in the direction of flow along each river, this resulted in richness being both higher and lower closer to the urban core. In contrast, for native plants and butterflies, the combination of land-uses and habitat heterogeneity along the riparian corridors of Sheffield maintains diversity at similar levels.

Our results emphasize that it is not appropriate to study a single transect if the aim is to understand how urban land-use and metrics of urbanization may affect species richness. Further, based on evidence presented here, it is unlikely that patterns observed in any one group may broadly represent how other taxa might be distributed across urban areas (Bräuniger *et al.*, 2010).

The lack of any relationship between butterfly richness and distance from central Sheffield along all seven riparian transects contrasts with the variety of patterns observed in birds and illustrates that the two cannot be reliably used as surrogates for one another in biodiversity surveys (cf. Blair, 1999), a conclusion that is likely to hold across other taxa not

surveyed here, such as small mammals or less mobile invertebrate groups. When considering the environmental drivers, butterfly richness responded differently to two measures of urbanization; peaking at intermediate levels of human population density (Hogsden & Hutchinson, 2004; Clark *et al.*, 2007), but declining with increasing sealed surface cover, the latter relationship is consistent with previous research indicating that, in general, invertebrate richness declines with increasing urbanization (Clark *et al.*, 2007; McKinney, 2008). One important factor might be that the provision of nectaring plants can promote butterfly diversity in urban areas (Clark *et al.*, 2007). While we did not measure this characteristic, butterfly richness increased with Habitat Diversity but was not positively correlated with plant richness. Previous studies of avian richness have demonstrated a consistent pattern of richness peaking at intermediate levels of urbanization (Chace & Walsh, 2006). Here, avian richness decreased with increasing coverage by sealed surfaces and showed little response to human population density. Avian richness did, however, respond negatively to increased Tree Cover and positively to Habitat Diversity (Fernandez-Juricic, 2004; Oneal & Rotenberry, 2009).

In cities, we may expect socio-economic factors and householder behaviour to affect species richness (Hope *et al.*,

2003; Fuller *et al.*, 2008; Loss *et al.*, 2009). However, richness in riparian zones is less likely to be associated with these variables than other urban areas. Although heavily influenced by industrial and commercial development, riverine areas in Sheffield do not feature large areas of domestic gardens. Where greenspaces exist, they tend to be publicly owned or managed, semi-natural in character and not dominated by domestic plant varieties or formal planting. For example, here, only 28% of plant species were neophytes, compared to over 70% of flora in domestic gardens (Loram *et al.*, 2008). Nevertheless, non-native plants can be more prevalent in urban riparian zones because of increased levels of disturbance and a high availability of propagules from the surrounding landscape (Moffatt *et al.*, 2004; Burton *et al.*, 2005; Loewenstein & Loewenstein, 2005). Here, neophyte richness increased in the direction of water flow along each river corridor where a relationship was present, consistent with non-native plant propagules being dispersed by running water (Säumel & Kowarik, 2010). Neophyte richness was higher with raised levels of built surface. In contrast, native plant richness showed only a weak relationships with the two measures of urbanization (sealed surface cover and human population density), but increased with variables representing semi-natural habitat quality (Habitat Diversity and Tree Cover).

## CONCLUSIONS

We can expect patterns of species richness observed along transects of increasing distance from city centres to reflect the complex interactions among environmental gradients, socio-economic characteristics of neighbourhoods, householder behaviour and species ecological traits (McKinney, 2008). To date, studies have failed to examine patterns from multiple taxa along many transects within the same region. Doing so allows us to assess the different responses of taxa to the same environmental variables and provide recommendations for how any management might benefit the broadest range of biodiversity. Only avian and plant species richness were not significantly correlated and a number of environmental variables have common effects. Avian, butterfly and native plant richness are all augmented by increased Habitat Diversity. Both avian and butterfly richness decline with increasing sealed surface coverage, while neophyte plant richness increases. Management actions across the riparian zones of Sheffield, such as improving the diversity of habitats and providing a greater amount of Natural Surfaces, will, therefore, act to enhance the species richness of the broadest range of taxa. However, without adequate strategies aimed at mitigating the negative effects of increased coverage by sealed surfaces, the growing call to densify UK cities (DCLG 2006) is likely to result in an urban environment that is home to an increasingly depauperate flora and fauna.

Urban planning regularly promotes preserving or enhancing greenspace along riparian corridors or other 'greenways' (Bryant, 2006; Fábos & Ryan, 2006; Mason *et al.*, 2007), despite a lack of evidence that corridors are beneficial to

biodiversity in cities other than through the habitat they provide. Greenways and riparian zones are undoubtedly an important part of the mosaic of urban habitats. However, land-use in the riparian zones of Sheffield demonstrates that the changes in tree and Natural Surface Cover with increased proximity to the urban core are no different from non-riparian zones. If we consider area of habitat alone, other forms of urban greenspace, such as domestic gardens, public parks or other linear features such as abandoned railway lines, could be equally able to enhance connectivity in urban settings.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Details of the Gradsect survey design.

**Appendix S2** Mean percentage cover of broad habitat types within the 40 m by 10 m plant and butterfly survey area across all surveyed points.

**Appendix S3** A list of all species of birds, butterflies and plants encountered during the surveys.

**Appendix S4** Relationship between species richness for five taxonomic groups and environmental variables along the riparian zones of Sheffield.

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## BIOSKETCH

This research forms part of a larger research project (Urban Rivers and Sustainable Living Agendas; 'URSULA'; website <http://www.ursula.ac.uk/>), which aims to investigate the sustainable development of urban river corridors.

Author contributions: M.D., J.R.R., P.R.A., L.L.M., P.H.W., K.J.G. conceived the ideas. M.D., A.M.J.S. and J.R.R. collected the data, and M.D. analysed the data and led the writing.

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