promoting access to White Rose research papers

Universities of Leeds, Sheffield and York
http://eprints.whiterose.ac.uk/

White Rose Research Online URL for this paper:
http://eprints.whiterose.ac.uk/78899

Published paper

**BIODIVERSITY
RESEARCH**

Species turnover and geographic distance in an urban river network

James R. Rouquette[1]*, Martin Dallimer[1,2], Paul R. Armsworth[1,3], Kevin J. Gaston[1,4], Lorraine Maltby[1] and Philip H. Warren[1]

[1]*Department of Animal and Plant Sciences, The University of Sheffield, Sheffield S10 2TN, UK,* [2]*Department of Food and Resource Economics, Center for Macroecology, Evolution and Climate, University of Copenhagen, Rolighedsvej 23, 1958 Copenhagen, Denmark,* [3]*Ecology and Evolutionary Biology, The University of Tennessee, Knoxville, TN 37996-1610, USA,* [4]*Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9EZ, UK*

[This is a revised copyright line on 5 March 2014.]

ABSTRACT

Aim Understanding the relationships between species turnover, environmental features and the geographic distance between sites can provide important insights into the processes driving species diversity. This is particularly relevant where the effective distance between sites may be a function of the habitat or topographic features of the landscape and the means of dispersal of the organism. River networks, in particular in human-modified landscapes, are a striking example of such a situation. Here, we use data for both aquatic and terrestrial organisms across an urban river network to examine patterns of species turnover and to determine whether these patterns differ between different taxonomic groups.

Location Sheffield area, UK.

Methods Aquatic (macroinvertebrates, diatoms) and terrestrial (birds, plants, butterflies) organisms were surveyed at 41 sites across an urban river network. We assessed the relationship between turnover and three alternative geographic distance measures (Euclidean, network and flow distance), whilst also taking into account the environmental distance between sites, using Mantel and partial Mantel tests.

Results Turnover of all taxonomic groups apart from butterflies was significantly correlated with at least one measure of geographic distance. The aquatic taxonomic groups showed the strongest correlations with the geographic distance measures, and in particular with network distance. Terrestrial taxa were more closely associated with environmental than any of the geographic distance measures, although network distance remained significant for birds and some plant groups after removing the effect of environmental distance. Water-dispersed and neophyte plant groups were significantly related to network and flow distance.

Main conclusions The results suggest that aquatic communities are strongly influenced by spatial processes occurring within the river network. Terrestrial taxa have a more complex relationship with distance, with different components of these communities displaying different responses. Nevertheless, it is clear that connectivity along the river corridor is important for both aquatic and terrestrial communities.

Keywords

Geographic distance, Mantel tests, riparian, river corridor, species turnover, urban ecology.

*Correspondence: James R. Rouquette, Department of Environmental and Geographical Sciences, The University of Northampton, St George's Avenue, Northampton, NN2 6JD, UK. E-mail: Jim.Rouquette@northampton.ac.uk

INTRODUCTION

Patterns in species turnover among sites, and in particular the relationships between species turnover, environmental features and the geographic distance between sites, can provide important insights into the processes driving species diversity at both local and regional scales (Soininen *et al.*, 2007a). The similarity of species composition between two sites typically decreases as the distance between them increases (Nekola & White, 1999; Tuomisto *et al.*, 2003; Soininen *et al.*, 2007b; Morlon *et al.*, 2008). Yet, the rate and nature of the decrease can differ according to the processes driving community composition and according to what determines the effective distance between sites (that is, the distance of the actual route by which organisms can move between them). This issue is particularly relevant where the effective distance between sites may be a function of the habitat or topographic features of the landscape, as well as the means of dispersal of the organism. Such distinctions are especially obvious where sites are connected by habitat corridors, to form a network. River corridors, in particular in human-modified landscapes, are a striking example of such a situation.

Geographic distance between sites in a river network can be measured in a number of different ways (Peterson *et al.*, 2006, 2007). Euclidean distance is the straight line distance between two sites (Fig. 1), but may not be ecologically representative because it fails to take into account the spatial configuration, connectivity, directionality and relative position of sites in a river network (Peterson *et al.*, 2006). Network distance takes into account some of these issues, because it measures the distance between two sites along the network, irrespective of flow direction. Flow distance takes into account the directionality of the network, as it measures the distance between sites along the network, where sites are only connected if water flows between them (Fig. 1). For sites that are flow-connected, flow distance is the same as network distance.

The significance of river networks is not confined to their role as a habitat for organisms living in the river itself but, by virtue of the associated riparian habitat, the river corridor also represents a habitat network for terrestrial organisms. This riparian network is most obvious, and potentially important, in habitats such as urban systems, where the river corridor may provide the only continuous elements of greenspace crossing entire urban areas. Increasing emphasis is being placed on landscape-scale planning for greenspace (especially in urban river corridors), designed to enhance connectivity, enable ecosystem rehabilitation and promote human welfare (Sandstrom, 2002; Findlay & Taylor, 2006; Tzoulas *et al.*, 2007). To do this effectively, we need to understand the spatial structure of ecological communities in such habitats, and in particular how, or if, this spatial structure relates to the different forms of connectivity the river network may provide.

Patterns of species turnover in an urban river system are likely to be complex, affected by the spatial configuration, connectivity and directionality of the network (Peterson *et al.*, 2006, 2007; Grant *et al.*, 2007; Brown & Swan, 2010), by changes in habitat associated with longitudinal changes in river character (Vannote *et al.*, 1980), by both current and historical disturbance at the site (e.g. Ward & Tockner, 2001) and by patterns of urbanization and land use. Furthermore, organisms with different modes of dispersal may be influenced by the characteristics of the network to different degrees, with the relative importance of Euclidean, network or flow distance determined by dispersal characteristics. In addition, the effects of geographic distance on communities can be confounded by the fact that sites that are closer together may be more likely to have similar environmental conditions. Given this complexity, detecting the signal of network spatial structure is likely to be challenging and require a substantial and systematic data set.

To date, very few studies have compared the use of different distance measures in river networks for freshwater taxa
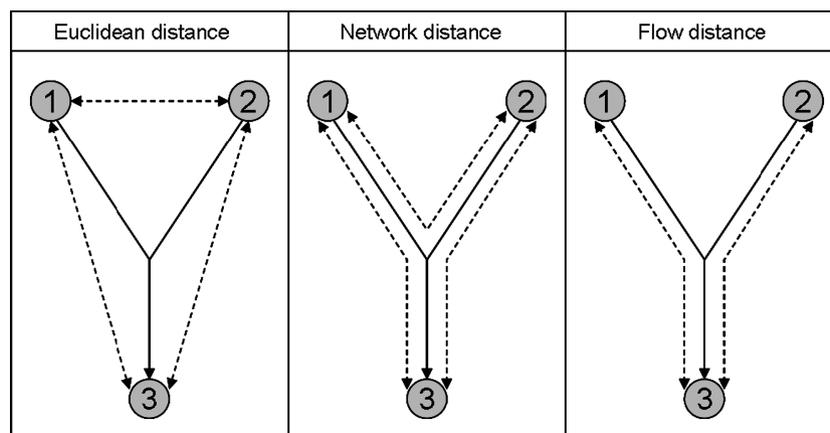

Figure 1 Three alternative geographic distances in river networks: Euclidean (straight line) distance, network distance and flow distance. The river network is represented by the solid lines, with the direction of water flow indicated by the arrow. Distance measurements are represented by dotted lines (from Dallimer *et al.*, 2012). Note that in our study, pairs of sites that are not flow-connected have been assigned a single large distance, equivalent to the largest flow connection distance in the river network.

(but see Brown & Swan, 2010; Peterson & Ver Hoef, 2010), and none have compared these for riparian organisms or across multiple taxa. Here, we use data for aquatic and terrestrial organisms across an urban river network to address the following questions: (1) Are there detectable relationships between species turnover and geographic distance, measured in different ways, across a dendritic river network? (2) Do patterns of species turnover differ between taxonomic groups, in particular between aquatic and terrestrial taxa?

If there are detectable relationships between community composition and network structure, we anticipate that these will be clearest for those organisms which are directly associated with the river itself – aquatic taxa or terrestrial taxa with strong riparian habitat requirements (e.g. wet conditions, water-dispersed seeds). Movements of such species, whether active or passive, are likely to be either in the stream itself (e.g. active movement, drift, seed dispersal), out of the water but following the water course (e.g. aerial dispersal of insects), or with water-associated vectors (e.g. waterfowl) (Johansson et al., 1996; Kristiansen, 1996; Bilton et al., 2001). A second group in which such patterns could occur, but where they may perhaps be weaker and less flow-direction dependent, are those organisms whose spread is facilitated by connectivity of vegetated habitat, but which are not necessarily limited to, or reliant upon, riparian habitat. This would include many terrestrial species with restricted abilities to move across nonvegetated or built environments. A final group of organisms that might show particular associations with network structure are those currently experiencing a phase of active spread: in particular non-native species expanding their ranges. River banks are subjected to regular disturbance and are often sites where neophyte species (recent colonizers) can most readily colonize (e.g. Crawley, 1987), and their distributions may therefore be more directly associated with dispersal corridors (DeFerrari & Naiman, 1994).

METHODS

Study area and site selection

The study was conducted on the River Don and its tributaries, in and around the city of Sheffield, UK (Fig. 2). Sheffield (53°22 N by 01°28 W) had a population of 552,700 at the 2011 census (ONS, 2012) and lies at the confluence of the Don with four tributaries: the Loxley, Rivelin, Sheaf and Porter. The study area ranged from highly urbanized, through suburban, to rural areas, with stream size ranging from 1st to 6th order (Strahler's stream order). The Don system is heavily impacted by humans, suffering from a legacy of industrialization, urbanization, mining and channel modification, although water quality has improved markedly in the last three decades (Firth, 1997). Detailed maps of environmental features across the city, including extent of green space, tree cover and housing density, are provided in Davies et al. (2008). Riparian areas in Sheffield have significantly greater tree cover and natural surface cover than nonriparian areas (Dallimer et al., 2012).

The entire survey area was first divided into 250 m by 250 m grid squares. For squares containing rivers, we determined the stream order of the watercourse, the presence or absence of a weir, the proportion of each square that was covered by sealed surface (all buildings and impermeable surfaces as defined within Ordnance Survey MasterMap) and the proportion of tree cover (derived from digitized outlines of tree canopies from aerial photographs). Each grid square was then classified according to the presence of a weir, four classes of stream order (1–3, 4, 5, 6), four quartiles of sealed surface cover and four quartiles of tree cover. Within our study area, 66 of these possible combinations of environmental variables occurred and a representative of each combination was randomly selected. Access limitations (where no alternative could be selected) and difficulties with sampling diatoms at some locations reduced the number of sites to 41. Sample locations were positioned as close as possible to the centre of the 250-m grid square.

Sampling protocols

At each site, the following taxonomic groups were sampled: aquatic macroinvertebrates, aquatic periphytic diatoms, birds, butterflies and terrestrial plants (forbs and woody plant species). A sample of the aquatic macroinvertebrate community was collected in April and October 2009 using standard UK Environment Agency methodology (EA, 1999). This involves collecting a kick/sweep sample over 3-minutes with a 1-mm mesh pond net, with sampling effort allocated proportionally between the different habitat types present. Samples were preserved in the field in 70% ethanol and then processed in the laboratory. Macroinvertebrates were identified to family level. A sample of the aquatic periphytic diatom community was collected at the same time as the macroinvertebrate samples, using standard methods (Kelly et al., 2008). Five cobbles were collected from mid-stream and placed into a tray with approximately 50 mL of stream water and the top surface of each was brushed with a toothbrush to remove the biofilm. The resulting suspension was collected in a plastic bottle, fixed with Lugol's iodine and stored prior to analysis. In the laboratory, samples were digested with hydrogen peroxide to remove organic material, and permanent slides were prepared using Naphrax as a mountant. Approximately 500 undamaged valves of nonplanktonic taxa were identified to species level using $1000\times$ magnification.

Bird surveys were carried out using standard methodology (Bibby et al., 2000; Fuller et al., 2009) on two separate visits in April–June 2009 to coincide with the breeding season, with the second visit at least 6 weeks after the first. Visits were only carried out in suitable weather conditions (low wind, no rain, no mist) and began between one and three hours after sunrise (the time of highest bird activity). During each visit, the identity of all birds that were seen or heard from the survey point was recorded over a five-minute period by a single observer. Any birds that flushed as the observer approached the survey location were also recorded as being present, but birds flying
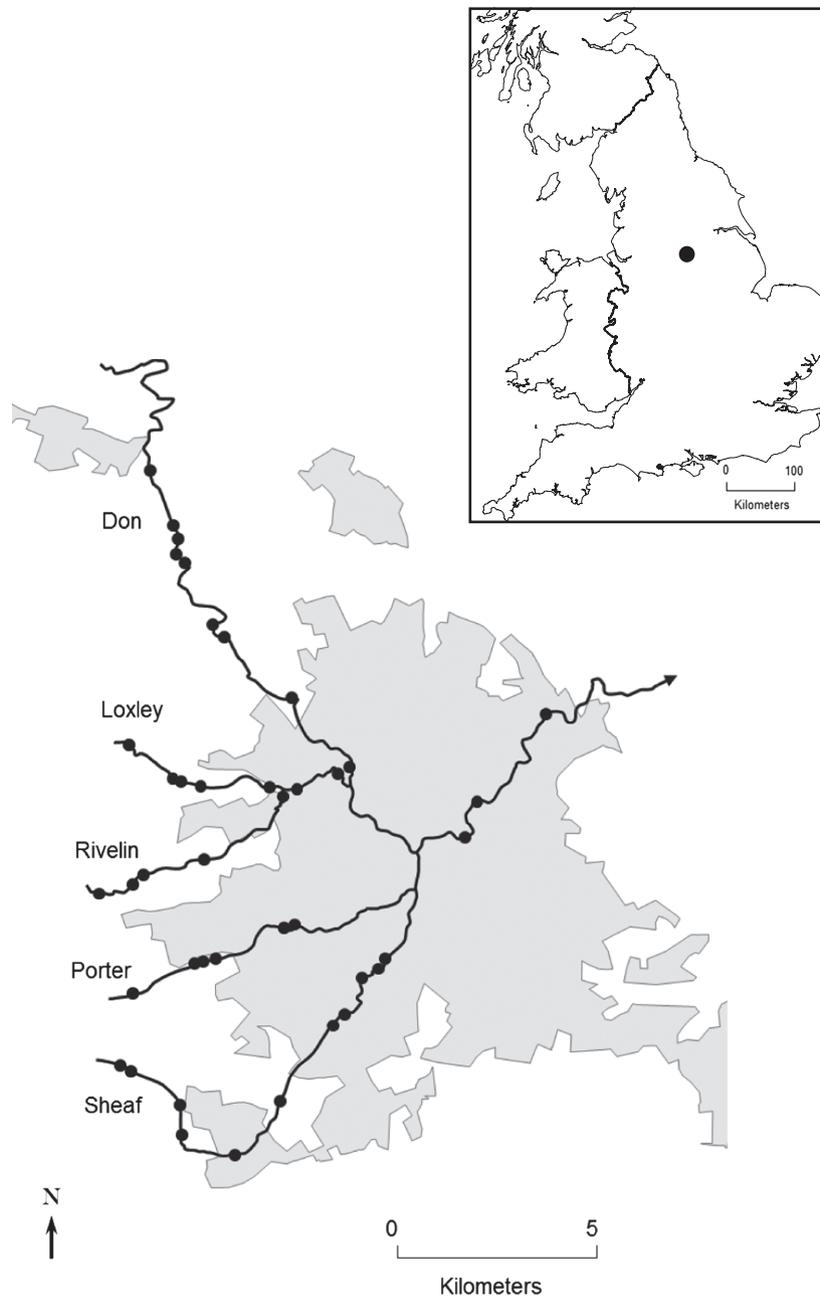
Figure 2 The River Don and its tributaries in Sheffield showing the survey points, the urban area (shaded), and the direction of river flow (arrow). The inset shows the location of the study area in the UK.

over the site were excluded. 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 three times (late May/early June, July and August) at each site. Surveys took place between 10.30 and 15.30, in suitable weather conditions (temperature above 17°C, 50% sunshine and wind speed below 4 on the Beaufort scale). A 40 m by 10 m area (long axis parallel to the river) was actively searched for butterflies for a fixed time period of 15 min. All butterflies observed within the survey area and time period were recorded. Whites (*Pieris*) were

recorded to genus level only due to difficulties with consistently identifying individuals in the field.

Plants were surveyed in the same 40 m by 10 m area as the butterflies. All forbs and woody plant species occurring in the survey area were recorded. For each taxonomic group, a single list of taxa was compiled for each site combining all sampling visits, thereby eliminating the issue of repeated measures.

Environmental characteristics

To describe the key environmental characteristics of the survey sites, water chemistry, river habitat and land cover vari-

ables were measured. Conductivity, pH, dissolved oxygen concentration and water temperature were recorded with hand-held metres at the same time as the macroinvertebrate and diatom sampling. A water sample was collected and analysed on return to the laboratory for alkalinity, nitrate (NO_3), nitrite (NO_2), ammonium (NH_4), phosphate (PO_4), hardness and colour.

At each location, channel width was measured, and water depth, flow (mean of 30 measurements), and silt and detritus depth were recorded at five locations across the channel. An average water depth, flow and silt depth were calculated for each site and used in subsequent analyses. The percentage cover of different substrate types (silt, sand, gravel, pebble, cobble, boulder, bedrock, concrete bed) was estimated in the field and later converted to a single measure of mean substrate size, using average phi sizes (Gordon *et al.*, 2004) for the first six substrate types, and a measure of the percentage of bedrock or concrete bed.

Land cover characteristics in a 50-m radius around each survey point were determined using Ordnance Survey MasterMap. Land cover was grouped into three categories – natural surface (including domestic gardens, allotments, woodland, and public parks), water bodies (rivers, ponds and reservoirs) and sealed surfaces (all buildings and hard surfaces). Tree cover was mapped in a geographic information system by manually tracing around the crown of each tree or group of trees shown in aerial photographs (Davies *et al.*, 2008). Finally, the percentage cover of habitat types was recorded across the same 40 m by 10 m area previously searched for butterflies and plants, and these were used to calculate the habitat diversity at each site using the Shannon diversity index. A description of the possible habitat types, with summary statistics, is provided in Appendix S1 in the Supporting Information.

Several of the 22 environmental variables were correlated; hence, a number of variables were dropped from further analysis, resulting in a final list of 12 variables (Table 1). The environmental variables were chosen to characterize the in-stream and riparian nature of the sites and hence derive environmental distance between sites. Our focus here is not on using the environmental data to explain variation in particular groups of organisms, but rather to remove its potentially confounding influence.

Data analysis

Species turnover was calculated using the Jaccard dissimilarity index. This is defined as the number of species not shared by a pair of sites as a proportion of the total number of species present in those sites and ranges from 0 (all species shared) to 1 (no species shared) (Tuomisto, 2010a,b). Jaccard dissimilarity was calculated for each pair of sites for each of the five taxonomic groups separately. Environmental distance was calculated by standardizing the 12 environmental variables and then computing Euclidean distance between each pair of sites. Geographic distance matrices were calculated

Table 1 Summary statistics for environmental variables included in the final environmental distance matrix

Variable	Min	Median	Mean	Max
Water chemistry variables				
Conductivity	53	327	288	425
pH	5.96	7.51	7.44	8.02
Dissolved oxygen concentration (mg L^{-1})	8.57	9.28	9.29	10.13
Water temperature (°C)	9.4	11.7	11.6	13.4
Nitrate (mg L^{-1} NO_3 corrected for nitrite)	0.20	1.63	2.38	8.49
River habitat variables				
Channel width (m)	0.9	6.6	8.3	30.1
Average water depth (m)	0.06	0.27	0.29	0.67
Average water flow (m^3 s^{-1})	0.04	0.22	0.23	0.50
Mean substrate size (phi)	−7.1	−5.2	−4.8	6.1
Land cover variables				
Proportion of sealed surface	0.00	0.08	0.18	0.78
Proportion tree cover	0.00	0.48	0.49	0.91
Habitat diversity of broad habitat types	0.00	0.81	0.83	1.84

between all sites using Euclidean distance, network distance and flow distance (see Fig. 1), with flow distance calculated in two ways. The first way was to standardize the distance between each pair of flow-connected sites between 0 and 1, and then to assign all unconnected pairs of sites the greatest standardized distance. This has the effect of making flow-unconnected relationships weaker. The second way was to construct an additional binary 'flow connection' matrix, coding each pair of sites as either flow-connected (0) or unconnected (1), to examine the importance of flow connection between sites without examining distance. To investigate the effect of assigning unconnected sites the same flow distance as the most distant connected site, three additional flow distance matrices were constructed using alternative and much greater values for the unconnected sites. Distances equivalent to 2, 10 and 100 times the maximum flow distance were tested, which progressively weaken the flow-unconnected relationships. The results produced by each matrix are shown in Appendix S2 in the Supporting Information.

We examined the association between species turnover of the five taxonomic groups, the three geographic distance matrices, and the environmental distance matrix with Mantel tests, using Pearson's product-moment correlation, and with significance assessed by 10,000 random permutations. Environmental distance was correlated (Mantel test) with all three geographic distance measures (Euclidean distance: $r = 0.434$, $P < 0.001$; network distance: $r = 0.327$, $P < 0.001$; flow distance: $r = 0.158$, $P < 0.001$). Therefore, partial Mantel tests were performed to ascertain the correlation between species turnover and each geographic distance measure whilst factoring out the effect of environmental distance. Partial Mantel tests were also performed using the binary flow connection matrix to test for an association between species turnover and flow connection, whilst taking environmental distance into

account. All statistical analyses were performed using the ecodist (Goslee & Urban, 2007) and vegan (Oksanen *et al.*, 2010) packages in R (R Development Core Team, 2011).

To further examine the role of dispersal in influencing patterns of species turnover, plants and aquatic macroinvertebrates were subdivided. Water-dispersed and nonwater-dispersed plants were examined separately (Fitter & Peat, 1994), as were native (arrived in the UK before the Neolithic period or independent of human activity), archaeophyte (introduced into the UK before 1500 AD) and neophyte (introduced into the UK after 1500 AD) species (Preston *et al.*, 2002). Aquatic macroinvertebrates were divided into insect and noninsect groups to give a crude indication of dispersal characteristics: most aquatic insects have adults that can disperse by flight in the terrestrial environment.

RESULTS

Distance measures

The number of pairs of sites in the distance matrices was the same for all distance measures (820 pairs), but only 254 of these pairs were flow-connected. The minimum separation distance between neighbouring sites was similar for all distance measures, but network distance had a larger median, mean and maximum value than Euclidean distance (Table 2). Median and mean flow distance was larger again when including all the unconnected pairs of sites in the matrix (with unconnected sites assigned a distance equivalent to the maximum flow-connected distance), but was less when considering only flow-connected sites. Euclidean and network distances were most correlated (Pearson's $r = 0.73$, $P < 0.001$), whilst Euclidean and flow distance had a Pearson's correlation of 0.42 ($P < 0.001$) and network and flow distance had a correlation of 0.66 ($P < 0.001$).

Species richness

A total of 55 bird species (mean 11.0, range 4–19 per site), 280 plant species (mean 43.8, range 19–89), 15 butterfly species (mean 2.7, range 0–7), 148 diatom species (mean 42.7, range 29–58), and 71 macroinvertebrate taxa (mean 30.5, range 15–38) were recorded at the 41 study sites. Of the

Table 2 Summary statistics for distance measures, in kilometres

Distance measure	N pairs	Min	Median	Mean	Max
Euclidean distance	820	0.159	5.93	6.35	17.22
Network distance	820	0.164	12.01	11.79	27.93
*Flow distance – all	820	0.164	20.11	16.12	20.11
Flow-connected sites only	*254*	*0.164*	*6.47*	*7.21*	*20.11*

*NB The summary statistics for flow distance includes 566 pairs of sites (of 820) that are not flow-connected but which have been assigned a distance equivalent to the maximum distance between two connected sites (20.11 km). Summary statistics for only those sites that are connected by flow are shown in italics.

plant species, 187 (67%) were native, 65 (23%) were neophytes, 26 (9%) were archaeophytes and 2 (1%) were of uncertain origin. Also, 27 (10%) of the plant species were water-dispersed. Of the macroinvertebrates, 54 (76%) were insect and 17 (24%) were noninsect taxa.

Patterns of species turnover

Taxonomic groups varied in their association with the geographic and environmental distance matrices (Table 3). Macroinvertebrate and diatom turnover was correlated with all the geographic distance measures (Table 3), with sites that were closer together also being more similar in their community composition. Turnover was most closely aligned with network distance for both macroinvertebrates ($r = 0.476$) and diatoms ($r = 0.431$), and this association remained highly significant when the effect of environmental distance was factored out ($r > 0.37$, $P < 0.001$). For macroinvertebrate subgroups, turnover in both insect and noninsect assemblages was also most strongly correlated with network distance (Table 4). When examining the importance of flow connection between sites, it became apparent that macroinvertebrate ($r = 0.146$) and diatom ($r = 0.186$) communities were significantly more similar at flow-connected sites than at flow-unconnected sites after removing the effect of environmental distance (Table 3). This pattern was apparent for the noninsect subgroup ($r = 0.115$, Table 4), but was not significant for the insect subgroup ($r = 0.099$).

Bird species turnover was correlated with both network ($r = 0.216$) and Euclidean ($r = 0.236$) distances, but only network distance remained significantly correlated when environmental distance was taken into account (Table 3). In contrast, butterflies displayed no correlation between turnover and any geographic distance measure ($r < 0.03$), but were significantly correlated with environmental distance ($r = 0.215$).

Plant species turnover was significantly correlated with all the geographic distances, but none of these relationships were significant when environmental distance had been taken into account (Table 3). Species turnover in water-dispersed plants (Table 4) was much more strongly correlated with network distance ($r = 0.221$) than with the other geographic distance measures ($r \leq 0.1$), and this correlation remained significant when environmental distance had been taken into account. In contrast, the group of plants that were not water-dispersed were much more strongly related to environmental distance ($r = 0.497$). Although turnover was significantly correlated with both network ($r = 0.237$) and Euclidean distance ($r = 0.225$), these correlations were not significant when environmental distance had been taken into account. Native plants showed the same pattern as the overall plant group (Table 4). For neophytes, turnover was most strongly associated with flow distance ($r = 0.197$), especially after factoring out environmental distance. Neophyte plants were also significantly more similar at flow-connected sites ($r = 0.124$) than unconnected sites. Archaeophyte species turnover was not significantly correlated with any geographic

Table 3 (a) Correlations between species turnover, four measures of geographic distance and environmental distance between all pairs of sites, and (b) partial correlations between species turnover and geographic distance after controlling for the effect of environmental distance. Based on Mantel tests of Jaccard dissimilarity.

	N pairs	Euclidean distance	Network distance	Flow distance	Flow connection	Environmental distance
(a) Correlations						
Macroinvertebrates	820	0.302***	0.476***	0.207***	0.131*	0.471***
Diatoms	820	0.240***	0.431***	0.273***	0.179**	0.279**
Birds	820	0.236***	0.216***	0.055	−0.043	0.340***
Butterflies	666	0.002	0.022	0.006	−0.024	0.215*
Plants	820	0.221**	0.262***	0.088*	−0.033	0.502***
			Corrected for environmental distance:			
(b) Partial correlations						
Macroinvertebrates	820	0.122	0.386***	0.152**	0.146*	
Diatoms	820	0.138*	0.374***	0.241***	0.186***	
Birds	820	0.104	0.119*	0.001	−0.048	
Butterflies	666	−0.117	−0.065	−0.031	−0.028	
Plants	820	0.003	0.120	0.010	−0.040	

Pearson's r is shown and the associated P-value (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

Table 4 (a) Correlations between species turnover, four measures of geographic distance, and environmental distance between all pairs of sites for plant and macroinvertebrate subgroups, and (b) partial correlations between species turnover and geographic distance, after controlling for the effect of environmental distance. Based on Mantel tests of Jaccard dissimilarity.

	N pairs	Euclidean distance	Network distance	Flow distance	Flow connection	Environmental distance
(a) Correlations						
Plants – not water-dispersed	820	0.225**	0.237**	0.076	−0.049	0.497***
Plants – water-dispersed	820	0.095	0.221**	0.084*	0.044	0.271**
Plants – native	820	0.206**	0.270***	0.080*	−0.023	0.491***
Plants – neophyte	741	0.131*	0.111	0.197***	0.124*	0.116
Plants – archaeophyte	210	0.146	0.104	0.043	0.007	0.205*
Macroinvertebrates – not insects	820	0.215**	0.391***	0.146***	0.108*	0.379**
Macroinvertebrates – insects	820	0.300***	0.427***	0.184***	0.091	0.433***
			Corrected for environmental distance:			
(b) Partial correlations						
Plants – not water-dispersed	820	0.012	0.132	−0.004	−0.059	
Plants – water-dispersed	820	−0.026	0.146*	0.043	0.045	
Plants – native	820	−0.009	0.133*	0.003	−0.029	
Plants – neophyte	741	0.091	0.082	0.183***	0.124*	
Plants – archaeophyte	210	0.096	0.079	0.036	0.018	
Macroinvertebrates – not insects	820	0.060	0.306***	0.094*	0.115*	
Macroinvertebrates – insects	820	0.137	0.335***	0.130**	0.099	

Pearson's r is shown and the associated P-value (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

distance measure and was only weakly correlated with environmental distance, although this may have been partly due to the small sample size of this subgroup.

DISCUSSION

There are clear associations between measures of geographic distance and differences in community composition of particular taxonomic groups across the urban river network in this study. Turnover in macroinvertebrates, diatoms, birds and some of the plant subgroups was significantly correlated with at least one measure of geographic distance, even after environmental differences had been taken into account. But there is variation in the strength of the correlations, and different taxa appear to be correlated to different aspects of distance. The remaining groups were not correlated with any

measure of geographic distance once environmental distance was included, but, with the exception of butterflies, appeared to be associated with spatially structured environmental variables.

Aquatic and riparian taxa can move through the network along two distinct pathways: movements within the river or corridor (within-network movement) or outside of the river corridor between river branches (out-of-network movement). Within the river corridor, movements can be upstream or downstream. For most aquatic species, within-network movements are likely to be the primary dispersal pathway (Kristiansen, 1996; Bilton *et al.*, 2001). Nevertheless, out-of-network dispersal is known to play an important role for some taxa, such as salamanders (Grant *et al.*, 2009), and some adult aquatic insects (Briers *et al.*, 2004; Finn *et al.*, 2006). Some previous studies have reported a decline in community similarity with geographic distance for aquatic macroinvertebrates (Thompson & Townsend, 2006; Shurin *et al.*, 2009; Brown & Swan, 2010), but others have not found consistent patterns (Lloyd *et al.*, 2005; Grenouillet *et al.*, 2008). These studies have used a variety of different distance measures, including network distance (Lloyd *et al.*, 2005; Grenouillet *et al.*, 2008) and Euclidean distance (Thompson & Townsend, 2006), but only Brown & Swan (2010) compared distance measures.

Patterns of species turnover in relation to geographic distance for diatoms have received less attention (but see Grenouillet *et al.*, 2008; Heino *et al.*, 2009; Shurin *et al.*, 2009). Until recently, the prevailing view has been that diatoms and other eukaryote microbes should show negligible variation across spatial scales, as a result of ubiquitous dispersal, with community variation driven by environmental differences (Finlay, 2002; Martiny *et al.*, 2006). But that view has been questioned recently, with evidence emerging of the importance of spatial patterns (e.g. Martiny *et al.*, 2006; Grenouillet *et al.*, 2008; Heino *et al.*, 2009). Our results support this latter view, suggesting that species turnover in diatoms is correlated with geographic distance, even after the effect of environmental distance had been removed. Our study provides new evidence that aquatic communities (macroinvertebrates and diatoms) were most closely correlated with network distance, which is consistent with our hypothesis that within-network connectivity is more important for these groups.

Macroinvertebrates were the only taxonomic group that were recorded at family rather than species level. However, we do not feel that this will have affected the overall pattern of the results, as previous studies (Melo, 2005; Marshall *et al.*, 2006; Heino & Soininen, 2007) have shown that trends in macroinvertebrate patterns at the species level tend to closely reflect those at the family level.

Patterns of distance decay in terrestrial taxa have been well demonstrated, particularly for plants (e.g. Nekola & White, 1999; Condit *et al.*, 2002; Tuomisto *et al.*, 2003; Qian *et al.*, 2005; Lichstein, 2007), but also for birds (Steinitz *et al.*, 2006; La Sorte & McKinney, 2007) and invertebrates (Steinitz

et al., 2006; Novotny *et al.*, 2007). Yet, none of the above studies examined turnover or distance decay along an ecological network, such as a river system, and all used Euclidean distance. In patchy terrestrial habitats, corridors are known to facilitate connectivity and movement between sites (Beier & Noss, 1998; Haddad *et al.*, 2003; Gilbert-Norton *et al.*, 2010). Although evidence from river corridors is much more limited, Gillies & St. Clair (2008) showed that movement in a species of bird was enhanced along a riparian corridor compared with nonriparian habitat. Our results show that at the relatively fine scale of our study system, species turnover of the riparian taxa was more closely correlated with environmental distance than with any measure of geographic distance. At least one measure of geographic distance did, however, remain significant for some components of the terrestrial communities after taking environmental distance into account.

Plants demonstrate a number of different relationships with geographic distance, which is representative of the large and diverse life history and dispersal strategies present across this group. We hypothesized that water-dispersed plants would show evidence of community composition correlated with the river network, and geographic distance was indeed significant for this group. However, the correlation was weak after factoring out environmental differences. Also, the water-dispersed plants were most strongly associated with network distance, which is somewhat surprising given that by definition, we might expect this group to be most closely correlated with flow distance. The large group of native plants were also significantly (although weakly) associated with network distance. This pattern is likely to be due to restricted abilities to move across nonvegetated or built environments and is consistent with previous studies that have shown that rivers enhance habitat connectivity of riparian plant communities at local to regional scales (Johansson *et al.*, 1996; Gurnell *et al.*, 2008).

The final group of organisms in which we expected to see an association with the riparian network were the neophyte species. In agreement with our hypothesis, the neophyte plant group was associated with geographic distance along the river network, in this case with flow distance. This group contained many species that are recent invaders and are in the process of spreading (e.g. *Fallopia japonica* and *Impatiens glandulifera*) and hence are more likely to display community patterns that reflect their recent dispersal history than native or well-established species. Although only 6% of the neophytes recorded in our study are primarily water-dispersed, water dispersal has been shown to function as a secondary dispersal mechanism for many other species (Truscott *et al.*, 2006) and evidence suggests that riparian zones facilitate the movement of exotic species through the landscape (DeFerrari & Naiman, 1994; Säumel & Kowarik, 2010).

In contrast to the macroinvertebrates, diatoms and some of the plant groups, species turnover in birds and butterflies appears to be less strongly associated with any measure of geographic distance. Bird communities were only weakly

correlated with network distance, and this correlation was not very different from the correlation with Euclidean distance (which was not significant) after factoring out environmental effects (Table 3). The weak patterns that are present are consistent with the view that both within-network and out-of-network movement pathways have a role to play (albeit weak), or that significant unaccounted environmental variables remain. The lack of a correlation with geographic distance for butterflies may at least in part be due to the fact that the butterfly sample size was very small, with only 15 species in total. Furthermore, eight of these species were only present at one or two sites, and the remainder were widespread, ubiquitous species, with excellent dispersal capabilities.

Comparing Euclidean and network distances in our study was straightforward as all of the sites occur on the same river network. But only 254 of 820 pairs of sites were flow-connected, which presented some methodological challenges when constructing the flow distance matrices. Flow distance is identical to network distance for flow-connected sites, so it was not possible to restrict our comparison to only flow-connected sites. To enable a comparison of all sites, it was necessary to assign an arbitrary large distance to flow-unconnected sites. The flow distance measure used here therefore represents both flow-connected and flow-unconnected relationships, but flow-unconnected relationships have been made weaker. The larger the arbitrary distance value applied to flow-unconnected sites, the less sensitive the measure becomes to geographic (network) distance between flow-connected sites and the more closely it resembles the binary flow connection matrix (Appendix S2).

CONCLUSIONS

By studying aquatic and riparian communities using a number of different geographic distance measures, together with environmental factors, we have shown that different taxa may be correlated with different aspects of geographic distance. Turnover in aquatic communities was most strongly correlated with network distance. Terrestrial taxa, on the other hand, were less strongly spatially structured. They displayed a more complex relationship with the alternative distance measures, with different components of these communities displaying different responses. Yet, network and flow distance remained significant for many of the terrestrial taxa, indicating that connectivity along the river corridor may be important for these communities.

These findings have implications for landscape-scale conservation and planning. Urban ecological networks have been perceived as especially important as they may provide the only opportunity for connectivity and wildlife movement in urbanized landscapes (Ignatieva et al., 2011). With increasing emphasis on landscape-scale planning of green infrastructure in urban areas (Sandstrom, 2002; Tzoulas et al., 2007), including the active development of green corridors for recreation and environmental enhancement (Fabos, 1995; Walmsley, 1995), it is important that understanding is improved of the relative importance of spatial patterns and connectivity in shaping plant and animal communities. Such an understanding is necessary to enable urban green infrastructure to be designed for the maximum benefit of both wildlife and people.

REFERENCES

Beier, P. & Noss, R.F. (1998) Do habitat corridors provide connectivity? *Conservation Biology*, **12**, 1241–1252.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H. (2000) *Bird census techniques*, 2nd edn. Academic Press, London.

Bilton, D.T., Freeland, J.R. & Okamura, B. (2001) Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, **32**, 159–181.

Briers, R.A., Gee, J.H.R., Cariss, H.M. & Geoghegan, R. (2004) Inter-population dispersal by adult stoneflies detected by stable isotope enrichment. *Freshwater Biology*, **49**, 425–431.

Brown, B.L. & Swan, C.M. (2010) Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology*, **79**, 571–580.

Condit, R., Pitman, N., Leigh, E.G. Jr, Chave, J., Terborgh, J., Foster, R.B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. *Science*, **295**, 666–669.

Crawley, M.J. (1987) What makes a community invasible? *Colonization, succession & stability* (ed. by A.J. Gray, M.J. Crawley and P.J. Edwards), pp. 429–453. Blackwell, Oxford.

Dallimer, M., Rouquette, J.R., Skinner, A.M.J., Armsworth, P.R., Maltby, L.M., Warren, P.H. & Gaston, K.J. (2012) Contrasting patterns in species richness of birds, butterflies and plants along riparian corridors in an urban landscape. *Diversity and Distributions*, **18**, 742–753.

Davies, R.G., Barbosa, O., Fuller, R.A., Tratalos, J., Burke, N., Lewis, D., Warren, P.H. & Gaston, K.J. (2008) City-wide relationships between green spaces, urban land use and topography. *Urban Ecosystems*, **11**, 269–287.

DeFerrari, C.M. & Naiman, R.J. (1994) A multiscale assessment of the occurrence of exotic plants on the Olympic

Peninsula, Washington. *Journal of Vegetation Science*, **5**, 247–258.

EA (1999) *Procedures for collecting and analysing macroinvertebrate samples*. BT001. Issue 2. Environment Agency, Bristol.

Fabos, J.G. (1995) Introduction and overview - the greenway movement, uses and potentials of greenways. *Landscape and Urban Planning*, **33**, 1–13.

Findlay, S.J. & Taylor, M.P. (2006) Why rehabilitate urban river systems? *Area*, **38**, 312–325.

Finlay, B.J. (2002) Global dispersal of free-living microbial eukaryote species. *Science*, **296**, 1061–1063.

Finn, D.S., Theobald, D.M., Black, W.C & Poff, N.L. (2006) Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Molecular Ecology*, **15**, 3553–3566.

Firth, C. (1997) *Domesday to the dawn of the new millennium: 900 years of the don fishery*. Environment Agency, Bristol.

Fitter, A.H. & Peat, H.J. (1994) The ecological flora database. *Journal of Ecology*, **82**, 415–425.

Fuller, R.A., Tratalos, J. & Gaston, K.J. (2009) How many birds are there in a city of half a million people? *Diversity and Distributions*, **15**, 328–337.

Gilbert-Norton, L., Wilson, R., Stevens, J.R. & Beard, K.H. (2010) A meta-analytic review of corridor effectiveness. *Conservation Biology*, **24**, 660–668.

Gillies, C.S. & St. Clair, C.C. (2008) Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences USA*, **105**, 19774–19779.

Gordon, N.D., McMahon, T.A., Finlayson, B.L., Gippel, C.J. & Nathan, R.J. (2004) *Stream hydrology: an introduction for ecologists*, 2nd Edn. John Wiley & Sons Ltd, Chichester, England.

Goslee, S.C. & Urban, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, **22**, 1–19.

Grant, E.H.C., Lowe, W.H. & Fagan, W.F. (2007) Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters*, **10**, 165–175.

Grant, E.H.C., Green, L.E. & Lowe, W.H. (2009) Salamander occupancy in headwater stream networks. *Freshwater Biology*, **54**, 1370–1378.

Grenouillet, G., Brosse, S., Tudesque, L., Lek, S., Baraillé, Y. & Loot, G. (2008) Concordance among stream assemblages and spatial autocorrelation along a fragmented gradient. *Diversity and Distributions*, **14**, 592–603.

Gurnell, A., Thompson, K., Goodson, J. & Moggridge, H. (2008) Propagule deposition along river margins: linking hydrology and ecology. *Journal of Ecology*, **96**, 553–565.

Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S. & Spira, T. (2003) Corridor use by diverse taxa. *Ecology*, **84**, 609–615.

Heino, J. & Soininen, J. (2007) Are higher taxa adequate surrogates for species-level assemblage patterns and species richness in stream organisms? *Biological Conservation*, **137**, 78–89.

Heino, J., Ilmonen, J., Kotanen, J., Mykrä, H., Paasivirta, L., Soininen, J. & Virtanen, R. (2009) Surveying biodiversity in protected and managed areas: algae, macrophytes and macroinvertebrates in boreal forest streams. *Ecological Indicators*, **9**, 1179–1187.

Ignatieva, M., Stewart, G.H. & Meurk, C. (2011) Planning and design of ecological networks in urban areas. *Landscape and Ecological Engineering*, **7**, 17–25.

Johansson, M.E., Nilsson, C. & Nilsson, E. (1996) Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science*, **7**, 593–598.

Kelly, M.G., Juggins, S., Guthrie, R., Prtchard, S., Jamieson, J., Rippey, B., Hirst, H. & Yallop, M. (2008) Assessment of U.K. rivers using diatoms. *Freshwater Biology*, **53**, 403–422.

Kristiansen, J. (1996) Dispersal of freshwater algae - a review. *Hydrobiologia*, **336**, 151–157.

La Sorte, F.A. & McKinney, M.L. (2007) Compositional changes over space and time along an occurrence – abundance continuum: anthropogenic homogenization of the North American avifauna. *Journal of Biogeography*, **34**, 2159–2167.

Lichstein, J.W. (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology*, **188**, 117–131.

Lloyd, N.J., Mac Nally, R. & Lake, P.S. (2005) Spatial autocorrelation of assemblages of benthic invertebrates and its relationship to environmental factors in two upland rivers in southeastern Australia. *Diversity and Distributions*, **11**, 375–386.

Marshall, J.C., Steward, A.L. & Harch, B.D. (2006) Taxonomic resolution and quantification of freshwater macroinvertebrate samples from an Australian dryland river: the benefits and costs of using species abundance data. *Hydrobiologia*, **572**, 171–194.

Martiny, J.B., Bohannan, B.J., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L., Horner-Devine, M.C., Kane, M., Krumins, J.A., Kuske, C.R., Morin, P.J., Naeem, S., Ovreas, L., Reysenbach, A.L., Smith, V.H. & Staley, J.T. (2006) Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology*, **4**, 102–112.

Melo, A.S. (2005) Effects of taxonomic and numeric resolution on the ability to detect ecological patterns at a local scale using stream macroinvertebrates. *Archiv Fur Hydrobiologie*, **164**, 309–323.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. & Green, J.L. (2008) A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters*, **11**, 904–917.

Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.

Novotny, V., Miller, S.E., Hulcr, J., Drew, R.A., Basset, Y., Janda, M., Setliff, G.P., Darrow, K., Stewart, A.J., Auga, J.,

Isua, B., Molem, K., Manumbor, M., Tamtiai, E., Mogia, M. & Weiblen, G.D. (2007) Low beta diversity of herbivorous insects in tropical forests. *Nature*, **448**, 692–695.

Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2010) *Vegan: community ecology package*. R package version 1.17-3. Available at: http://CRAN.R-project.org/package=vegan (accessed 29 July 2013).

ONS (2012) *2011 Census: number of usual residents living in households and communal establishments, local authorities in England and Wales*. Available at: http://www.ons.gov.uk/ons/publications/re-reference-tables.html?edition=tcm%3A77-257414 (accessed 29 July 2013).

Peterson, E.E. & Ver Hoef, J.M. (2010) A mixed-model moving-average approach to geostatistical modeling in stream networks. *Ecology*, **91**, 644–651.

Peterson, E.E., Merton, A.A., Theobald, D.M. & Urquhart, N.S. (2006) Patterns of spatial autocorrelation in stream water chemistry. *Environmental Monitoring and Assessment*, **121**, 571–596.

Peterson, E.E., Theobald, D.M. & Ver Hoef, J.M. (2007) Geostatistical modelling on stream networks: developing valid covariance matrices based on hydrologic distance and stream flow. *Freshwater Biology*, **52**, 267–279.

Preston, C.D., Pearman, D.A. & Dines, T.D. (2002) *New Atlas of the British & Irish Flora*. Oxford University Press, Oxford.

Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, **8**, 15–22.

R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Sandstrom, U.G. (2002) Green infrastructure planning in urban Sweden. *Planning Practice & Research*, **17**, 373–385.

Säumel, I. & Kowarik, I. (2010) Urban rivers as dispersal corridors for primarily wind-dispersed invasive tree species. *Landscape and Urban Planning*, **94**, 244–249.

Shurin, J.B., Cottenie, K. & Hillebrand, H. (2009) Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia*, **159**, 151–159.

Soininen, J., Lennon, J.J. & Hillebrand, H. (2007a) A multivariate analysis of beta diversity across organisms and environments. *Ecology*, **88**, 2830–2838.

Soininen, J., McDonald, R. & Hillebrand, H. (2007b) The distance decay of similarity in ecological communities. *Ecography*, **30**, 3–12.

Steinitz, O., Heller, J., Tsoar, A., Rotem, D. & Kadmon, R. (2006) Environment, dispersal and patterns of species similarity. *Journal of Biogeography*, **33**, 1044–1054.

Thompson, R. & Townsend, C. (2006) A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology*, **75**, 476–484.

Truscott, A.M., Soulsby, C., Palmer, S.C.F., Newell, L. & Hulme, P.E. (2006) The dispersal characteristics of the invasive plant Mimulus guttatus and the ecological significance of increased occurrence of high-flow events. *Journal of Ecology*, **94**, 1080–1091.

Tuomisto, H. (2010a) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33**, 2–22.

Tuomisto, H. (2010b) A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography*, **33**, 23–45.

Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, **299**, 241–244.

Tzoulas, K., Korpela, K., Venn, S., Yli-Pelkonen, V., Kazmierczak, A., Niemela, J. & James, P. (2007) Promoting ecosystem and human health in urban areas using Green Infrastructure: a literature review. *Landscape and Urban Planning*, **81**, 167–178.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.

Walmsley, A. (1995) Greenways and the making of urban form. *Landscape and Urban Planning*, **33**, 81–127.

Ward, J.V. & Tockner, K. (2001) Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology*, **46**, 807–819.

SUPPORTING INFORMATION

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

Appendix S1 Habitat types recorded at each site, with summary statistics.

Appendix S2 Additional information and analyses of alternative flow distance matrices.

BIOSKETCH

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

Author contributions: J.R.R., M.D., P.R.A., K.J.G., L.M. and P.H.W. conceived the ideas. J.R.R. and M.D. collected the data, J.R.R. analysed the data and led the writing, and L.M. and P.H.W. contributed to manuscript preparation, including discussion of data analysis and interpretation.

Editor: Ralph Mac Nally