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An analysis of ecological connectivity in London using terrestrial habitat-proxy species

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Abstract

In cities, nature sits at the nexus of the wild and the domestic. Efforts to understand it in these settings often neglect how it operates within and across urban landscapes. While most policies and strategies focus on structural components like canopy and greenspace cover, this paper adopts a functional approach. This study conducts a landscape-level assessment of connectivity for four proxy species in London using Omniscape, and compares the results with greenspace cover and canopy assessments as used in the London Environmental Strategy and London Plan. Functional connectivity maps did not always corroborate expected outcomes based on the percentage of greenspace or canopy cover. The analysis also revealed pinch points that could guide protected area designation. Additionally, 10% of total connectivity crossed borough boundaries. This highlights the need for urban policymaking to consider nature through a functional lens rather than one defined by governance boundaries. The evidence provided in the landscape connectivity assessment emphasises the importance of governance structures that work across administrative boundaries. The results of this study could support decision-making for a multi-scalar ecological recovery network.

Keywords: Urban Ecology, Connectivity, Omniscape, Landscape Ecology, Proxy Species

1 Introduction

Over 55% of the global population resides in urban areas, a proportion expected to grow over the next century [1]. Although studies have examined urban ecological processes, they often employ a granular approach. Only in recent decades have urban

areas been accepted as significant sites of ecological activity. This is due to cultural preconceptions of these areas as "human" and "unnatural" [2–5], or of wildlife as impure and "*too human*" to have constituency [6], or the historical difficulties of performing ecological experimentation in these settings [7, 8]. As such there are biases to overcome and contemporary research is behind in understanding these locations. In fact, recent research has shown these areas to be biodiversity hotspots [7, 9, 10], and not simply "*the abyss of the human species*" [11]. This paper builds towards recognising these spaces as natural. To draw on notions raised by [12, 13], this paper challenges the distinction between the "human" and "non-human" worlds. Compounded by the historical lack of research into urban ecology, there are many understudied phenomena of nature within urban landscapes with significant implications. Among them: the ability of organisms to adapt and grow accustomed to these sites [14, 15], the role urban areas can play in biotic homogenisation [16, 17], the catalysis of species invasion and proliferation [18, 19] and the role that urban areas can play in alienating humanity from Nature [20, 21]. To better understand these phenomena, it is necessary to develop a more complete understanding of these localities. This can be done using pre-existing theories relevant to ecology, biogeography, and conservation biology and treating these highly fragmented landscapes similarly to "natural landscapes".

Given the density of urban populations and the framing of these spaces as purely human, reconfiguring our perspective would aid in breaking down the false dichotomy of "the Human" and "the Natural". Adding to this, these are areas of large populations that would benefit from the employment of nature-based solutions. The Greater London Authority (GLA) acknowledges the role of green infrastructure in "*improving biodiversity and ecological resilience*" [22], but also admits these benefits "*are economically valuable, but are not widely understood*" [22]. GLA policy suggestions prioritise increases in the number of Sites of Importance for Nature Conservation (SINCs) and in tree cover from 20% to 22% by 2050 [22, p. 167]. When determining the value of London's nature, they employ assessments that use greenspace cover and canopy cover as proxies, measuring their performance through carbon accounting and ecosystem service valuations.

In these assessments, biodiversity does not sit at the forefront. Rather, it is treated as an emergent property of greenspace coverage. However, biodiversity does not emerge after the fact - it is the precondition of ecosystem functioning, a series of attributes that span levels of organisation from the genetic to the landscape-level [23]. Biodiversity impacts and is impacted by the state of the ecosystem. Recognising nature as a multifaceted, complex system, allows one to consider nature as greater than the sum of its parts. This is a perspective adopted by landscape ecology which accounts for this complexity both spatially and disciplinarily [24, 25].

Landscape ecology considers cities not simply in a modular manner but as functional and interconnected landscapes [26–29]. It approaches ecosystems as existing in a complex state of flux [30, 31] - as an interplay between the ecology and the processes that occur. This bidirectional influence of structure and services is integral to a landscape-level understanding [25, 32]. It considers broad spatial scales and the effects and patterns that determine ecosystems across them [26]. Landscape ecology is commonly used to study non-human areas, but not widely employed to understand the

way nature functions in anthropogenic landscapes, although its value has been noted [19, 32, 33].

This paper aims to show that employing a functional approach with respect to London can provide a more robust basis for ecological planning than the disconnected and broad picture that policymaking currently offers. We employ a circuit-theory model to assess how proxy species could interact with the landscape and compare these results with borough rankings of greenspace and canopy cover. This contributes to expanding the view that nature is greater than the sum of its parts [34] - it is a highly complex system that must be understood both at its finest levels and as a connected and interacting system [35–37].

Both the theoretical and ecological components of this analysis demonstrate gaps in the management focus of urban policymaking and provide avenues for reevaluating our opinions of urban areas. By providing an in-depth, landscape assessment of London, and employing functional assessments, this paper challenges prevailing notions of *The Urban*. This application of ecological techniques to Greater London made it possible to determine: 1) whether greenspace and canopy cover is a valid proxy for functional connectivity of the landscape; 2) whether an assessment using connectivity of the landscape provides a more nuanced approach to assessing urban nature; and 3) what role this sort of assessment could play in SINC designation or further management policy to build a nature-smart city.

2 Methods

2.1 Study Region

With over 9 million people, London has the largest concentration of people in the United Kingdom [38]. The administrative area of Greater London has a total area of 1,569 km² [39] and is composed of a mosaic of political units, including 33 local government districts (32 boroughs and the ceremonial county of the City of London) each with a dedicated council. Each borough has its own environmental strategy and some have a Biodiversity Action Plan (BAP) guided by the London Environment strategy [40] and the requirements of the London Plan [22]. BAPs often include priority species and habitats, but they focus on individual boroughs.

It has been 26 years since the emergence of the London Biodiversity Action Plan [41], yet many areas within the city still suffer from intense ecological deprivation [22, 40]. Despite being designated the first “National Park City” in 2019, approximately 68% of adults live in an Area of Deficiency to SINC^s [42]. While policy frameworks aim to address ecological deprivation, pollution, and nature deficits [22, 40] they focus predominantly on climate change and achieving net-zero, with less priority given to nature within the city [43]. While Policy G5 of the London Plan requires a 10% net gain in biodiversity and the implementation of an urban greening factor [22], this has been shown to be an ineffective means to capture value of invertebrate habitats, and potentially to be a cause of increased fragmentation and reduced habitat quality [44, 45]. It has also been associated with the proliferation of relatively common habitats (eg. grasslands and scrubs) [46] and relies upon adequate monitoring and maintenance that was shown to be absent in 27% of cases [47] due to a lack of ecological expertise

within councils [48]. As such, there is strong a need for a considered and ecologically informed agenda.

While the idea of approaching cities from a landscape-level has been explored in cities such as Geneva [49], Jinzhong [50], and Boston [51], London has mostly been considered from a localised and granular level or meta-analytically [52, 53]. The only model applied at a landscape-level in London used citizen science data to assess habitat suitability correlatively [54, 55], and not functional modelling of connectivity.

Assessments of connectivity and species networks within London’s landscape are absent from policy [22, 40, 56]. They mention corridors, however, fail to account for the conditions needed to generate them. This absence illustrates a broader trend in conservation: research and management take place within geopolitical boundaries rather than ecological ones, a trend that this research questions [57, 58].

Outside of academia, there is a lack of consideration for the role that biodiversity plays in facilitating a functioning ecosystem and bolstering the services it can provide. Connectivity is one way that biodiversity can be maintained and improved [26, 59, 60]. By considering the natural landscape, this research is able to quantify the extent of interconnectivity between boroughs for focal species.

2.2 Mapping and Modelling

There are multiple methods to quantify and map landscapes and their habitats for species. These models are broadly typified as correlative models, process-based models, and connectivity models (which can be further delineated by least-cost path (LCP), circuit theory, graph theory, and agent-based models). Correlative models use observation data and environmental information to predict the probability of occurrence based on abiotic or biotic criteria [61, 62]. Process-based models generate predicted distributions based on species’ limits to abiotic factors [63, 64]. Connectivity modelling, on the other hand, seeks to identify corridors and model how the landscape is connected.

One study has considered London at a landscape scale to assess habitat suitability for organisms [54]. However, this study used correlative regressions and citizen science. The species assessed here are similar but [54] only looked at mammals. In this paper, rather than looking for gradients of preference the goal with connectivity models is to use the data of habitat suitability - habitat preference or urbanisation tolerance - to determine the corridors these individuals might use in the landscape. Proxy species can serve as stand-ins for species with similar habitat preferences, even those of different genera or phyla [65, 66]. The variation in habitat preference and dispersal threshold offers a range for assessing the degree of connectivity across various iterations. In doing so, this paper provides a broad, evidence-based scope for the way that an array of species might interact with the landscape, comparing a focus on green-coverage to one that considers functional use of the landscape and whether there is a sufficient network for biodiversity across London.

In circuit theory models, the landscape is treated as an electric circuit. The researcher applies a resistance value to each habitat type and current is run through providing an output of all possible movement paths not just between nodes but across

the entire landscape [67, 68]. Of these models, the main proponents are the Circuitscape and Omniscape models, the latter of which performs an omnidirectional assessment compared to the former’s pairwise assessment [69–71]. Omniscape was used given its tiling function as a result of the omnidirectionality. This allows a landscape to be divided into sections and assessed. Since Circuitscape determines pairwise connectivity between nodes it has issues with tiling. This makes Omniscape better for larger rasters [69–71]. Based on the critiques levelled by [72] against researchers neglecting to explain their process, decisions behind resistance values, and visualisation techniques these will be explained in detail. Any choice of models is a decision of the researcher and frames results in a specific manner. Transparency around variable choices and motivation is necessary.

2.2.1 ArcGIS

To begin, it was necessary to create a detailed map of London that would serve as the basis for Omniscape, and could provide a detailed understanding of the habitat composition. As a part of the Agile Initiative at the University of Oxford, the Nature-based Solutions (NbS) Knowledge Hub was developed to provide tools to generate maps that can inform policy and provide opportunities for different types of NbS based on biophysical and socio-economic data [73]. The maps are based on over 40 different publicly available maps such as the Ordnance Survey Maps, Priority Habitat Inventory, various Department for Environment, Food & Rural Affairs (DEFRA) maps, the Crop Map of England (CROME), and Natural England open data. These are combined in ArcGIS using the open-source software developed by [73]. From this, it was possible to generate a detailed (1m resolution) preliminary base map. However, it lacked any information about trees, and so was overlaid with Bluesky’s National Tree MapTM (NTMTM) that maps every tree over 3m tall. The only trees included were those trees that intercepted sealed surfaces - in other words, the woodland was already considered so BlueSky data provided information on stand-alone street trees. This was necessary given the Agile toolkit has mostly been used in rural sites, and not in urban contexts where street trees are significant contributors to the urban ecosystem [74, 75].

The Agile tool was also capable of providing summary statistics for the landscape composition. In total there were 93 different habitats which were too extensive for the models and were therefore simplified following a review of the literature to 9 categories encompassing as many as ecosystems as possible. The map was therefore rasterised to a 6m resolution (the finest value that was able to take into account the width of roads) with values corresponding to the average of those therein. This map was then further simplified through use of fewer habitat categories, following best-practice when using Omniscape [70]. In the literature the extent of this simplification varies from three to over a dozen habitat types [49, 71, 76, 77]. Based on computational constraints and the need to capture habitat diversity, 9 categories were chosen. The aim was to have enough variation in habitats that the species proxies could be used to cover a sufficient array of specialism and habitat preference.

2.2.2 Omniscape

A tiling analysis was used for Omniscape with a core of 2000x2000 pixels and a buffer around the tile proportional to the dispersal threshold of the species. This meant that any artefacts from the chosen dispersal distance could be removed by overlapping each of these tiles to focus on cores. The tiling was carried out in a spiral starting in the centre of the raster and working outwards. This overcame the crashing that occurred when too many NoData values were present in the raster - as tiles approached the edge of the raster the core was reduced and the extent of overlap increased. In this way within 41 tiles the raster was able to include all the core necessary and minimise issues from NoData. The tiles were then compiled into a mosaic of core areas, and in ArcGis a colour gradient was applied to the cumulative current output using the Classify symbology with 10 Natural Breaks (Jenks) from lowest to highest current value to give the final results seen in figure 1.

2.3 Study Species

The species were chosen as proxies for guilds of species that occupy certain habitat types [78–80]. Proxies are often used and have been shown to effectively inform the protection and monitoring of surrogate species [65, 81]. Given the highly complex and interconnected nature of the urban environment, proxies facilitate the application of ecological techniques by simplifying the assessment and avoiding the need for agent-based modelling [65, 66]. While there is room for additional species this was also a function of time given the raster had to be reconfigured, and Omniscape had to be rerun for each. Additionally, the species were chosen so that they would both cover a breadth of dispersal distance thresholds, variation in IUCN Red List status, both vertebrates and invertebrates, and both generalists and specialists of woodland and grassland habitats. This information is conveyed by the resistance values, and preference or lack thereof for certain habitats. The species were as follows:

- European Badger (*Meles meles*) - Woodland Generalist
- European Stag Beetle (*Lucanus cervus*) - Woodland Specialist
- European Hedgehog (*Erinaceus europaeus*) - Grassland Generalist
- Small Heath Butterfly (*Coenonympha pamphilus*) - Grassland Specialist

According to the literature there are a few ways of determining the resistance values: through sampling sites to determine preferences, through expert opinions, or through a literature review. For this research employed the literature review technique. This allowed the inclusion of papers not directly related to connectivity modelling but to the Hutchinsonian niche [82] as well as life history traits of species. The benefit of this is that it allows researchers to compile the various values as well as ecological drivers behind habitat preference and to overcome the Wallacean shortfall that can occur when using citizen science to locate cryptic or similar species [83]. The table of resistance values is visible in the supplementary material (Supplementary Table 1) and the references that motivate the choice of resistance values can be found in Table 1.

The use of a resistance value of 1000 over water may seem errant for the Small Heath Butterfly given their ability to fly, but the literature showed that they tend to

fly very close to the ground in a step-wise manner between flowers - no further than 20m per short flight [84, 85]. While the rest of the literature review reflected that they could fly much further distances over the course of a day, the short manner of individual flights and reliance on places of rest precluded any travel over water-bodies. Especially given the River Thames varies between a width of about 50m to over 600m across London it was important to prevent this from being included as a viable form of connection.

A sensitivity analysis was run for each species by repeating the model for one central tile, assessing ten values between the upper and lower limits of dispersal distances found in the literature as well as the chosen value for use in the final output (either the median value or the literature consensus depending on whether the species had been modelled before). The figures of the sensitivity analysis can be found in the Supplementary Material, and are further discussed in the Results.

2.4 Metrics

Following the Omniscape assessment, boroughs were ranked by current per m² for each species. On top of this each borough was ranked by proportion of canopy cover and greenspace (including canopy cover) following an MSPA analysis performed using the Guidos Toolbox Workbench software provided by the European Commission [86]. These ranks were then compared to the Omniscape rankings, and a Spearman's correlation was used to determine whether the ranks for canopy and greenspace cover were able to predict the rankings for each species. On top of this, the number and location of pinch points for each species (or areas of high current within a width of 50 pixels), as well as the betweenness centrality (BC) of boroughs were determined. These analyses provided additional information gleaned from the Omniscape model and using the Guidos workbench.

3 Results

3.1 GIS Results

The mapping revealed that 60.29% of London is green, 22.78% of the total cover is gardens, and 15.17% are highly managed greenspaces (Table 2). The Agile mapping revealed that 2,194ha of London (1.38%) comprises golf courses while 893ha (0.56%) is devoted to Allotments. Additionally, 63,294ha (39.69%) of London is sealed surface, and 3,880ha (2.44%) is made up of hydrological features such as rivers, ponds, and lakes.

The London Environment Strategy states that at the time of its publishing the area of SINC's across its jurisdiction is 30,697ha, an increase of 824ha within the previous 20 years. These SINC's include the entirety of the River Thames and all public waterways, as well as all parks as Metropolitan sites of Importance. In terms of protected areas designated for nature, Special Protected areas (SPAs) are set aside for the conservation of birds and Special Areas of Conservation (SACs) are protected more generally for flora and fauna under the European Commission Directive 92/43. The former consists of 1281.6ha of the Southwest bodies of water and the Lee Valley basin only. This

value is almost the same as the amount of land currently under development. The SACs consist of Wimbledon Common, Richmond Park and Epping Forest, and make up 2,829.3ha, only just larger than the area of golf courses in the city.

3.2 Omniscape Results

First, the sensitivity analysis showed no artefacts dependent on the distance, nor arbitrary variation in results due to chosen values. The current output increased linearly with increasing dispersal distances (see Supplementary Material).

Figure 1 shows the Omniscape outputs: London-wide maps and part of the central tile with two Royal Parks. These demonstrate what would be expected from a generalist versus specialist species where the former shows a greater extent of coverage. Figure 1 also shows examples of pinch points - the narrow areas with high current representing narrow, highly-traversed passageways. To compare these maps with the current London policy, a bump chart was made (Figure 2). The MSPA generated the extent of greenspace or pure canopy cover in each borough. In accordance with this the boroughs were ranked, and the bump chart shows the variation between the greenspace and canopy rankings on the left, and the species current rankings on the right. Figure 2 shows that rankings diverge, indicating that structural proxies do not perfectly predict functional connectivity - none of the rankings are a 1 to 1 overlay (except the City of London). Figures 3 and 4 show the results of the Spearman's ranking. The darker red sections show higher correlations - with Stag Beetle having the lowest correlation with greenspace, and Small Heath Butterfly having the lowest correlation with canopy (note both are specialists).

Because rankings alone do not fully capture the Omniscape results, BC, number of pinch points, and the extent of inter-borough flow were used to plot a connectivity network between the boroughs [87] and assess the connection between administrative boundaries. Betweenness centrality is the measure of a node's importance in a network determined by how often it lies on the shortest paths between other nodes [87]. The pinch points assessed were those with the highest 2% of current given a 50 pixel moving window. These assessments were performed given the results of the Spearman's rank analysis revealed that there is a moderate correlation, especially among specialists (Stag Beetle, Small Heath) between policy rankings and the connectivity rankings. Total greenspace had a stronger correlation than the canopy cover, the latter was still positive, but the limits were between 0.53 and 0.66 compared to 0.47 to 0.86 for greenspace cover.

While the relationship is moderately positive, it is weakly positive for some specialists. This suggests that connectivity assessments are valuable in providing more refined assessment and can provide a deeper perspective of the way the landscape is used by more choosy species.

3.3 Post-Omniscape Analysis Results

These analyses considered the extent of inter-borough current flow and pinch points for each species. Using the circuit-based heat maps in Figure 1 it was possible to assess the flow of current across the landscape. This revealed that for woodland species (Stag

Beetle and Badger) over 10% of total current flows across borough boundaries. While lower in grassland species it is still 7.0% for European Hedgehogs and 8.3% for Small Heath Butterflies. These results show the value that a landscape level approach provides compared to borough-siloed policy which can substantially impact the landscape as a network if not thoroughly considered.

The Omniscap assessment also identified pinch points some of which are visible as high current foci in Figure 1. The list of pinch points provides a more elaborate toolkit for potential SINC designation, through determining areas of high current bottlenecks that ought to be prioritised for maintaining the landscape connection. Further analysis could identify the exact location of these and explore the impacts of expanding the habitat or focusing conservation efforts on these areas. These pinch points demonstrate the difference in using generalist versus specialist proxies where the former resulted in higher numbers (6,169 Badger; 8,285 Hedgehog) than the latter (5,781 Stag Beetle; 7,371 Small Heath), details seen below:

- European Badger - 11.6% cross boundary flow - number of pinch points: 6,169
- European Stag Beetle - 11.8% cross boundary flow - number of pinch points: 5,781
- European Hedgehog - 7.0% cross boundary flow - number of pinch points: 8,285
- Small Heath Butterfly - 8.3% cross boundary flow - number of pinch points: 7,371

This assessment was able to produce comprehensive maps of potential grassland and woodland species movement across the landscape, and produce far more detailed results than a mere landscape cover assessment - some of which were contradictory. Additionally, this output was used to create networks of connectivity to demonstrate the borough-by-borough flow. Omniscap produces an output that reveals emergent properties of connectivity. Some lower-ranked boroughs by structural cover are significantly more important when connectivity is the lens one uses to assess. For instance, Kensington and Chelsea ranks 30th and 29th for greenspace and canopy but bumps up to 13th and 9th for Badger and Stag Beetle ranking by current. The difference between a connected network and an assessment of greenspace/unit area can be seen in figure 4. The x-axis here shows the amount of current that flows into other boroughs, and the betweenness centrality is on the y. The presence of the City of London as the highest BC is a function of its small size. What this figure shows is that there are some boroughs with incredibly large currents, but they do not serve the network as a whole. Such an analysis as a connectivity assessment allows us to see the importance that central boroughs play to the network, even if they experience less green cover. Westminster and Wandsworth, for example, have frequently some of the highest BCs. While not the most verdant boroughs they often sit on the shortest path between two other boroughs. While some of the greener boroughs that can be found in the bottom left, with a BC of 0, only connect to one other borough, making an assessment of BC impossible.

Figure 3 shows a heat map of the correlations that outlines the range in positive correlations between 0.47 (Stag Beetle:Greenspace) as the weakest, and 0.86 (Small Heath:Greenspace) as the strongest. The Stag Beetle correlation with canopy cover ranking was only 0.54 suggesting that this specialist species is weakly correlated with both of the metrics used in the legislation. This weak positive correlation suggests

that the use of canopy cover or greenspace as a measure of viable habitat for specialist woodland species is insufficient at capturing the specificities of habitat for these individuals. The correlations suggest that greenspace is a good proxy for grassland species, but this is not the case for woodland specialists, and that canopy is a moderate proxy for all, with every species ranking between 0.53 and 0.66. Given woodland species include mammals, birds, and invertebrates many of which, by virtue of their status as specialists, are protected, this suggests that the standards for nature in London must be expanded upon to accommodate. Habitat proxy species could be used as to provide an alternate framework for assessing boroughs and local areas that not only includes a more refined consideration of habitat but can also take into account the functional connection between local sites both at a fine and broad scale.

Figure 6 shows the extent of inter-borough connectivity represented as a network map of the city. This format represents the paucity of connection between certain boroughs as well as the interference by the Thames in its eastwards, estuary-direction. Such a map could be used for network governance [88] and represents a novel means of demonstrating the importance of meso-scale considerations of cities by highlighting the connection or lack thereof between administrative boundaries, this concept has been noted on broader scales as having the potential to enhance management as it relates to the essential components of ecological connectivity [89].

4 Discussion

A major output of this research is a high-resolution Agile Map. A version without BlueSky canopy data will be made openly available in line with Agile software requirements. This provides a detailed spatial dataset and enables assessment of flooding and potential erosion risks. However, given this was not done using NDVI but instead used the land cover designation types from Natural England, it does not account for a recent study by the Royal Horticultural Society (RHS) and Gentian Ltd. which showed up to 60% of gardens in the UK are paved over [90]. This suggests that the value of gardens may therefore be overestimated in this dataset.

The Omniscape assessment demonstrates that connectivity rankings are not fully predicted by greenspace or canopy cover. The relatively weak correlations indicate that structural proxies alone do not adequately capture how species interact with urban landscapes. This highlights the importance of incorporating functional connectivity into urban ecological assessments, particularly for informing urban ecological strategies.

London, as a global megacity and the largest city in Europe [39], provides an important case for urban ecological assessments. While the analysis here focuses on local policy, the implications extend to other urban systems characterised by fragmented governance and heterogeneous land cover - features common to cities globally. However, this study extends the discussions of ecological connectivity by demonstrating that modelling can reveal systematic mismatches between structural indicators and functional ecological networks. While structural and functional approaches are complementary, both must be explicitly assessed to provide robust ecological insights.

Further, this study demonstrates that detailed connectivity modelling is not only useful for fast-growing, rapidly urbanising regions, but also mature cities. These findings demonstrate that connectivity-based approaches are applicable not only in rapidly urbanising regions, but also in mature urban systems; furthermore they suggest that reliance on structural proxies may be a widespread limitation in urban ecological planning, rather than a context-specific issue.

As [91] states, "*urbanization is both part of the problem and part of the solution for sustainable development*". If we hope to develop sustainable Nature-smart cities it is vital to integrate these techniques into global urban policy. Cities emerge through a series of historical decisions around land tenure, legal structures, immigration, and emigration. While this is more important as it relates to ecosystem services for nature and people, it is important to bear in mind with ecosystem assessments as well. This paper provides a deep dive into the structure of London, a city much larger than Geneva, Bedford, Luton, Glasgow, Braunschweig [49, 92–94], all of which have been considered previously. This demonstrates that it is now possible to use such models, at high enough resolutions to account for urban roads and fragmentation, to achieve meaningful results. If we are to use them as sites of innovation for biodiversity and nature, cities must be a focal point of landscape ecological research.

Structural and functional approaches are complementary [95], but both must be explicitly assessed to provide a robust understanding of urban ecosystems. Advances in modelling and spatial data now make it feasible to apply such approaches at high resolution in complex urban environments. This study demonstrates that connectivity-based assessments can be applied at city-wide scales, providing insights relevant to both rapidly developing and long-established urban contexts.

Cross-borough flow provides additional insight into the functional structure of the landscape. A substantial proportion of connectivity occurs across administrative boundaries, indicating that ecological processes are not confined to borough-scale governance units. The higher levels of connectivity observed for woodland species may reflect the role of linear features such as street trees in facilitating movement [19, 75].

When borough BC is ranked (Figure 5) it adds another layer beyond the current rankings. For instance, the top 5 boroughs for BC are the City of London, Tower Hamlets, Wandsworth, Greenwich, and Westminster. The top 5 current rankings, however, are Hillingdon, Havering, Bromley, Hounslow, and Kingston. This highlights the difference between boroughs with large areas of suitable habitat, and the landscape-level significance of boroughs in the overall connection of the network. Plots of hub importance against total cross-borough flow further highlight the contribution of smaller boroughs to overall connectivity - an aspect not captured by current-based rankings. If priority were only assigned to low-canopy ranking boroughs that appear higher for Stag Beetle functional connectivity (e.g. the borough of Kensington and Chelsea) then this would neglect the higher-BC-ranking boroughs such as Hammersmith and Fulham, Brent, or Wandsworth. The BC results and inter-borough flow combined with the current rankings create a picture of a landscape of deep interconnectivity, and adequate LNRS or SINC designation ought to reflect this.

Connectivity models provide a mechanism to demonstrate the modularity (and connectivity despite this) across the urban landscape, highlighting the need to generate adequate recommendations and conservation targets. The proportion of flow crossing borough boundaries gives credence to the importance of generating city-wide, landscape-level strategies. There were several instances in Figure 2 where very green boroughs were overtaken by middle- to low-ranked competitors, such as Hounslow appearing in the top 4 for both Badgers and Stag Beetles compared to its 13th (Greenspace) and 26th rankings (Canopy). Likewise, relatively high boroughs occasionally appeared far lower than expected, such as Sutton which appeared in 6th for Greenspace and 11th for Canopy but dropped to 22nd for Badger connectivity and 25th for Stag Beetle. These rankings draw attention to a complex and context-dependent aspect of ecological systems, especially in cities: the complex way in which organisms interact with and inhabit ecosystems must be explicitly considered in restoration planning.

Additional species groups, such as semi-aquatic taxa, would likely reveal further patterns. The network analyses showed that the river plays an important role in cutting off eastern boroughs from each other in the north-south direction, and also that the modularity of green cover in the central boroughs often prohibits cross-borough migration, shown in Figure 6 especially.

Connectivity modelling identified weaknesses not only in the assessment based on canopy or greenspace, but delineations based on administrative boundaries. The landscape approach employed lends itself to generating more connected forms of governance, interlinking top-down, bottom-up, and cross-boundary decision-making, one such governance technique is that of Network Governance [96]. Generating multi-scalar environmental networks has been proposed as a way of addressing the complex nature as well as management required for environmental legislation [97]. Research has given relatively limited attention to the meso-scale, with most focusing on regional- or local-level [88, 98]. In keeping with the outcomes of [88] in Stockholm, this paper provides a justification for the role of scale-crossing brokers and the implementation of network governance. The landscape level of an urban assessment such as this is an example of a meso-scale network that is frequently ignored. [59] identify that cities hold under-explored potential for urban design, and that social and ecological boundaries are prevalent. This paper demonstrates how the importance of administrative boundary-crossing processes can be quantified as well as what an outcome of the meso-scale assessment of a city as a landscape could look like. While administrative boundaries can have profound effects on, and in turn create their own, ecological boundaries [99], it is vital to be aware of the interplay of these processes. [89] identified that cross-boundary consideration enhances connectivity of management structures and therefore benefits the vital component that is ecological connectivity. This paper shows how one can employ landscape level models to achieve outputs that would enhance such network governance.

This paper stresses the importance of prioritising function over structure in environmental strategy. When viewing the landscape not only as a consequence of its percentage green cover, but in a way that is considerate of the way organisms interact with it, the outcome identifies that the picture painted by administrative documents

such as the London Plan or London Environmental Strategy risk misappropriating resources based on simplified judgements. Cross-boundary considerations at the scale of boroughs can also facilitate regional cross-boundary connections [100], this paper represents the role that connectivity modelling can play in such a goal, and the importance of such considerations in highly (administratively and ecologically) fragmented urban landscapes.

Previous studies have extended similar approaches to corridor optimisation [101], and future work could build on this by exploring optimisation and the effects of spatial resolution. This study provides a high-resolution and comprehensive assessment of London’s ecological connectivity, representing a first step towards more functionally informed urban planning.

While socio-politically justifiable to think of these regions in a segmental manner, it is clearly important to consider the way species interact not only with the ecosystems within these segments but across the landscape as a whole. Network governance is a growing means of actualising landscape conservation and recovery [96] and is highly applicable to urban areas, as is shown in this paper’s demonstration of strong and weak inter-borough connectivity.

While administrative boundaries are important for governance, ecological processes operate independently of them. This study demonstrates the importance of considering cities as interconnected landscapes, and highlights the role that connectivity modelling can play in supporting more effective urban environmental management. Adding to the strength of governance networks, landscape ecology is a view that must be employed to adequately understand urban spaces - localities that often exceed expectations in their ecological capacity.

5 Limitations

Further research could consider other species proxies, or layer this research with a correlative species distribution model (SDM) performing regressions based on citizen science against urbanisation, climate, or traffic. This could both further verify the findings, and provide further information about the role of urbanisation in influencing functional networks. Additionally, there is room to use models that allow for node addition to optimise the network. Finally, the Agile map was limited in its translation to be used in Omniscape. 9 categories were the broadest that could be used at this scale. Future work could run these models for a longer period using more land-use types, providing greater detail to the species habitat networks.

6 Conclusion

This paper reframes nature in our cities, and the way urban policy-making should better account for the landscape-level connectivity of nature. Contemporary urban policymaking often gives greater weight to structural proxies than to functional ecological connectivity. As seen in the [22] and [40], this is especially true in London, where the variables used to assess and monitor urban nature are greenspace or canopy.

This paper offers a different approach, re-envisaging London as an ecological landscape, and comparing the results of a functional assessment to those of greenspace and canopy cover.

This research demonstrates that intention is vital to restoration. We illustrate how the value of habitat changes based on a few representative proxy species. This could be expanded further to include ecosystem functions that benefit humans, or still more niche species. When performing assessments of nature, the task is constantly shaped by explicit or implicit values. The current policy does not admit to this and as such relies on coarse proxies that do not necessarily capture the intricacies of specialisation. Research such as this serves to enhance the picture we create in ecosystem assessments, with explicit consideration of values. As more research is done into these spaces, more values must be made explicit - through this it is possible to assess and improve on nature for both the flora and fauna therein, as well as for people.

The results corroborate key findings from similar studies in other cities: urban management policies often neglect components of nature crossing administrative boundaries, and the differences between a meso-scale vs regional-level approach [59, 98]. This supports the suggestions by [88] that urban policymaking should bring local management actors or brokers who bring border-crossing elements of nature into decision-making. The connectivity assessments demonstrated that the assumptions made by canopy and greenspace cover are sufficient indicators for generalist species, but not for specialist interactions with the landscape. This suggests that a more nuanced approach to urban nature management is necessary. Such an approach would move beyond administrative boundaries and consider the urban sprawl as a natural landscape not isolated within boroughs or reduced to simple foci like canopy or greenness.

This study challenges the dominant assumptions informing environmental policy-making in the densest inhabited areas. Despite entrenched beliefs that these areas are exclusively human domains, they are also deeply ecological. Cities are not only metabolically reliant on the work of nature in distant ecosystems, but influence and exist within the limits of nature. Recognising this can reframe urban and environmental policy to succeed in preserving and improving nature within cities and reaffirm our position in the biosphere. It is through this activity, the reintegration of nature into the lives of urban communities, that we can not only benefit from the services ecosystems provide but also reaffirm the ontology of our naturalness. Nature is not far-off and unhuman, but present even in our most human localities. Nature-smart cities are a necessary step in aligning ourselves with the ecological principles that sustain and are beholden to us. If we are to adequately green cities, connectivity models as well as cross-boundary planning must play a role in design and decision-making.

7 Figure Captions

1. Clockwise top 4 from top left these show the output maps of the Omniscape analysis for the European Badger, European Hedgehog, Small Heath Butterfly and European Stag Beetle. The legend shows the values of the 10 Jenks Break bands for cumulative current of each pixel. Bottom 4 show the Omniscape outputs for the four proxy species, but zoom in on the central tile around Hyde Park and Regent's Park to demonstrate the differences in output both between specialists vs generalists, and woodland vs grassland proxy species
2. This bump chart is the output of ranking the boroughs by average cumulative current/m² for each of the species versus the rankings of greenspace and canopy cover per m². The borough names are labelled by the first few letters, but the colours are consistent for each borough and visualise how these rankings change. Note the red boroughs which rank very low for greenspace appearing in the top ten and the blue boroughs which rank highly for greenspace in the bottom ten for stag Beetles.
3. This shows the Spearman's rank matrix between each of the proxy connectivity rankings and the canopy and greenspace rankings. The paler colours indicate a weaker positive as the correlation tends closer to 0 - or random correlation.
4. The top 4 graphs visualise the rankings for greenspace vs species ranking, and display the spearman's correlation value and degree of significance above. The bottom 4 graphs visualise the rankings for canopy vs species ranking, and display the spearman's correlation value and degree of significance above.
5. For each species, these show the connectivity hubs on the left displaying the betweenness centrality for each of the top 15 boroughs. On the right the total cross-borough flow has been plotted against the betweenness centrality to display the variation in total current flowing out of boroughs compared to their betweenness centrality or how often they serve as midpoints between two boroughs.
6. These four maps show the connectivity network based on the inter-borough connectivity for the top 90% of current flows (i.e. ignoring the very lowest amount of connectivity to capture boroughs that have negligible connections). Node size and colour corresponds to the amount of total inter-borough current flow, while the thickness of the blue lines corresponds to the flow between two specific boroughs

8 Tables

Table 1 Indicator Species

Species	Habitat Preference	GB IUCN Red List status	Dispersal Distances /m	References
European Hedgehog (<i>Erinaceus europaeus</i>)	Grassland Gardens Allotments, Cemeteries & Churchyards	Vulnerable to Extinction	1000	[94], [55], [102], [103], [104], [105], [106]
European Badger (<i>Meles meles</i>)	Arable Grassland Woodland,	Least Concern	1250	[107], [108], [54], [109], [110],
Small Heath Butterfly (<i>Coenonympha pamphilus</i>)	Grassland Highly Managed Greenspace	Vulnerable	700	[111], [112], [84], [85], [113],
European Stag Beetle (<i>Lucanus cervus</i>)	Woodland Allotments, Cemeteries & Churchyards	Near Threatened	800	[114], [115], [116], [117], [116], [118],

Table 2 Pixel label analysis of Greater London 9 Category map with 6m resolution

Label	Land Cover Type	Count	Percentage
1	Woodland & Forest	52,932,337	13.28%
2	Semi-natural Grassland & Heathland	20,702,186	5.19%
3	Wetlands & Hydrological Features	11,948,300	3.00%
4	Allotments, Cemeteries & Churchyards	4,835,156	1.21%
5	Gardens	90,782,087	22.78%
6	Highly Managed greenspace	60,457,172	15.17%
7	Passable Artificial Surfaces	80,829,690	20.28%
8	Impassable Artificial Surfaces	65,467,156	16.43%
9	Arable land	10,598,181	2.66%

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All maps created using Agile Opportunity Maps software from the Oxford Martin School. These maps incorporate OS data (©Crown Copyright and database rights 2024 Ordnance Survey AC0000851941) and Open Government License data.

All maps created using canopy data that is Copyright © Bluesky International Ltd 2025 ALL RIGHTS RESERVED.

GuidosToolbox is available at the following web site: <https://forest.jrc.ec.europa.eu/en/activities/lpa/gtb/>.

Ethics, Consent to Participate, and Consent to Publish declarations. not applicable

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Data Availability. The datasets generated and/or analysed during this study are derived from a combination of publicly available and licensed data sources, including Natural England, Ordnance Survey, DEFRA, and Bluesky National Tree Map™ data. Due to licensing restrictions, some datasets cannot be shared publicly. Processed data supporting the findings of this study are available from the corresponding author upon reasonable request, subject to data access agreements.

Supplementary information. Please see Supplementary Information for details on resistance values and sensitivity analyses

Supplementary Figure 1 caption: These graphs demonstrate the variation in mean cumulative current and coefficient of variation (top to bottom) between each species across the range of dispersal thresholds found in the literature. They demonstrate that the changes in cumulative current and variation are dependent on the dispersal distance threshold and not artefacts of the model - therefore depending on accurate choice of dispersal thresholds which are shown as the vertical dotted lines.

Supplementary Figure 2 Caption: These show the difference between the smallest and largest dispersal values chosen for the stag Beetle (top) and small heath butterfly (bottom) when mapping the central tile. They demonstrate how much the output varies and the far-right map shows the largest differences in these areas. As with supplementary Figure 1 they show that the choice of dispersal distance is important and reliant upon accurate and informed decisionmaking.

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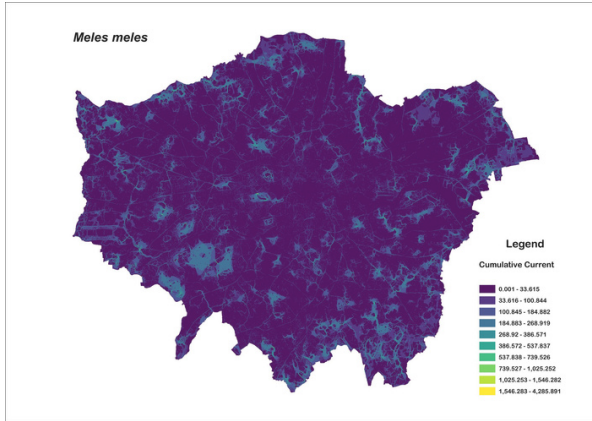
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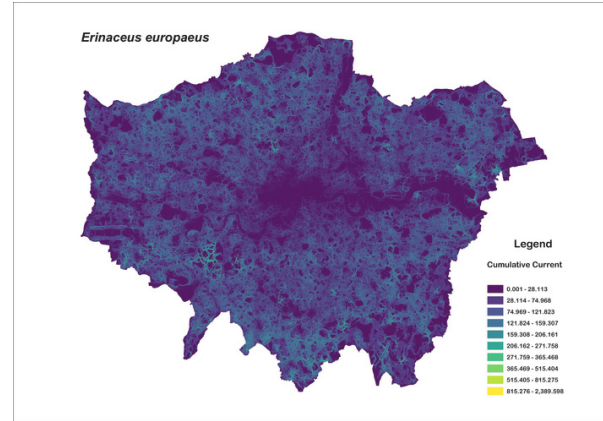
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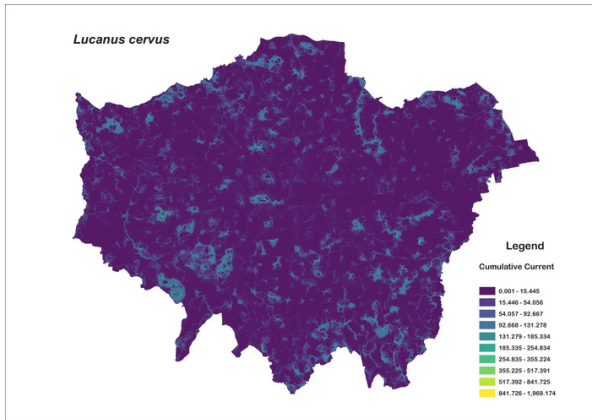
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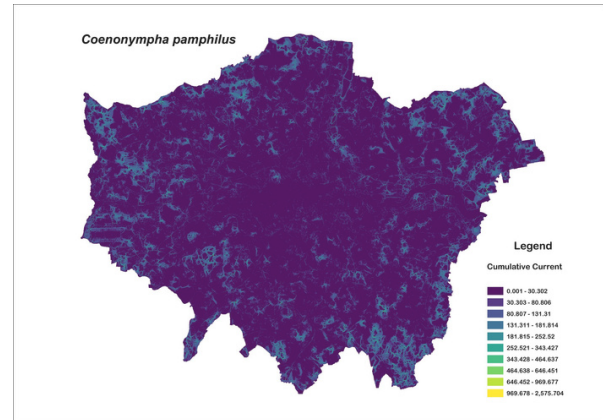
(a) European Badger



(b) European Hedgehog



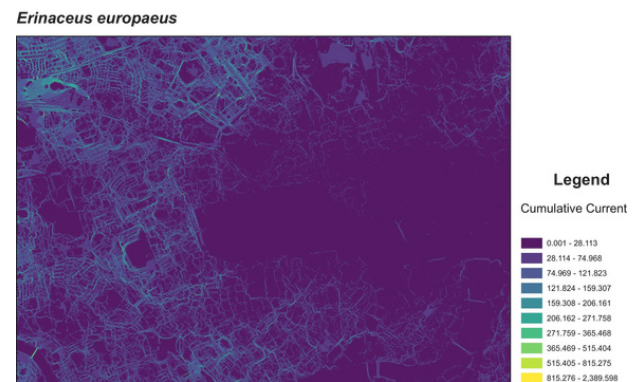
(c) European Stag Beetle



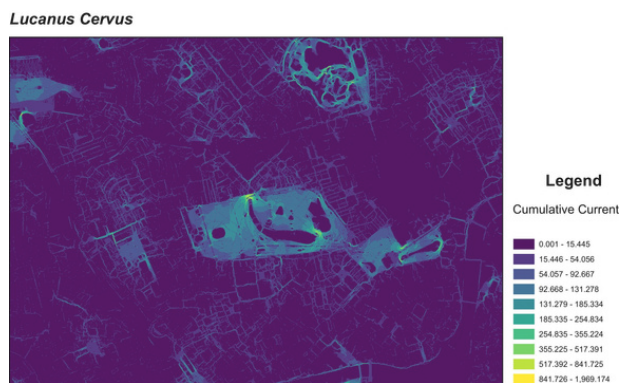
(d) Small Heath Butterfly



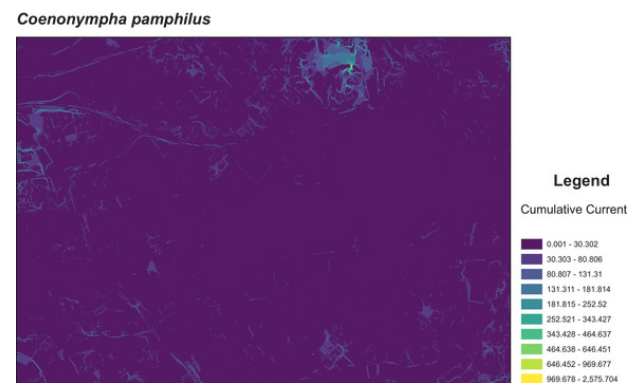
(a) European Badger



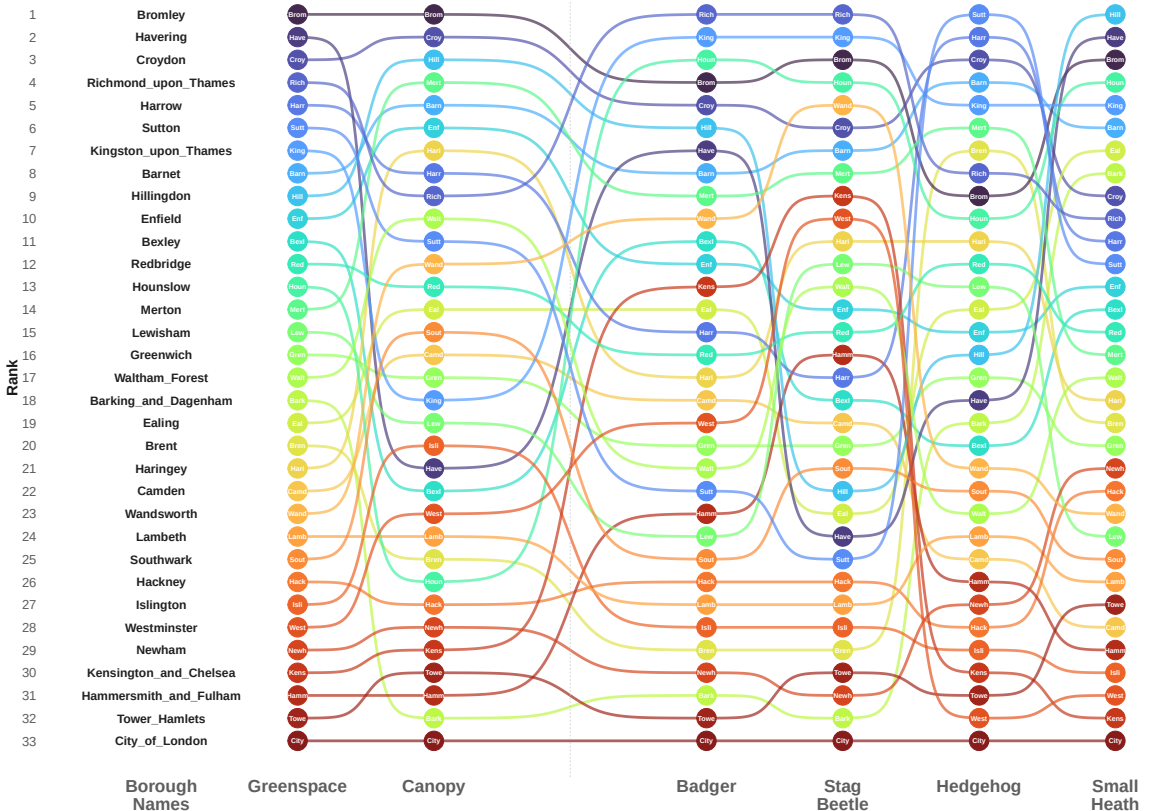
(b) European Hedgehog



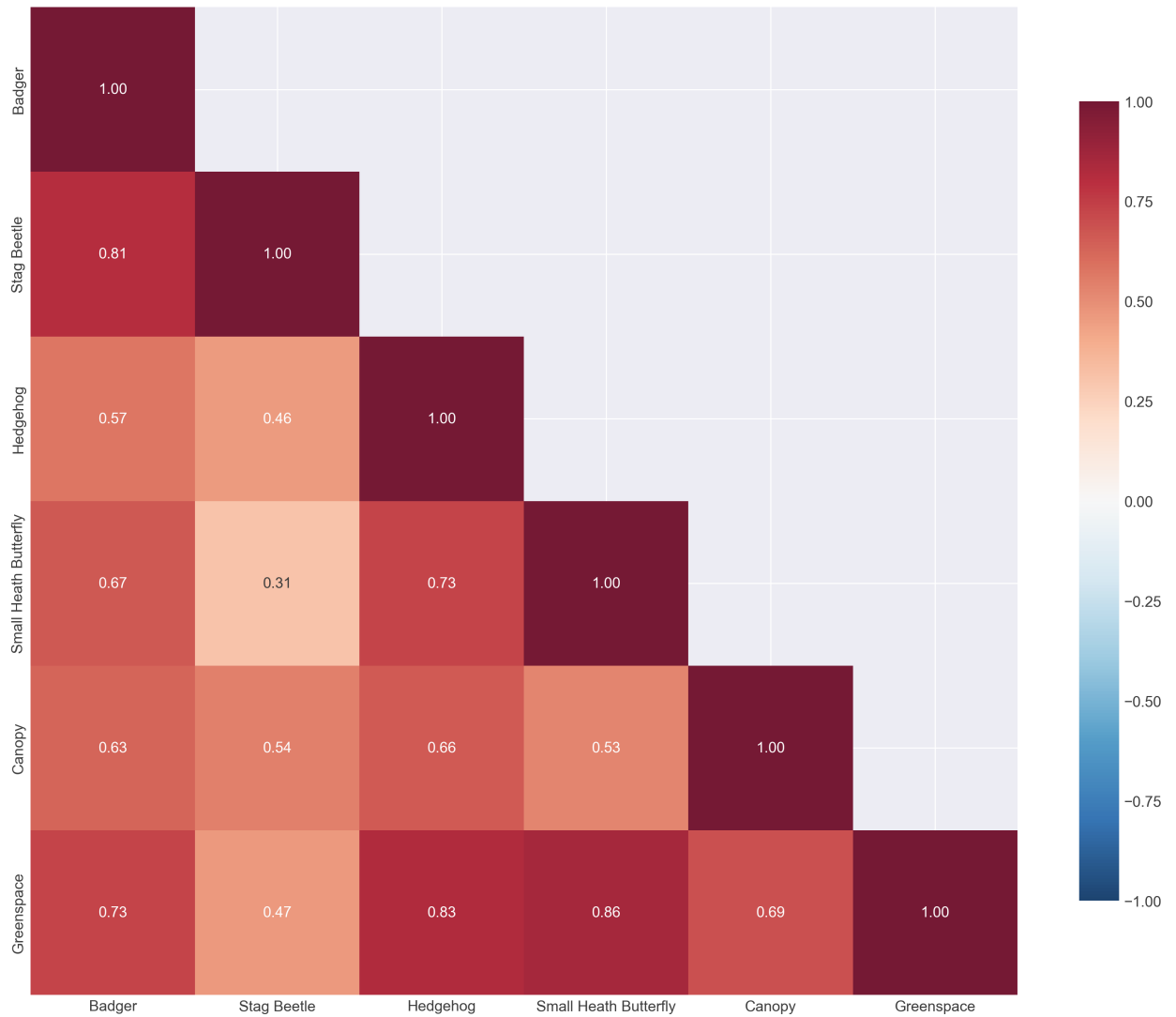
(c) European Stag Beetle



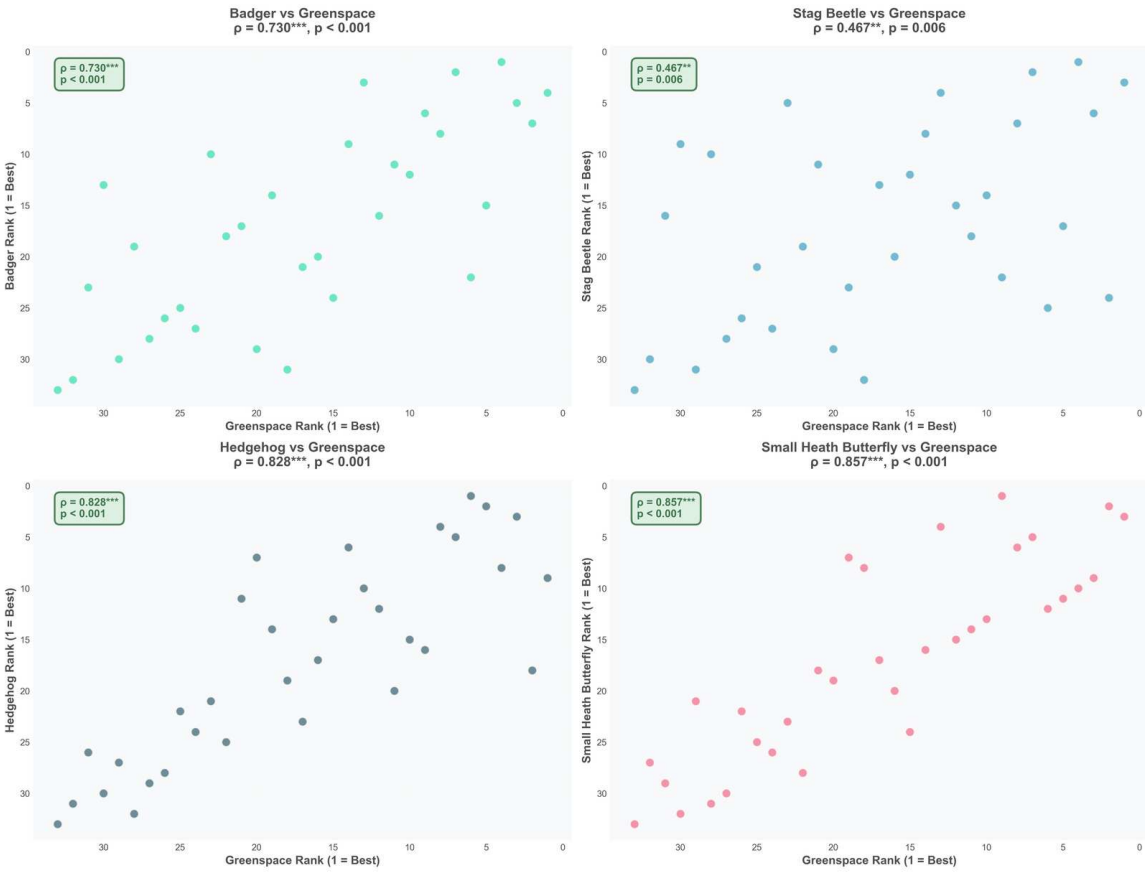
(d) Small Heath Butterfly



Spearman Correlation Matrix of All Rankings



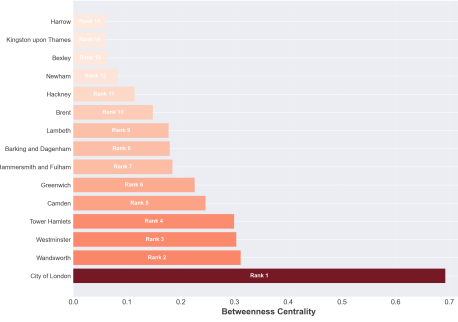
Species Connectivity vs Greenspace Rankings



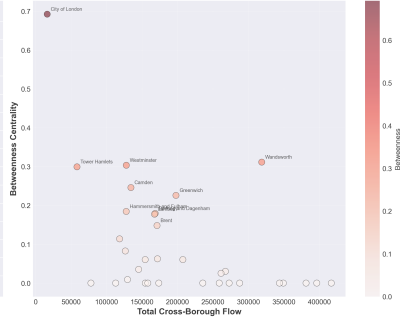
Species Connectivity vs Canopy Cover Rankings



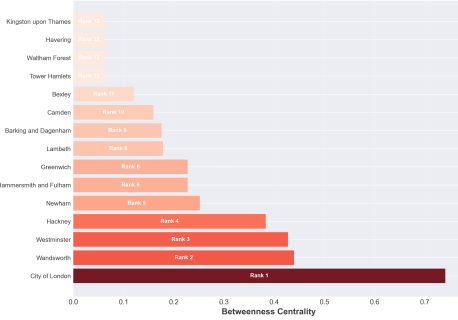
Top 15 Connectivity Hubs
Badger



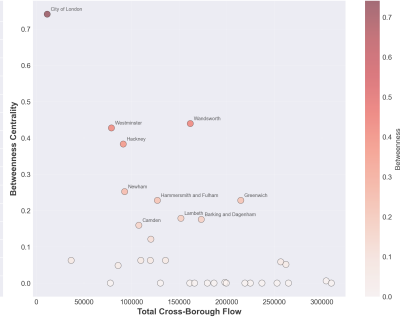
Hub Importance vs Flow
Badger



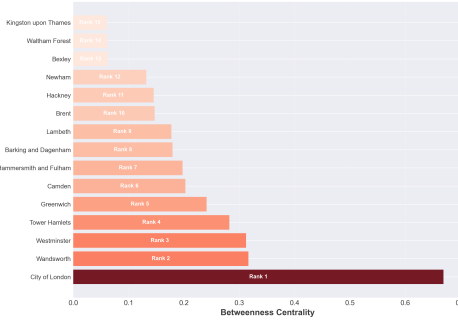
Top 15 Connectivity Hubs
Hedgehog



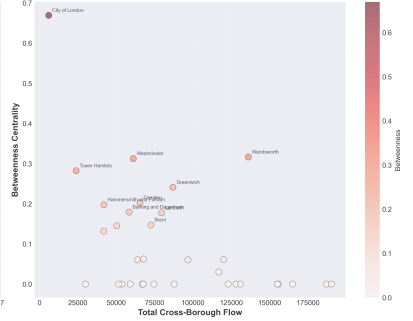
Hub Importance vs Flow
Hedgehog



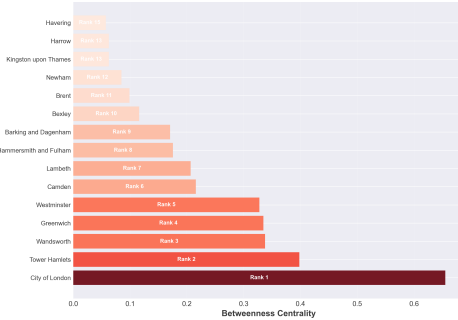
Top 15 Connectivity Hubs
Stag Beetle



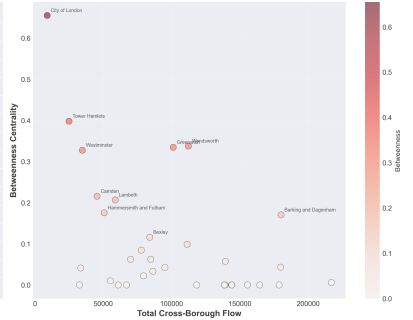
Hub Importance vs Flow
Stag Beetle



Top 15 Connectivity Hubs
Small Heath Butterfly



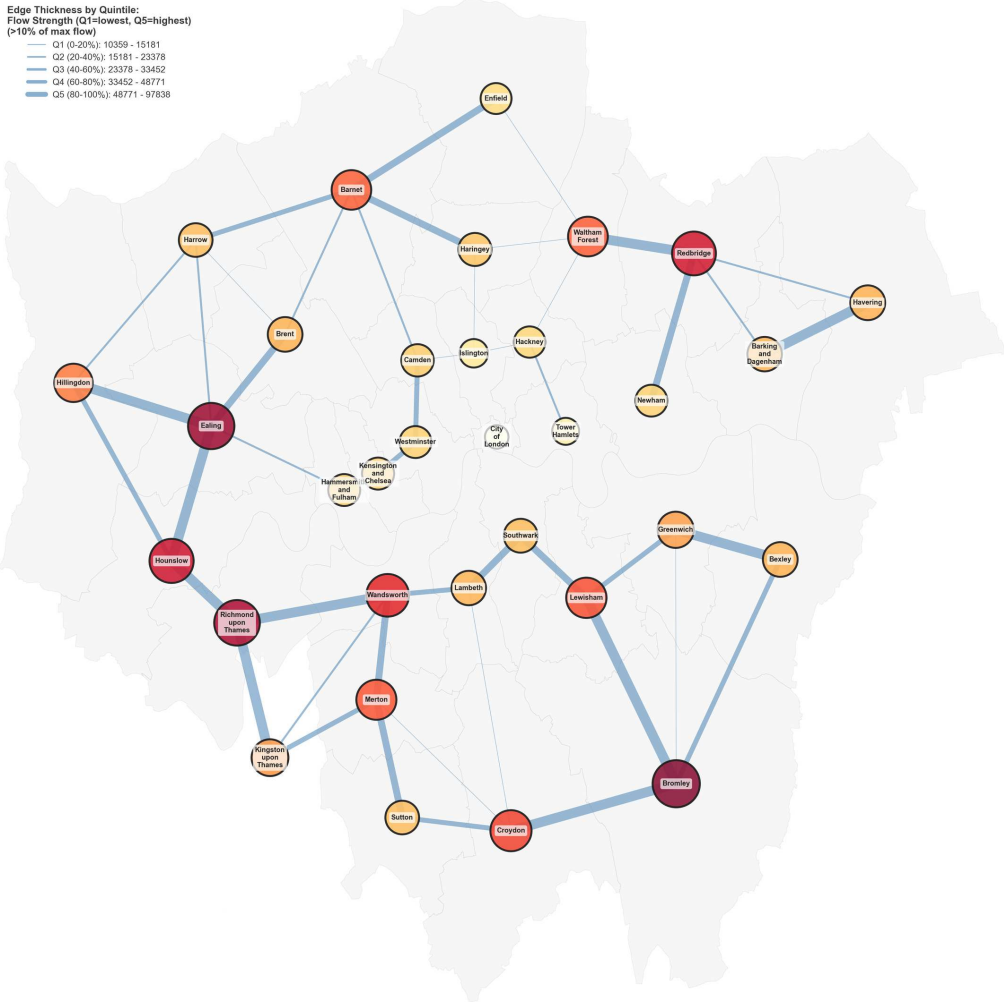
Hub Importance vs Flow
Small Heath Butterfly



Cross-Borough Connectivity Network: Badger
All 33 Boroughs | Edges: flows >10% of maximum (classified by quintiles)

Edge Thickness by Quintile:
Flow Strength (Q1=lowest, Q5=highest)
(>10% of max flow)

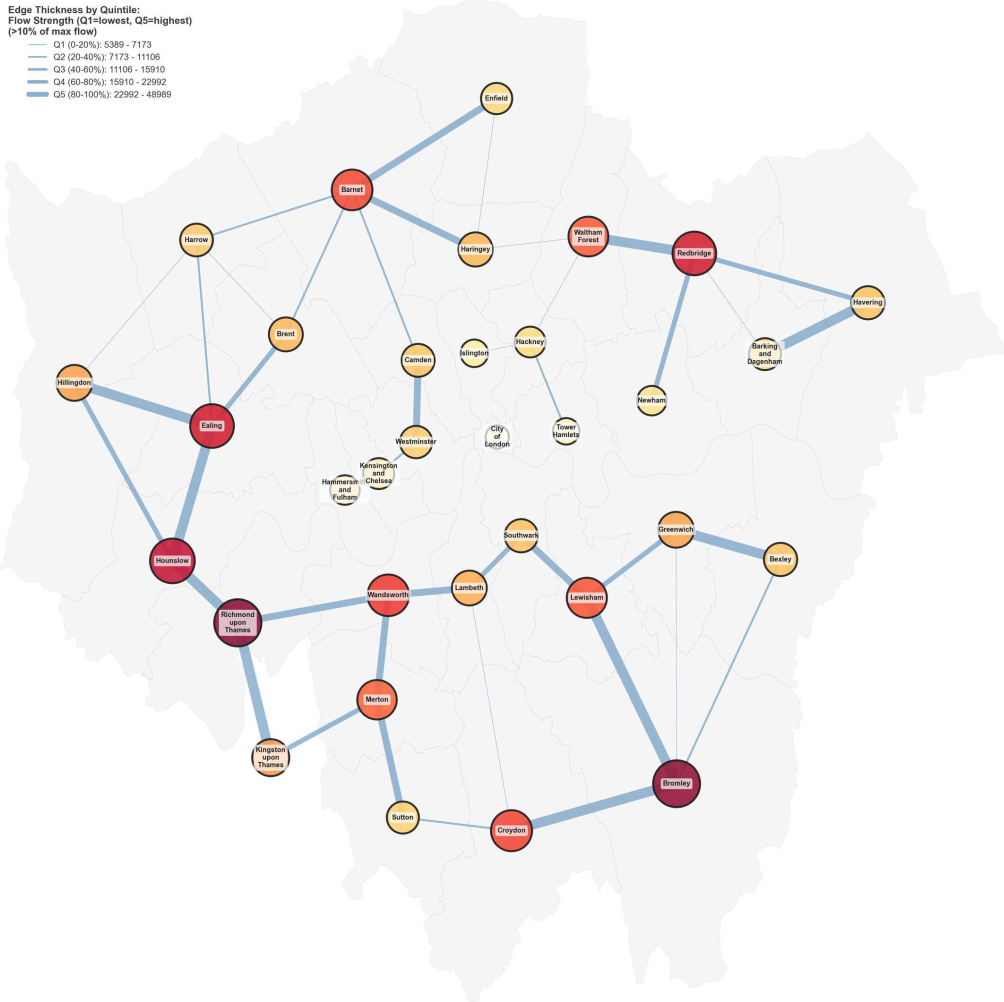
Q1 (0-20%):	10359 - 15181
Q2 (20-40%):	15181 - 23378
Q3 (40-60%):	23378 - 33452
Q4 (60-80%):	33452 - 48771
Q5 (80-100%):	48771 - 97838



Cross-Borough Connectivity Network: Stag Beetle
All 33 Boroughs | Edges: flows >10% of maximum (classified by quintiles)

Edge Thickness by Quintile:
Flow Strength (Q1=lowest, Q5=highest)
(>10% of max flow)

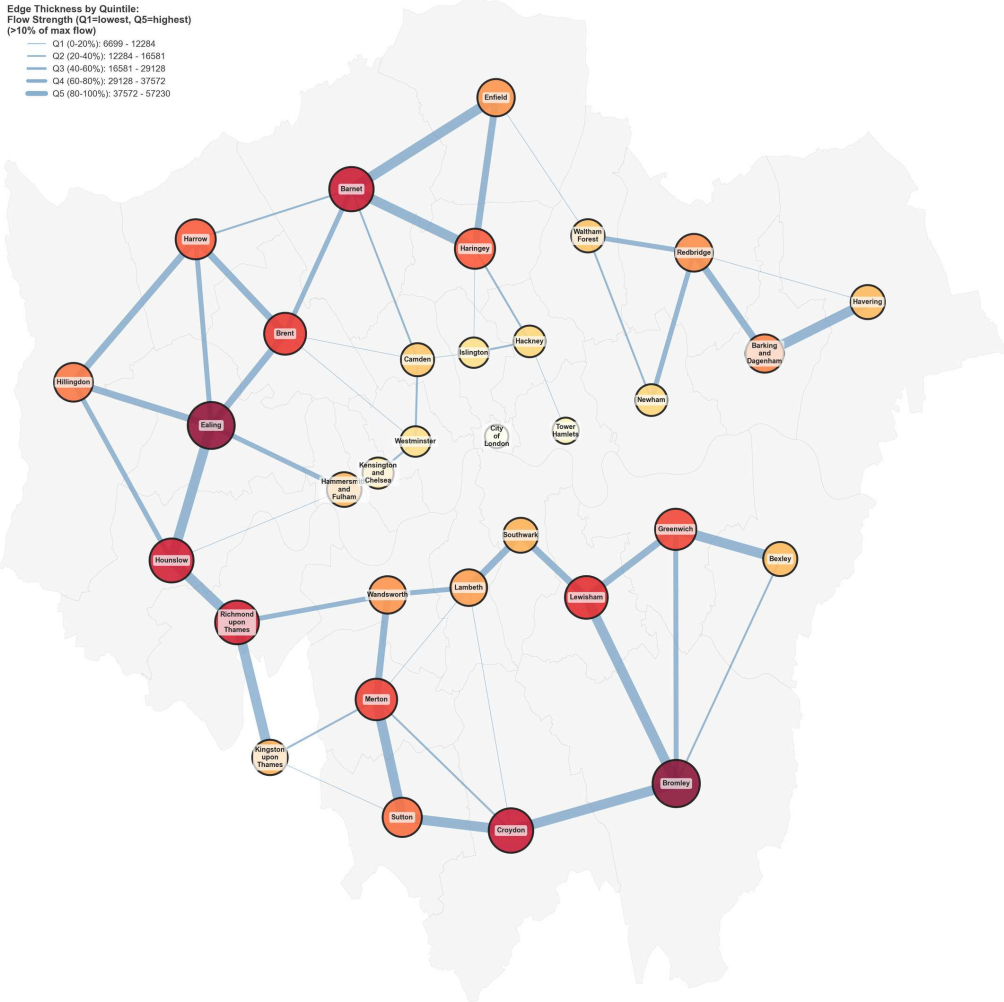
Q1 (0-20%):	5389 - 7173
Q2 (20-40%):	7173 - 11106
Q3 (40-60%):	11106 - 15910
Q4 (60-80%):	15910 - 22992
Q5 (80-100%):	22992 - 48989



Cross-Borough Connectivity Network: Hedgehog
All 33 Boroughs | Edges: flows >10% of maximum (classified by quintiles)

Edge Thickness by Quintile:
Flow Strength (Q1=lowest, Q5=highest)
(>10% of max flow)

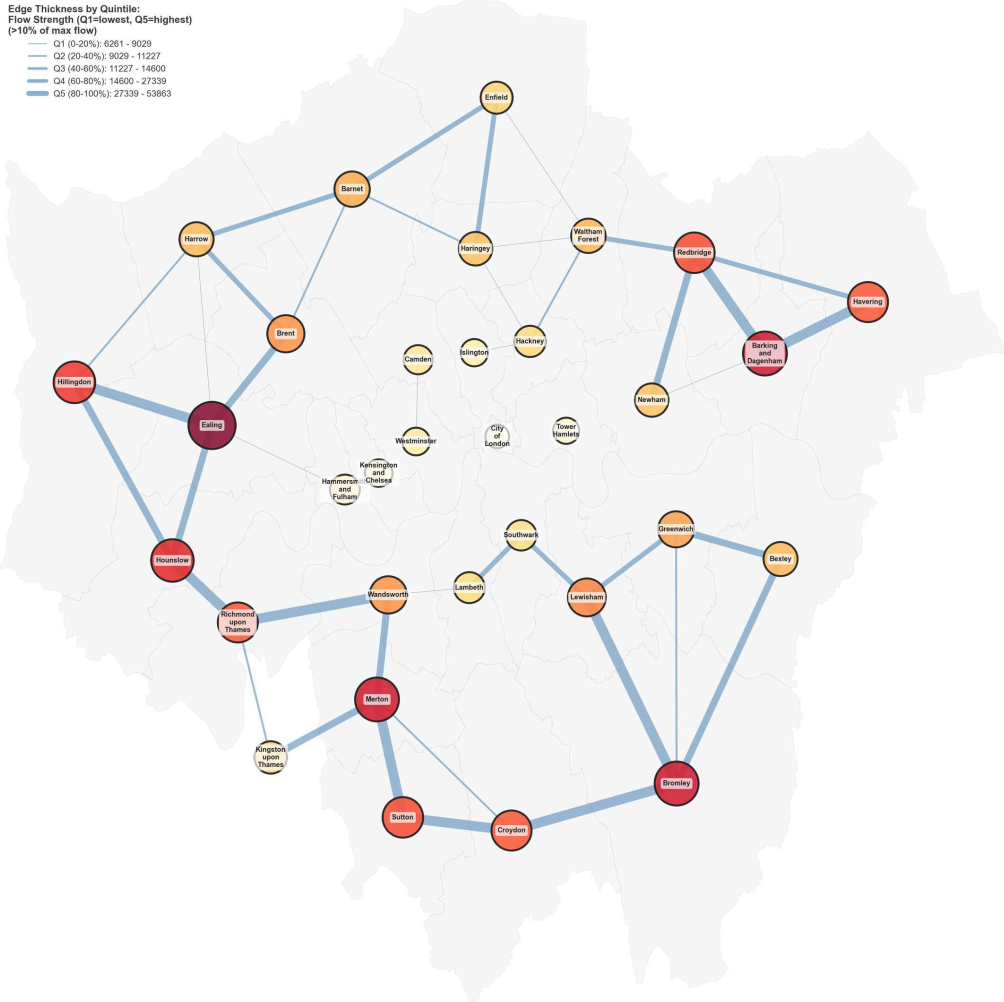
Q1 (0-20%):	6699 - 12284
Q2 (20-40%):	12284 - 16581
Q3 (40-60%):	16581 - 29128
Q4 (60-80%):	29128 - 37572
Q5 (80-100%):	37572 - 57230



Cross-Borough Connectivity Network: Small Heath Butterfly
All 33 Boroughs | Edges: flows >10% of maximum (classified by quintiles)

Edge Thickness by Quintile:
Flow Strength (Q1=lowest, Q5=highest)
(>10% of max flow)

Q1 (0-20%):	6261 - 9029
Q2 (20-40%):	9029 - 11227
Q3 (40-60%):	11227 - 14600
Q4 (60-80%):	14600 - 27339
Q5 (80-100%):	27339 - 53863



Supplementary Files

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