INSTITUTE FOR GLOBAL PROSPERITY

Studying the impact of urbanisation on global and local insect populations

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Abstract

Rapid urbanisation is leading to devastating decreases in global biodiversity. While cities expand economic opportunities and foster diversity and inclusion for humans, the conversion of land into urban space is one of the primary drivers of biodiversity loss around the world. To develop cities that can provide habitats for all living species, we must better understand the influence of urbanisation on biodiversity. This study has two focuses: global insect biodiversity and London butterfly biodiversity, each in relation to the challenges presented to them by different urbanisation variables: impervious surface area, artificial light at night and land cover. These relationships were studied with regression analysis and modelled with generalised linear mixed effects models. At the global level, only certain land uses exerted a significant influence over changes in insect biodiversity, with signals from the urbanisation variables being too weak to draw any conclusions regarding their impact. In the London case study, butterfly species richness fluctuated significantly with changes in the value of each urbanisation variable, as well as changes in land cover. This study calls attention to the importance of context when studying urbanisation's impact on insect biodiversity. Though drawing patterns at the global scale was largely precluded due to external variables, at the single-city level butterfly species richness was determined by both landscape and local conditions. This study contributes to building our understanding of how changes in the built and natural environment can impact biodiversity, a crucial piece of knowledge in our increasingly urban world.

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Glossary of Terms

Artificial Light at Night (ALAN): The presence of human-made light in the environment during nighttime hours, usually associated with urban and suburban areas. ALAN can disrupt natural light-dark cycles and affect wildlife behaviour and ecosystems.

Backwards stepwise selection: A statistical method for model selection that starts with all predictor variables and iteratively removes the least significant variable until all remaining variables are statistically significant. This was the method used for model selection during statistical analysis.

Chi-squared (χ2): A statistical test used to determine the difference between the expected and observed outcomes of different variables. This value is used to determine the significance of a variable in a statistical model.

Degrees of freedom: In statistics, the maximum number of independent variables used to calculate a statistic, often referred to in relation to χ2 values.

Gaussian distribution: Also known as the normal distribution, it is a symmetric probability distribution that follows a bell-shaped curve. It is often used to model natural phenomena in various fields, including biology and ecology.

GeoTIFF: A file format for storing georeferenced raster imagery. It embeds geographic information within a TIFF file, allowing for spatial analysis and mapping.

Heteroscedasticity: occurs when the standard errors of a variable are not constant over time

Impervious Surface Area (ISA): The percentage of land covered by impenetrable surfaces such as buildings, roads, and parking lots, preventing water infiltration into the soil. ISA is associated with urban development and pollution of waterways due to run-off.

Negative Binomial Model: A discrete probability distribution used for modelling count variables. It is a generalisation of the Poisson regression, used when the variance in the data exceeds the mean. It is often used for overdispersed count data.

Overdispersion: when the variance of the response variable is greater than what is predicted by the statistical model.

p-value: The probability of obtaining the observed results, and that there is a relationship between the two variables being studied. It is used to determine the statistical significance of results, with lower values signifying greater statistical significance. P-values of 0.05 or lower are generally considered significant.

Poisson distribution: a discrete distribution that measures the probability of a given number of events happening in a specified time period. Poisson regressions are used to model count variables, assuming these variables occur with a known average rate, and independently of the time since the last event.

Raster: A gridded matrix of cells (or pixels) organized into rows and columns, where each cell contains a value representing information, such as elevation, temperature, or land cover type. In this study, all rasters contain geographic/spatial information.

Shapefile: A geospatial data format for geographic information system (GIS) software. It stores the geometry and attribute information for spatial features like points, lines, and polygons.

Spatial join: A GIS operation that appends data from one feature layer to another based on the spatial relationship between the features, such as intersection or proximity. This paper references 'spatial joins' when referring to joining two sets of data, generally urbanisation data to biodiversity data in their spatial formats.

Species Abundance: The number of individuals of a particular species in a defined area or community.

Species Richness: The number of different species represented in an ecological community, landscape, or region.

Urban Heat Island (UHI): An area (usually within a city) that is significantly warmer than its surrounding rural areas due to human activities and urban development, characterized by higher surface and atmospheric temperatures.

Zero-inflation: When a data set has more zeros than expected by a Poisson distribution. The word "inflation" emphasizes that the probability mass at zero is greater than what a standard parametric distribution would allow. Zero-inflation is a common symptom of overdispersion, and accounting for zero-inflation doesn't always remove overdispersion.

List of Abbreviations

ALAN – Artificial Night At Light
BC – Butterfly Conservation
BNM – Butterflies for the New Millennium
GHSL – Global Human Settlement Layer
GI – Green Infrastructure
GLA – Greater London Authority
ISA - Impervious Surface Area
IUCN – International Union for the Conservation of Nature
PREDICTS - Projecting Responses of Ecological Diversity In Changing Terrestrial Systems
UHI – Urban Heat Island

List of Figures and Tables

Unless otherwise stated, all figures, tables and visualisation were created by the author.

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1 | INTRODUCTION

Economic opportunities, arts and culture, and the broad acceptance of different religions and ethnicities found in cities all contribute to the increasing urbanisation of our world. Today, roughly 56% of the world's population live in urban areas; by 2050, that share is expected to increase to 70% of the total global population (World Bank, 2024). In many ways, living in a city is considered the more environmentally-friendly option: city-dwellers tend to walk, cycle or take public transport, whereas those in the countryside often need to drive to get around. Urban accommodation is smaller per capita than rural housing, requiring less energy to heat in winter and cool in summer. As the population grows—which it is projected to do until at least 2080—and the development needs of many around the world increase, it is considered more ecologically sound to build *up* rather than *out*, to develop on land that has already been converted from primary vegetation, rather than exploiting wild habitat anew (Dale and Newman, 2009). In this way, urban development and expansion could be seen as less destructive for wildlife than development alternatives in rural areas.

Despite this, through industry, transport and the concentration of wealth that accumulates in urban areas, cities account for 70% of the total emissions of greenhouse gases (Environment, 2017), which, by changing our climate, intensifies weather patterns, modifies habitats, and warms the planet and seas, disrupting diverse biological functions (Otero *et al.*, 2020). It is estimated that 24% of the species on the International Union for the Conservation of Nature (IUCN) Red List are threatened by commercial and residential infrastructure expansion (zu Ermgassen *et al.*, 2022), which is unavoidable as millions of people look to settle in urban areas. Other indicators of urbanisation—such as light pollution, impervious surfaces and habitat fragmentation—have been directly linked to wildlife and biodiversity loss (Fenoglio *et al.*, 2021).

Due to urbanisation and humans' unrelenting pressure on the environment, the world's biodiversity is under threat. There are more than 157,000 species on the IUCN Red List, of which over 45,000 are species threatened with extinction. This includes 12% of birds, 26% of mammals, 34% of conifer trees and 36% of reef corals (*The IUCN Red List of Threatened Species*, 2024). Though difficult to quantify, it is estimated that the current rate of species extinction is at least tens—and up to hundreds—of times higher than the average rate over the past ten million years. Furthermore, the rate of extinction is accelerating (Ceballos *et al.*, 2015). One class of species particularly vulnerable to our changing climate and urbanising world are insects. Insects make up 75% of all plant and animal species globally (van der Sluijs, 2020), play vitally important roles in our lives, but are under severe threat, disappearing at alarming rates around the world (Sánchez-Bayo and Wyckhuys, 2019; van der Sluijs, 2020; Wagner, 2020). The IUCN has named 'housing and urban areas' as the number one threat to insects (*The IUCN Red List of Threatened Species*, 2024), and it's estimated that roughly one third of all insect species are threatened, with as many as 41% suffering some level of decline (Sánchez-Bayo and Wyckhuys, 2019).

Within the planetary boundaries framework, biodiversity is considered one of the processes vital to maintaining a stable Earth system (Richardson *et al.*, 2023). Continued biodiversity loss due to human activity places undue strain on our planet, which already suffers from a host of anthropogenic pressures, such as land-use change and climate change, both of which are connected to genetic diversity of species. Healthy, biodiverse landscapes are crucial for the planet and all living species to thrive, and they provide a wide range of ecosystem services, such as water filtration, air purification, carbon storage, nutrient cycling, pollination, natural pest control, and climate stability (Alho, 2008).

It may be unsurprising, then, that biodiversity has been positively correlated with gains in human health and wellbeing. The more biodiverse the planet's ecosystems, the better able they are to provide humans with some of their core needs, as defined by Maslow (Maslow, 1943). At a basic level, ecosystems supply our physiological needs: food, water, shelter, as well as the air we breathe. Going one step up, healthy ecosystems can provide us with safety and security, such as medicine and jobs, while a loss in biodiversity can lead to an increase in the transmission of infectious diseases (Keesing *et al.*, 2010). Finally, interactions with nature—often, explicitly biodiverse nature—bestows wide-ranging social, cultural and psychological benefits, including increased self-esteem, social cohesion and spiritual wellbeing (Sandifer, Sutton-Grier and Ward, 2015). In cities in particular, time spent in more biodiverse landscapes—as measured by species richness of plants, birds and butterflies—is associated with greater psychological benefit than time spent in less biodiverse parks and green spaces (Fuller *et al.*, 2007).

Finally, biodiversity has intrinsic value, just like any living thing; much of it existed long before humans did, and it should continue to exist long after. Protecting biodiversity is our imperative for the 21st century. The challenge then becomes how to fulfil the needs of humans—particularly those in regions undergoing rapid development—while ensuring the highest levels of biodiversity as possible. The world must continue to urbanise to meet the needs of the growing human population, yet the number one driver of habitat loss around the world is land use change (Hanski, 2011), including the conversion of land into urban space. As cities grow, humans displace wildlife, leaving them with nowhere to live. But what if cities could be habitats not only for people, but for wildlife too? In an increasingly urbanised world, understanding patterns and drivers of urban biodiversity loss will be necessary for developing healthy, sustainable cities for all living species.

Public awareness of both biodiversity in general, and biodiversity in cities specifically, has grown in recent years, and there has been increasing recognition of the importance of urban spaces for wildlife 'as cities become viewed as novel ecosystems rather than anthropogenic sinks devoid of nature' (Collins, Magle and Gallo, 2021, p.56). This recognition is vital so that public and private entities may work together in the important task of building the kinds of places that benefit people as well as wildlife. Cities could provide important habitat in a world becoming increasingly urbanised, but as yet there is a knowledge gap concerning the role of urban systems to protect and conserve biodiversity. City planners and government need to know how biodiversity responds to different forms of urbanisation, but more research is needed to make recommendations to protect biodiversity in urban settings.

This study aims to fill that gap by identifying and better understanding the relationship between insect biodiversity and urbanisation. Using a global database of biodiversity surveys (the PREDICTS database), I analyse the impact of key urbanisation metrics and land use on insect biodiversity at the global scale. Datasets for artificial light at night and impervious surface area serve as proxies for urbanisation and human pressures on the environment. After modelling the effects of urbanisation on insect biodiversity globally, I zoom into the local level and use London as a case study to measure the impacts of urbanisation drivers on butterfly biodiversity. Through my research, I seek to deepen our understanding regarding the extent to which cities can act as habitats for wildlife and contribute positively to biodiversity, and more specifically, how we can develop cities in ways sensitive to insect populations. My research will add to the emerging field of urban ecology and the growing body of work assessing the impact of urbanisation on insect biodiversity.

There are two main questions this study seeks to answer:

1) How does global insect biodiversity respond to light pollution and impervious surface area, two measurable drivers of urbanisation?

2) How is butterfly biodiversity in London impacted by features of the natural, built and social environment?

The global study looks at both species richness and total species abundance, while the London study examines only total abundance. These questions will also be enriched by examining interactions between land use and urbanisation drivers. Armed with this knowledge, how might we develop more sensitive cities, and incorporate nature into their planning? It is crucially important that decision-makers and stakeholders have as much data available to them as possible, to help guide the development and preservation of wildlife-friendly, biodiverse cities.

Based on the findings of previous studies, overall biodiversity is expected to decline with increasing levels of urbanisation (Faeth, Bang and Saari, 2011). However, some studies—specifically on Aves and Arthropods—showed an increase in overall abundance, but a decrease in species richness, due to an increase in urban generalist or synanthropic species, but a decrease in specialist species. This study will explore these findings, and assess the hypothesis that overall biodiversity declines with urbanisation. Further, it seeks to either confirm or challenge some of the existing thinking that landscapes heavily dominated by humans are depleted of wildlife (Soanes *et al.*, 2019).

Section 2 of this paper explores a wide range of concepts relating to urban ecology, briefly delving into its history and covering the theoretical basis upon which it was built. This section also looks at the concept of cities as habitats and explores some of the unique features of urban landscapes, such as brownfield sites. There is a subsection on the implications of urban ecology research on urban planning, and how the existing knowledge can be used to inform these decisions. I expand on the state of urban biodiversity research today and then home in on insects and butterflies as the focus of this paper. Section 3 describes in detail my methodology for analysing both global and local datasets using RStudio, as well as the rationale behind the data and any key assumptions made in the process. In section 4, I present the results from the study, and I discuss and interrogate the outcomes in section 5, where further research is suggested and possible policy implications and recommendations are presented, along with the limitations I encountered in my study and analysis. Section 6 concludes the paper and wraps up my findings.

2 | LITERATURE REVIEW

The following review explores common features of urban environments that influence biodiversity and identifies factors that are later addressed in the analysis. At the outset of research, several broad topics emerged relating to urban biodiversity: gardens, birds, brownfield/wasteland/vacant lots, and green infrastructure. There is a large body of work on frameworks, recommendations and lessons using landscape ecology and its related theories to understand urban biodiversity patterns and behaviour, as well as the potential of these frameworks to influence urban planning. There is also substantial research on 'softer' components, such as the psychological benefits of biodiversity and urban green space, and an exploration of human perceptions of biodiversity in the city. The number of papers returned from searches including the term 'biodiversity' when paired with the words 'urban' or 'cities' was significantly higher than when these same words were paired with the term 'wildlife conservation'. This might indicate that, though there has been substantial research on trends and observations of biodiversity in urban areas, 'wildlife conservation' is still seen as something that is done outside of cities.

2.1 | The nature-culture dualism

Urban ecology as a disciplinary field did not gain serious attention until the 1970s (Magle *et al.*, 2012). For most of the 19th and 20th centuries, wildlife—at least as conceived in much of Europe and North America—was something that happened 'out there,' away from the hustle and bustle of city life (Adams, 2013). At first, nature was feared—it was rough and dangerous and could bring a person's life to a swift close—and then it was revered, beautiful and mysterious, the subject of poetry and lore (Adams, 2013). But still, it was 'away': somewhere to visit and then leave behind. This kind of thinking pitted wilderness and humanity against each another and created a space for the nature-culture dualism that dominated the European imagination for centuries (Haila, 2000). It was from within this chasm that European settlers felt empowered to colonise 'wild', 'empty' land, to preserve in all its 'pristine' glory, and to remove the very people who had stewarded it for generations (Adams, 2013). This systematic separation of natural processes from humanity, of 'putting nature in a box', was painfully wrought—and with lasting repercussions—in the great expanses of the western United States, whose national parks are an embodiment of our obsession with—and misunderstanding of—nature.

In the late 1800s, Yellowstone National Park in Wyoming, as well as other parks around the United States, were created with an explicit goal of providing an experience of 'uninhabited wilderness' to wealthy tourists (Spence, 1999). What was perhaps less explicit was the forced removal of native people from this land, and the acknowledgment that the land that was viewed by Europeans as pristine wilderness was in fact shaped for millennia by the very people they were removing (Spence, 1999). In recent decades, this fatal misunderstanding has been recognised, and many wildlife organisations acknowledge their historical role in excluding indigenous peoples from conservation efforts on their own land (Lee, 2016). Today, the rhetoric around nature conservation has shifted, and rather than further embedding the nature-culture dichotomy into our ways of thinking, the 2022 Kunming-Montreal Global Biodiversity Framework from the Convention on Biological Diversity frames indigenous people as 'custodians of biodiversity' ('Kunming-Montreal Global Biodiversity Framework', 2022), recognising the value of people in the natural landscape.

The latter part of the 20th century saw ecologists growing increasingly concerned with the impacts of humans on the natural world, and with this, their attitudes towards studying urban ecosystems changed (Niemelä, 1999b). Since the 1990s, publications focusing on urban wildlife have increased dramatically, and new educational programmes have emerged (Collins, Magle and Gallo, 2021), helping to legitimise the field of urban ecology. Yet as recently as 2001, urban ecology was viewed as a 'soft science', with conservation measures carried out in urban areas described by professional ecologists as 'highly experimental and without any guarantee of success' (Harrison and Davies, 2002, p.103). Government funding of urban biodiversity studies lags well behind those from academic institutions, with the majority of public funds for wildlife conservation funnelled to rural areas (Collins, Magle and Gallo, 2021).

Though the nature-culture dualism has weakened significantly, its roots are still embedded in much of the environmental literature, and in many minds (Haila, 2000). Misconceptions about nature conservation abound, with human-dominated, urban landscapes considered far less valuable, in conservation terms, than their sparsely populated, rural counterparts—a narrative that pervades 'policy, practice and the public psyche' (Soanes *et al.*, 2019). While it is true that urbanisation poses real and significant threats to biodiversity, there has been too much focus on the negative impacts of urbanisation, with not enough research or effort being funnelled into the opportunities it might create through intentional design (Spotswood 2021). Rather than solely looking to our 'wild' landscapes to help us conserve some of our rare and threatened species, we might think to turn our focus inward, to the very landscapes we inhabit, so we might harness the positive impacts of urbanisation into a more thoughtful, inclusive conservation (Lepczyk, 2023). The expansion of urban ecology as a legitimate field of study is part of the process of weakening the nature-culture dualism, as we acknowledge that 'wilderness' and humanity are not distinct entities; in today's rapidly urbanising world, they must necessarily interact and be treated as connected phenomena.

2.2 Urban ecological theory

Urban ecology does not have an explicit theoretical basis, but borrows from various existing ecological theories in order to make sense of urban ecosystem dynamics (Spotswood *et al.*, 2021). Though traditionally the natural and social sciences have been siloed, urban ecology demands their intermingling, and the 1990s gave rise to an integration of these two sides, and a recognition of the importance of both (Blood, 1994). Thus emerged a 'socioecology' of urban systems, whereby social, cultural and economic dynamics are connected to physical and biological processes (Pickett *et al.*, 1997).

In early work, ecologists tried to understand the patchy nature of urban green spaces by applying Island Biogeography Theory, claiming that habitats within cities acted like islands and responded to external factors in the same way. Faeth and Kane, and David and Glick, who first suggested this analogy in their papers published on the topic in 1978, introduced us to relevant terminology of urban ecology: that of 'habitat islands,' 'stepping stones' and wildlife 'corridors' (Davis and Glick, 1978; Faeth and Kane, 1978). Conceiving of urban spaces in this way continues to influence how we think about urban systems and habitats today. Many studies support the use of Island Biogeography Theory as a framework for urban ecology through their findings of a positive relationships between habitat 'patch' size and species richness, for example that by Beninde et al (2015) (Beninde, Veith and Hochkirch, 2015).

Another theoretical underpinning of urban ecology is Metapopulation Theory, which hypothesises frequent local species extinction at the habitat patch level, coupled with species recolonisation at the landscape level (Wu, 2008). This dynamic highlights the importance of connectivity between habitat patches to support viable populations of species (Wu, 2008). Breuste et al. draws connections between Metapopulation Theory and species dispersal in urban areas, where the patchiness of habitats—disconnected parks, gardens and small green spaces—creates risks for certain species, especially those with low mobility (Breuste, Niemelä and Snep, 2008). Metapopulation Theory, then, acknowledges Island Biogeography dynamics, but expands upon the theory by highlighting the importance of the wider landscape in determining species richness (Lepczyk *et al.*, 2017).

Understanding the impact of these spatial ecological concepts—local, patch effects vs. a larger landscape or 'matrix' model—on urban biodiversity is crucial, and ecologists need to better comprehend their relationship to one another in order to manage urban environments more effectively (Angold *et al.*, 2006).

Norton et al. explores this relationship through the lens of 'city-level' and 'within-city' biodiversity. City-level biodiversity is analysed by looking at the city's size—which can predict land use, resource flows and economic activity—its age, and context. A city's context includes the composition of its native biodiversity, its climate, and the degradation of the surrounding area, all of which contribute to landscape-level dynamics. Within-city analysis examines the finer-scale spatial variation across an urban area, as well as fragmentation and the ‘urban matrix.’ Temporal dynamics can also play a significant role in a city’s biodiversity, especially on smaller parcels of land, which tend to have more rapid turnover of management, from a park manager to an at-home gardener. Given that the type and quality of urban habitats are reliant on human desires—which can quickly change—they are frequently colonised by early-successional plant species that thrive in high-turnover landscapes. (Norton, Evans and Warren, 2016)

2.3 Global biodiversity knowledge

Urban biodiversity studies have expanded greatly in the past decade, but there is still a dearth of data describing global patterns and observations between different regions (Werner, 2011). This has led to a bias in our existing knowledge, with most of our studies originating in North America and Europe, from cities with major universities. This is hardly representative of the world’s biodiversity, nor of the world’s cities. Further, approximately 66% of all papers published on urban biodiversity study birds and higher plant species only, neglecting the myriad other species that make up cities’ diverse assemblages. This geographic deficit is referenced by Collins and Beninde as well (Beninde, Veith and Hochkirch, 2015; Collins, Magle and Gallo, 2021), both noting that we have a significant knowledge gap for Asia, South American and Africa. This is problematic not only for the imbalance in our collective body of research, but also because these are the very continents that will experience the highest levels of urbanisation in the coming decades (Beninde, Veith and Hochkirch, 2015).

For these quickly urbanising regions, the speed of change might introduce an additional variable to measure. In one study observing the decline of bird species in different regions around the world, it was found that the negative relationship between the extent of human settlement and bird species richness—essentially, the impact of urbanisation on biodiversity—was greater in many parts of Asia than it was in western Europe (Sultana, Corlatti and Storch, 2023). With large swathes of Asia’s population moving to cities in search of opportunity (as illustrated by the concept of the ‘arrival city’ – (Saunders, 2011)), this relationship could be indicative of the more destructive impact of a rapid urbanisation occurring in many regions in the global South. With less time to adapt to urbanisation’s heavy footprint, many species may find themselves at even greater risk. These geographic nuances make it even more essential that urban biodiversity research is as far-reaching and diverse as the species it aims to understand.

2.4 Insect biodiversity

Along with regional bias, the field of biodiversity research suffers from severe taxonomic bias, wherein some species receive great levels of attention, while others don’t receive very much at all, preventing a holistic view of biodiversity at the global level, and impeding coordinated conservation efforts (Troudet *et al.*, 2017). The majority of this discrepancy is due to societal preference for some species over others, influencing the direction of research and providing funding for particular areas of interest. For example, relative to the number of known species, the class Insecta is the most under-studied of all classes, whereas Aves has received outsize consideration. Bird species have been over-represented in scientific and academic studies since the middle of the twentieth century, and this excess—as well as insects' shortfall—continues to grow. Perhaps as a direct result of this relative lack of focus on insect biodiversity, only about 10% of all insect species are even known by name, meaning that many of them are disappearing before we even know their importance (van der Sluijs, 2020). It is up to researchers to correct this bias and make more space for a diversity of research. Insects, though under-studied, are vital components of our natural world, making up nearly two-thirds of all terrestrial life on Earth (Sánchez-Bayo and Wyckhuys, 2019).

Aside from the nearly $60 billion value that insects are estimated to provide to the US economy alone (Losey and Vaughan, 2006), they are central to a wide range of ecological services upon which we are dependent, like pollination, pest control, seed dispersal, and nutrient cycling (Scudder, 2017). Insects also tell us about the state of our environment and world. Insects are highly sensitive to changes in their environment, and as they are the most abundant and widely distributed species found on the earth, in the air, and in water, they act as biological monitors across all habitats (Parikh, Rawtani and Khatri, 2021). Within this class, butterflies are often used as bioindicators, as their environmental sensitivity requires them to rapidly adapt and modify their behaviour, making them effective indicators of climate change (Vickery, 2008). In this way, butterflies can act as a proxy for biodiversity and help scientists better understand the state of the health of the environment. Further, their high detectability qualifies them as suitable subjects of citizen science surveys, an increasingly important tool in measuring biodiversity over time (Cooper *et al.*, 2024).

In the UK, the climate is the main influencing factor for the extent of a butterfly's range—whether too warm in the south, or too cold in the north. Over the twenty-year period from 1988-2008, the average temperature in the midlands region of the UK increased by 1.5 degrees Celsius (Vickery, 2008). This meant that 25% of the butterflies at their northern limit in the south of England were able to extend their limits northwards. However, 'colder' butterfly species like the Scotch Argus, already at their southern limit, lost ground, and had to decrease their ranges by up to 100km northward (Vickery, 2008). In the mountains of central Spain—where temperatures have risen on average 1.3 degrees C over a similar period—16 butterfly species have receded into the mountains, moving to higher altitudes and cooler temperatures (Vickery, 2008).Though it can be exciting to see more butterflies—and more species of butterflies—in areas where they previous weren't, they can only survive if they have suitable habitat, and in our urbanising world, this is becoming increasingly unlikely. While generalist species might be able to adapt, flying longer distances for suitable habitat, specialist species will find that habitat is either too fragmented, or no longer exists, leading to their local extinction (Vickery, 2008).

2.5 Drivers of urbanisation

In her 2021 paper, Fenoglio and her colleagues define five key drivers of urbanisation and identify them as the leading causes of biodiversity loss—specifically of terrestrial insects—in urban areas. These key metrics are outlined below (Fenoglio *et al.*, 2021).

1. Impervious surfaces: the sealing over of soils by impermeable substances, usually concrete. Impervious surfaces are considered a 'transversal' driver and are correlated with the other urbanisation drivers, influencing their intensity and impact on the landscape. Impervious surfaces block the pollutant processing completed by soil, contribute to waterway contamination through surface run-off, and are strongly correlated with urban heat islands (S.V. Chithra *et al.*, 2015).
2. Habitat fragmentation: the splintering and removal of habitat into smaller and more disconnected areas due to development, creating habitat patches that vary in size, quality and connectivity. Habitat loss through fragmentation impacts biodiversity directly—through decreases in species richness, abundance and genetic diversity—but also indirectly, altering species interactions, predation, breeding, and animal behaviour (Fahrig, 2003)
3. Urban heat island effect: the phenomenon whereby urban areas can be up to 12 degrees Celsius hotter than the adjacent rural areas. While some insects can expand their range with warmer temperatures, others area affected by lack of cold areas for overwintering, while others still simply cannot survive once they reach their critical thermal maximum.
4. Pollution: light, air and sound pollution abound in urban centres, but artificial light, particularly at night, poses the biggest threat to insects. Artificial light at night (ALAN) can severely impact on wide-ranging biological processes—from feeding to growth to reproduction—all of which are dependent on natural light cycles (Gaston and Miguel, 2022).
5. Exotic plant species: urban gardens are home to a wide range of exotic and invasive flora, which tend to sustain lower levels of abundance and diversity of species when compared with native plant varieties. Invasive plants can alter ecological processes and ecosystems and influence the survival and productivity of their native counterparts (Shabani *et al.*, 2020).

This study and others like it focus on drivers linked to humans, highlighting their centrality in biodiversity's decline. Though this is a new focus for biodiversity studies, it is an increasingly significant one, especially as the field of urban ecology expands.

2.6 Cities as unique habitats

Though human expansion is often connected with declines in biodiversity, human-dominated urban landscapes can create unique habitats not found anywhere else, creating environments in which to examine the impacts of humans on nature (Niemelä, 1999a). Some cities serve as a refuge to certain species due to their unique features and habitat gradient (Lepczyk, Aronson and La Sorte, 2023), these 'novel ecosystems' forming out of a wide range of selection pressures and different levels of management and economic input throughout a city (Lepczyk *et al.*, 2017). Cities can even act as key conservation areas for certain species, like the Lima leaf-toed gecko, which is critically endangered and whose last remaining population is found within habitat patches in Lima, Peru (Lepczyk, Aronson and La Sorte, 2023). They and other species may find refuge within city limits due to factors including: increased resources like food and water, as well as less competition for them, freedom from predators and human overexploitation, increased growing seasons and higher temperatures, reduced chemical inputs compared to agricultural land, and higher prey abundance (Lepczyk, Aronson and La Sorte, 2023). For these same reasons, cities may be appropriate places to reintroduce threatened species, as was the case with the kaku, a forest-dependent parrot that was reintroduced to Wellington, NZ (Lepczyk, Aronson and La Sorte, 2023).

Though undoubtedly part of what makes urban areas so unique, the multiple 'land managers' of urban green space—in the form of parks staff, volunteers and home gardeners—are also what makes habitat management extremely complicated, as stakeholders act independently and rarely coordinate their efforts across the wider cityscape (Cooper *et al.*, 2024). From gardens to parks to nature reserves, the different scales at which urbanisation and habitat features influence different species must be considered, with a multi-scale, spatially-explicit perspective (Lepczyk *et al.*, 2017). For example, connective corridors are more effective than 'stepping stones' for helping species disperse, but even small habitat patches throughout a city can connect highly mobile species like butterflies (Lepczyk *et al.*, 2017). Aronson notes that the wider urban matrix must be considered in order to connect disparate habitat patches, and suggests the city-wide management of parks as a solution to the patchy nature of urban habitat (Aronson *et al.*, 2017). In cities where councils, charities, businesses and individuals all manage different types of green spaces, reflecting different human priorities, this kind of shift could radically alter how wildlife moves around their urban home.

In addition to the importance of the city-wide matrix, the landscape *outside* a city can be crucial in determining how biodiversity responds to the city itself. In her 2021 paper, Spotswood and her colleagues challenged the notion of cities as 'biological deserts', and explored what it might mean for cities to actually increase the genetic diversity in a region and foster populations that may be better able to tolerate threats like climate change (Spotswood *et al.*, 2021). Spotswood et al. offer five pathways through which cities can benefit regional ecosystems, by: releasing species from pressures of the surrounding landscape, increasing regional habitat heterogeneity, acting as stopover sites or stepping stones during migration, contributing to species' genetic diversity and adaptability, and enabling engagement with humans, which in turn encourages stewardship and better habitat management. These factors, however, are more or less important depending on what land use surrounds the urban area. If an urban area is surrounded by agricultural land or plantations, then a city can provide species relief from high chemical use, offer more heterogenous habitat, and introduce them to more genetic diversity. If an urban area is surrounded by wild land, then cities can offer higher levels of inter-species interactions and an abundance of prey (Spotswood *et al.*, 2021). These studies are critical in illustrating that, though urbanisation decreases biodiversity *on average*, there are a multitude of factors that determine how species respond to human pressures.

2.7 Brownfield biodiversity

In a city like London, the value of 'wasteland' is slowly being accepted, and it's now common to see roadside verges, gardens and park borders filled with long grasses and wildflowers. This practice of encouraging green space to 'go wild', which has also been termed 'benign neglect', is a management approach geared towards species and habitat richness (Niemelä, 1999a). Yet there is still pushback on the messy aesthetics of wildlife-friendly spaces (Lampinen *et al.*, 2021), clashing as it does with the English sensibility of 'neat and tidy'.

These tensions are elucidated in the arena of brownfield conservation, which brings into harsh relief the conflict between the scientific and social goals of wildlife conservation (Harrison and Davies, 2002). The term 'brownfield' refers to land that has been abandoned—for days, months or years—for one reason or other, after previously being developed or serving as a site of industrial activity (Lorimer, 2008). The land may be completely abandoned, closed off by a fence, or it may have been adopted by the community as a makeshift park, but the low levels of human input and nutrient-poor soil create unique habitats for diverse ecological assemblages. In Bonthoux et al's review of the existing literature around wasteland biodiversity, they found that wastelands can foster higher diversity of species than other urban green spaces, and the highest diversity of flowers in some regions (Bonthoux *et al.*, 2014).

Many sectors of the population still might judge brownfield sites as having low social or amenity value, but we've come a long way since they were portrayed as 'wasting assets' by the UK's Urban Task Force in 1999 ('Towards an Urban Renaissance', 1999). Brownfield sites are recognised by wildlife conservation charities as important habitats for a wide range of rare species, where biodiversity can reach some of the highest levels in urban areas (Buglife, The Wildlife Trusts, and others). However, their location in the city centre or near old docklands makes them appealing sites to clean up and create parks, or often makes them targets of heavy development pressure (Lorimer, 2008). Some data suggests that the majority of new development in the UK is occurring on brownfield sites (Dixon, 2007), and while there are benefits to redeveloping ex-industrial sites, including easing development pressures elsewhere and preventing urban sprawl (Couch and Dennemann, 2000), brownfield represents habitat in its own right, and that must be taken into account when assessing their suitability for development.

A deeper appreciation of the value of brownfield sites for conservation could greatly benefit wildlife in cities like London, and all around the UK. In a country deemed 'one of the most nature-depleted countries on Earth' (*State of Nature*, 2023), brownfield sites are as close as we might get to near-natural or wild spaces in the expanding urban landscape. Fields of shorn green grass might be aesthetically pleasing, but they are often devoid of life and absent the dramatic seasonal changes that might occur in a more natural landscape (Harrison and Davies, 2002). Brownfield sites might be yellow and purple and pink—or more often than not, merely brown—but they support far more life than the 'green deserts' of some urban parks and gardens (Harrison and Davies, 2002). Brownfield can even have a positive impact on wildlife in nearby areas. In a paper by Angold and colleagues in 2005, they found that proximity to the nearest 'derelict' site was one of the most influential characteristics for increasing species richness, and that when these sites are closer to other similar sites, they had more distinctive flora than when they were isolated (Angold *et al.*, 2006).

2.8 Urban planning implications

Urban ecology naturally and inevitably has a societal component, as any kind of intervention or conservation action will affect the people for whom the city is also habitat. It is for this reason that urban ecology research lends itself to urban planning (Niemelä, 1999a). However, this collaboration assumes the appropriate knowledge on both sides, an interest to communicate and share across disciplines, and the will to implement the recommendations. One of the key ways that ecological research can play a role in urban development is through the provision of green infrastructure (GI). GI can be understood as the integration of nature into the built environment—traditionally 'grey' infrastructure—through a range of features like green roofs, green walls, and sustainable drainage systems (Filazzola, Shrestha and MacIvor, 2019). As well as possibly providing habitat or a green corridor for more mobile species, green infrastructure helps alleviate some of the pressures of urbanisation and climate change, providing permeable surfaces, improving air quality and reducing the urban heat island effect (Ying *et al.*, 2022). Sinnett states that 'green infrastructure is the primary way that biodiversity is protected and enhanced in the built environment' (Sinnett, 2015, p.198), and though GI should not be viewed as a replacement for natural systems and habitats (Filazzola, Shrestha and MacIvor, 2019), high-quality green infrastructure can benefit people, wildlife, and the built environment itself.

There exists a strong case for green infrastructure to foster urban biodiversity, as well as statutory guidance at various levels of governance in the UK, but to date there are few examples of quality green infrastructure in new developments (Jerome et al. 2019). This may be because there are multiple goals for green infrastructure, and cultivating biodiversity is rarely the main priority (Filazzola, Shrestha and MacIvor, 2019). In their green infrastructure literature review from 2019, Filazolla et al. found that 91% of green infrastructure projects were focussed on providing ecosystem services, human well-being, or aesthetic value. Evidence of green infrastructure having a significant positive impact on biodiversity in heavily urbanised areas is limited (Murkin *et al.*, 2023), but as are the projects which explicitly prioritise wildlife. Going forward, biodiversity must be the central priority for green space planning, provision and management (Sinnett, 2015).

Jerome and their colleagues present a framework for assessing the quality of green infrastructure, and outline three essential principles for conserving nature through GI (Jerome *et al.*, 2019):

1) GI should convey lasting ecological improvement so the built environment can play a role in reversing declines in biodiversity.
2) GI should help create, restore and enhance habitats and the linkages between them.
3) GI should support populations of key species, as identified in local biodiversity plans and targets.

Since we know that biodiverse spaces improve people's health (Fuller *et al.*, 2007), prioritising biodiversity during the provision of green infrastructure should also lead to GI that enhances human wellbeing. Underpinned by ecological theory, Hostetler et al lean on systems-thinking to advocate for coordinated, landscape-level management of green infrastructure, informed by the greater ecosystem and socio-ecological processes that govern it (Hostetler, Allen and Meurk, 2011). Hostetler says this would require a city-wide understanding of biodiversity, and an aligned philosophy for its management. This may be a lofty goal, but it is perhaps necessary if we are to overcome the chasm that exists between policy and practice (Roe and Mell, 2013).

3 | MATERIALS AND METHODS

In this study, I examined the influence of urbanisation on biodiversity, exploring both species richness and total species abundance. Drawing on the paper by Fenoglio et al (2021), I looked at the impact of some key drivers of urbanisation on insect biodiversity, namely light pollution and impervious surface area. In the global study, I also analysed the urban heat island effect, and in the London study, 'green cover' data served as a proxy for habitat fragmentation. The study employed R ('R Core Team', 2024) for all data preprocessing, data manipulation and statistical analysis, and apects of the process were aided by the use of an AI language model ('Claude 3.5 Sonnet', 2024).

3.1 | Global

3.1.1 Global biodiversity data: The PREDICTS database

The PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) database collates 3.2 million records dating back to 1970, sampled at over 26,000 sites around the world and representing over 47,000 species (Hudson *et al.*, 2017). The data represents a broad range of taxa and species, covering all major plant, fungal and terrestrial animal groups, and has wide-ranging geographical reach. These records are classified into one of nine land use types: primary vegetation, secondary vegetation (mature, intermediate, young, unknown age), plantation forest, pasture, cropland, or urban (Hudson *et al.*, 2014). The data comprises species abundance, presence/absence, and species richness measures as proxies for biodiversity. PREDICTS provides a wide range of high-quality biodiversity data from sites representing varying levels of human disturbance across many different taxa and regions. This presents the opportunity to model changes in biodiversity due to human pressure on a global level, but at local scales. (Lorimer, 2008)

From the full dataset, which combines PREDICTS releases 1 and 2 (Hudson *et al.*, 2023), I subset the dataset to only the class Insecta, which reduced the number of observations to 1,037,499. Each observation has spatial information attached to it, allowing the data to be aggregated and reorganised to site-level metrics, creating a row for each site and summarising how many species and individuals have been recorded at each unique site. The site-level biodiversity metrics of interest were within-sample species richness and total species abundance. Species richness was calculated as the number of unique taxa found at a given site, using a standardised sampling unit known as species density, and total abundance was calculated as the sum of the measures of abundance of all taxa at each site (Newbold *et al.*, 2015). When sampling effort varied within a study, it was corrected by rescaling the sampling efforts of each study, assigning the most-sampled site a value of 1, and then dividing the raw abundance measurements by the relative sampling effort (Newbold *et al.*, 2015). This step was completed before reorganising the data by site.

After cleaning and reorganising the data, 8,242 insect sites remained. Figure 1 shows the distribution of insect sites around the world. Though sites are spread across continents, there is a clear bias towards Europe, with significant studies also in Latin America. Africa is underrepresented, and there are very few sites in central Asia.

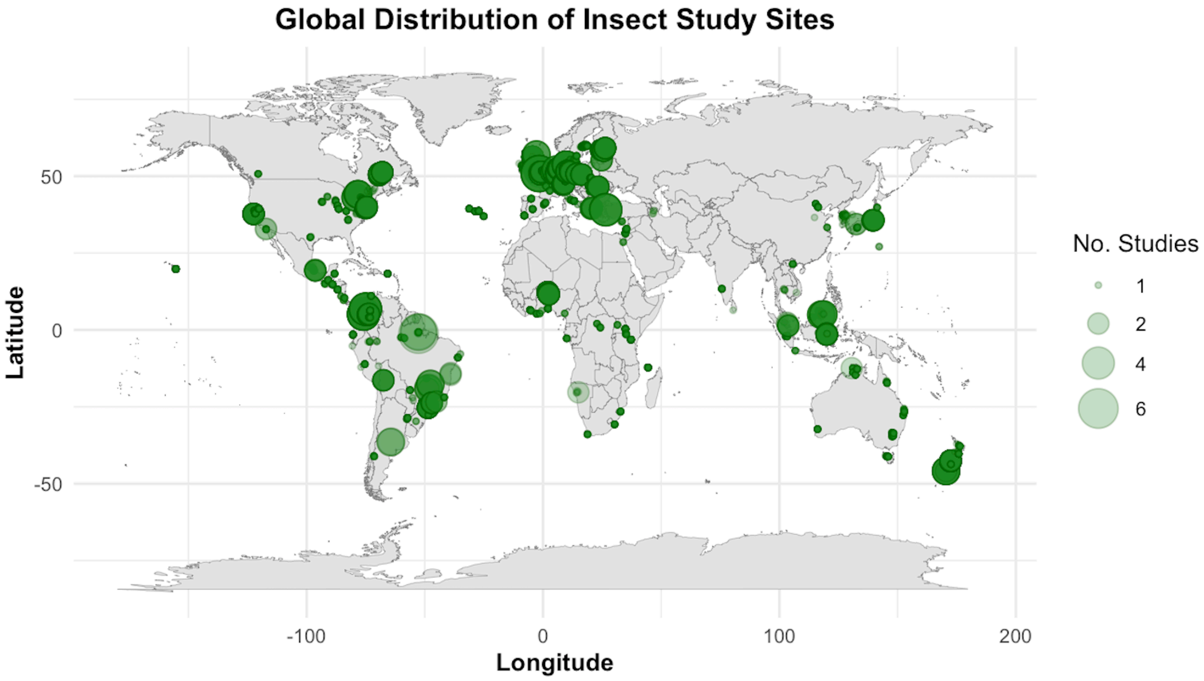


FIGURE 1: Global distribution of insect sample sites, with the size of the green dot representing the number of studies at each site.

Though there is a predominant land use category classified as ‘urban’ in the PREDICTS data, all land use types were included in the analysis. This allowed for a richer investigation of the *drivers* of urbanisation, rather than solely of pre-defined urban areas. It also allowed for analysis of potential interactions between land use and urbanisation variables, and to assess in which environments urbanisation might impact insect biodiversity to a greater or lesser degree. The external urbanisation data sets utilised for the global analysis were artificial light at night, impervious surface area, and urban heat island effect. The PREDICTS data spans more than 50 years, so to ground the data temporally, the sample midpoint was calculated for each site. Both the mean and the median sample midpoint for all sites reporting on insect biodiversity was 2005, so where possible, urbanisation data from 2005 was used to compare data of similar temporal resolutions.

Total abundance and species richness were analysed separately, and these metrics were broken out into separate data sets, as some of the insect sites did not have measures of abundance. The final data sets included 8,242 observations of insect species richness and 7,716 observations of total insect abundance. Before joining external datasets to the PREDICTS data, insect site locations were extracted as latitude/longitude coordinates and converted to spatial points using the *terra* package in R (Hijmans *et al.*, 2024).

3.1.2 Landscape-level data: Artificial light at night

The data used to study the impact of artificial light at night (ALAN) on global insect biodiversity is from Li and Zhou (2017) and was downloaded from Figshare (figshare.com/dataset/nighttime_light). It is a calibrated time series from 1992-2021 of nighttime light data obtained from the National Oceanic and Atmospheric Administration (NOAA) (ngdc.noaa.gov/). The raw data has been used in countless studies investigating the impact of artificial light, including social, economic and environmental research—specifically for studies looking at urbanisation and electricity use—but the lack of systematic calibration for the data had made it difficult to apply across temporal and spatial resolutions (Li and Zhou, 2017).

In their 2017 paper, Li and Zhou explain their approach to improving the consistency of ALAN time series data derived across different time periods or different satellites, to produce a globally calibrated and long-term time series (Li and Zhou, 2017). Their stepwise calibration scheme accounts for over- and under-estimation of the satellites used in the initial data collection and captures annual cloud-free observations of light measured from cities, towns and other areas suffering from continuous nighttime light (Li and Zhou, 2017). The full range of possible nighttime light values are digital numbers from 0 to 63, and have a spatial resolution of 30 arc seconds, or 1 kilometer, with a coverage of -180 to 180 degrees in longitude, and -65 to 65 degrees in latitude.

The data was available in GeoTIFF file formats for each year from 1992 to 2021. The 2005 data was used for this study, and the GeoTIFF was read into R as a spatial raster, whose values ranged from 0 to 61. Spatial data points were extracted from the ALAN raster using the *terra* package in R (Hijmans *et al.*, 2024) and matched to the insect sites. The

PREDICTS insect sites covered the full range of ALAN values, implying a diverse geography of sites that represent a broad range of potential impacts from this urbanisation metric. Figure 2 illustrates the range of artificial light at night across the globe, with varying intensities displayed using a colour gradient from dark grey, representing no artificial light, through to yellow and white, indicating heavy light pollution.

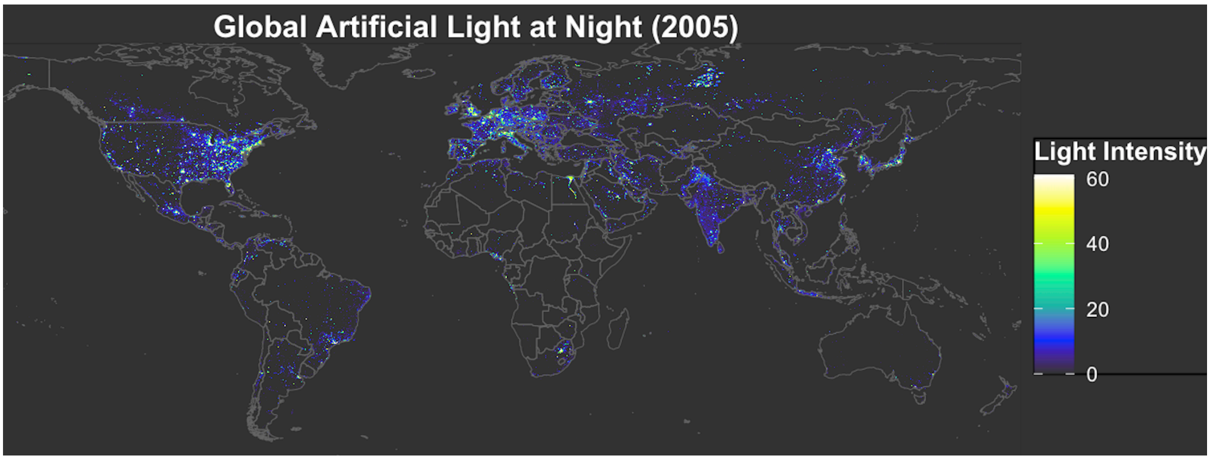


FIGURE 2: Global distribution of artificial light at night.

3.1.3 Landscape-level data: Impervious surface area

The 'built' layer from the Global Human Settlement Layer (GHSL) project can be downloaded from the GHSL website (human-settlement.emergency.copernicus.eu). This project produces spatial data and analytics on a global level to help better understand the impact of human presence on the planet (European Commission. Joint Research Centre., 2023). The GHS-BUILT-S spatial raster dataset, used in this study as a proxy for impervious surface area (ISA), is a representation of the estimated distribution of built-up surfaces around the world, in five-year intervals from 1975-2030. The data was created through a spatial-temporal interpolation of a collection of multi-sensor satellite imageries from Landsat and Sentinel-2. Built-up surface, which will represent impervious surface area, is defined as the 'gross surface (including the thickness of the walls) bounded by the building wall perimeter with a spatial generalization matching the 1:10k topographic map specifications' (European Commission. Joint Research Centre., 2023).

The data was available as individual shapefile tiles at 3- or 30-arc seconds, or as a GeoTIFF for global coverage, at 30-arc seconds/1 kilometer. For the global study, a full download of the worldwide GeoTIFF at 1 kilometer for the year 2005 was used. Data was uploaded to R as a raster and values were extracted and matched to insect sites using the *terra* package (Hijmans *et al.*, 2024). The built-up values are expressed as 32-bit integers, with possible minimum and maximum values ranging from 0-1,000,000, for the total built-up surface area in square meters that falls within each 1 square kilometer grid cell. Though the maximum value of the raw GHSL data for the year 2005 is 926,652 meters, the distribution of values is heavily skewed towards zero, with a value of 607 meters occupying the 90th percentile of the dataset. As urban areas only make up 2% of the world's land cover, this data accurately represents the predominantly non-built-up state of the world. The range of built-up values matching the PREDICTS insect sites ranges from 0-455,923 square meters. In any 1 square kilometer area around an insect sites, less than 50% of the area is considered built-up, as defined by this dataset. Figure 3 shows the full built-up cover data set for the year 2005. The condensed areas of built-up cover are signified by colours reaching towards orange and red.

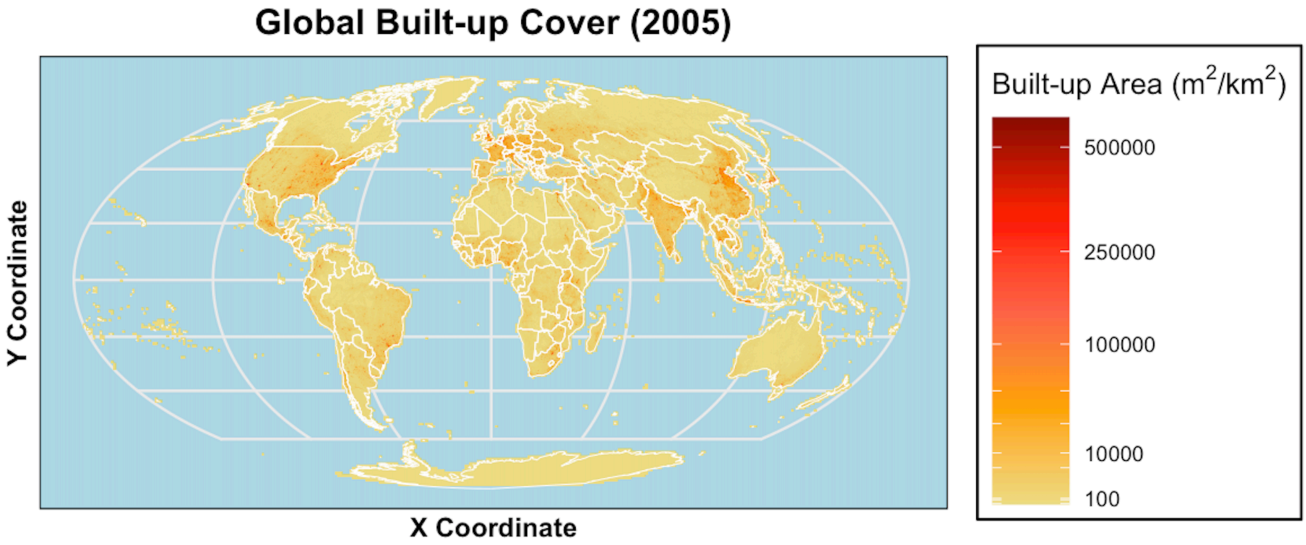


FIGURE 3: Global Human Settlement Layer - Built-Up Cover. This image was projected using the original CRS of the GHSL raster, which at 1km is the Mollweide pseudocylindric projection.

3.1.4 Landscape-level data: Urban heat island effect

Urban heat island (UHI) data is from the Yale Center for Earth Observation (YCEO) and can be downloaded from Nasa's Socioeconomic Data and Applications Center (SEDAC – sedac.ciesin.columbia.edu). The most recent version combines urban extent data from Natural Earth (https://www.naturalearthdata.com/), land cover data from the European Space Agency Climate Change Initiative (ESA CCI), and Land Surface Temperature estimated from the Moderate Resolution Imaging Spectroadiometer (MODIS), from Nasa's Terra and Aqua satellites (Chakraborty and Lee, 2023). The full data set comprises annual Surface Urban Heat Island (SUHI) intensities averaged across the years 2003-2018, for both daytime and nighttime, for more than 10,000 global urban extents. The data was uploaded as a gridded raster, but only pixels for the 10,000 urban clusters are connected to UHI values, so the data was not continuous. This is because it was necessary for the authors to designate 'urban' and 'rural' references, which they only did around the urban clusters (Chakraborty and Lee, 2023). The raw UHI data has both positive and negative values, with negative values indicating that there are some urban areas that are colder than the surrounding are. This could be due to various factors, such as bodies of water or urban parks with significant vegetation. However, the mean and median values of the UHI data are both positive, signifying that urban areas tend to follow the hypothesis of being warmer than their rural surroundings. The range for the daytime UHI is greater than the nighttime range, with a minimum value of -3.75 degrees C and a maximum value of 2.86 degrees C. However, the data indicates that the effect of nighttime UHI is more intense, signified by a higher maximum temperature difference of +2.98 degrees C, and a warmer lower reach of -1.3 degrees C.

There were a significant number of NA values in the raw UHI data, which is explained by a few factors: either there is not an urban or rural pixel for a certain area as detected by the ESA CCI land cover product, the pixel is not useable, or there is a limitation of the urban extent data used in the algorithm (Chakraborty and Lee, 2023). These limitations are significant, and in joining the data, only 5% of the global insect sites were able to be matched to UHI values, with the results excluding all of the sites in Africa, Australia, central America and Canada, as well as much of Asia. Due to this substantial gap in the data, the UHI variable was removed from the analysis. Figure 4 illustrates the distribution of useable UHI pixels against insect sites, of which only 473 were matched.

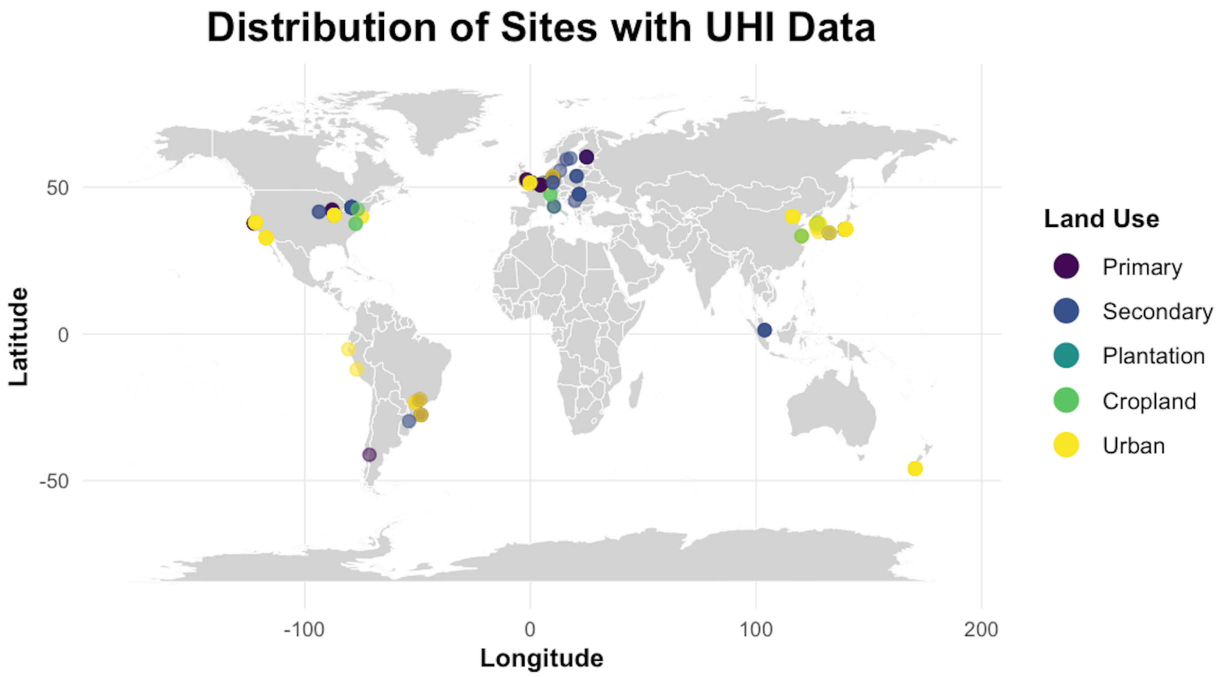


FIGURE 4: Distribution of UHI data after matching to PREDICTS insect sites.

3.1.5 Statistical modelling

All statistical analyses were conducted using R version 4 (‘R Core Team’, 2024). The abundance and richness response variables were modelled separately, each with a generalised linear mixed effects model. The urbanisation variables were scaled to their centre points so the values were standardised, and the primary land use categories were converted to factors with 6 levels: primary vegetation, secondary vegetation, plantation, pasture, cropland and urban. Land use, impervious surface area and artificial light at night variables were inputted into the model as fixed effects. Added to both studies was a random effect of spatial block, to account for the spatial arrangement of each site, as well as study identity, to account for differences in overall abundance and richness between regions and different methods of sampling (Newbold *et al.*, 2015). In the richness model only, site identity was added to the random structure, in the case of overdispersion (Newbold *et al.*, 2015). Before running the model, total abundance was log-transformed to correct for skewness and to better fit the model. The abundance GLM model was fitted with a Gaussian distribution, and the species richness model used a Poisson fit.

Two sets of models were run—one without any interactions between the variables, and one with an interaction between both land use and impervious surface area, and land use and artificial light at night. An interaction model was initially chosen under the hypothesis that the impact of urbanisation metrics on insect biodiversity might be more or less influential based on the land use type. This is in keeping with studies that show the importance of landscape-level and other contextual factors in determining the response of certain species to human pressures (Angold *et al.*, 2006; Spotswood *et al.*, 2021). However, this model was abandoned after performing backwards stepwise selection of the fixed variables. Firstly, there were many warning signs indicating rank deficiency due to insufficient observations per factor level to estimate every model term. This was confirmed when plotting the interaction model, which showed that many of the land types dropped off as urbanisation variable values increased.

Further, there was high multicollinearity between the variables in the interaction model, which was tested using the 'vif' function from the *car* package in R (Fox *et al.*, 2023). No variables were retained after the backwards stepwise selection processes, so this model was not deemed a good fit to represent the relationship between urbanisation and insect biodiversity. This was true for both total abundance and species richness.

Backwards stepwise selection was then performed on the non-interaction model, where land use, impervious surface area and artificial light at night were all inputted to the model with a purely additive relationship. The function ran without any warnings and returned the final model, whose only variable was land use, indicating that the addition of ISA and ALAN did not improve the model fit. In checking the assumptions of the model, it was found that both the ALAN and ISA variables demonstrated some non-linearity, as well as heteroscedasticity. To address this, polynomial terms were added for these two variables, and the species richness model was fitted with a negative-binomial distribution instead. However, these did not improve the fit of the model, so the original GLM model was used for simplicity.

The GLMER function was used for all models, which is part of the *StatisticalModels* package (version 0.1, Tim Newbold), which is dependent on *lme4* (Bates *et al.*, 2024). The final models are presented in Appendix A.

3.2 | London

3.2.1 London biodiversity data: Butterflies for the New Millennium

Butterflies for the New Millennium (BNM) is a butterfly database created and co-managed by the charity Butterfly Conservation, and all data was provided courtesy of Butterfly Conservation. BNM is the most comprehensive source of verified butterfly records across the United Kingdom, with inputs dating back to 1917 and comprising observations from the following national surveys: Butterfly Transects, Wider Countryside Butterfly Survey, National Moth Recording Scheme, Big Butterfly Count, iRecord Butterflies, and the namesake of the database, Butterflies for the New Millennium (*Butterfly Conservation*, 2024). BNM contains observations of every species of butterfly found in the UK, including specialist species most likely to be impacted by urbanisation and environmental changes. Though BNM contains some data from transect surveys, for the most part it is unstructured, presence-only data. Therefore, for this portion of the study, only species richness was analysed, as absence records are required to infer abundance.

The data set I started with was already limited to the Greater London area, so no geographical subsetting was required. Though the data contained observations from as early as 1917, all entries before 2010 were removed so that analysis could be performed on more relevant observations gathered through consistent and contemporary means, such as apps like iRecord. This updated data set would also be more reflective of the current state of biodiversity in London. The sample midpoint for each site was calculated as the mean value from the earliest and latest sample year recorded for each site. Both the median and mean sample midpoint across all sites is 2017, showing a slight skew towards more recent years across the 10-year time span. The full data set had 543,276 observations, which decreased to 315,714 when subsetting to just 2010 onward. 44 unique butterfly species were observed in Greater London between 2010 and 2021. During this time, the ten most frequently recorded species were, in descending order, the Meadow Brown, Gatekeeper, Small White, Large White, Speckled Wood, Ringlet, Common Blue, Marbled White, Green-veined White, and the Holly Blue. These butterflies are illustrated in that order, starting from the left for both the top and bottom rows, in Figure 5. These figures were calculated by summing the total number of observations of each species recorded in each survey over time.

Figure 5. The 10 butterflies recorded in the BNM data most frequently from 2010-2020 across all sites in Greater London. This may not be reflective of the actual abundance of

these species, as the records are presence-only, and are likely to be skewed by surveyors' ability to identify certain species, how often each site was surveyed, as well as dynamics at each individual survey site. Image credit for all butterflies: Butterfly Conservation.

Site-level metrics were created by reorganising the data by geographic location. As the BNM data is comprised of multiple different surveys, the spatial resolution was inconsistent across entries, with resolutions ranging from 1 to 100 meters. To work across a consistent data set, all entries were aggregated to 100-meter grid cells, using the 6-digit Ordnance Survey (OS) National Grid reference. There were 32,372 such 'sites'. Site-level species richness was calculated by aggregating the number of unique species present within each 100-meter grid. Plotting the survey sites onto a map revealed that the geographic extent of the BNM data fell well outside the extent of Greater London, stretching significantly further to the south. To prevent the occurrence of NA values when matching the butterfly sites to London urbanisation data, and to restrict the study to only the area of Greater London, the BNM data was cut to match London's specific coordinates. This more precise data, organised by 100-meter grid references, yielded 19,454 sites. Figure 6 shows the distribution of butterfly survey sites in Greater London, aggregated to 1 kilometer for less cluttered plotting.

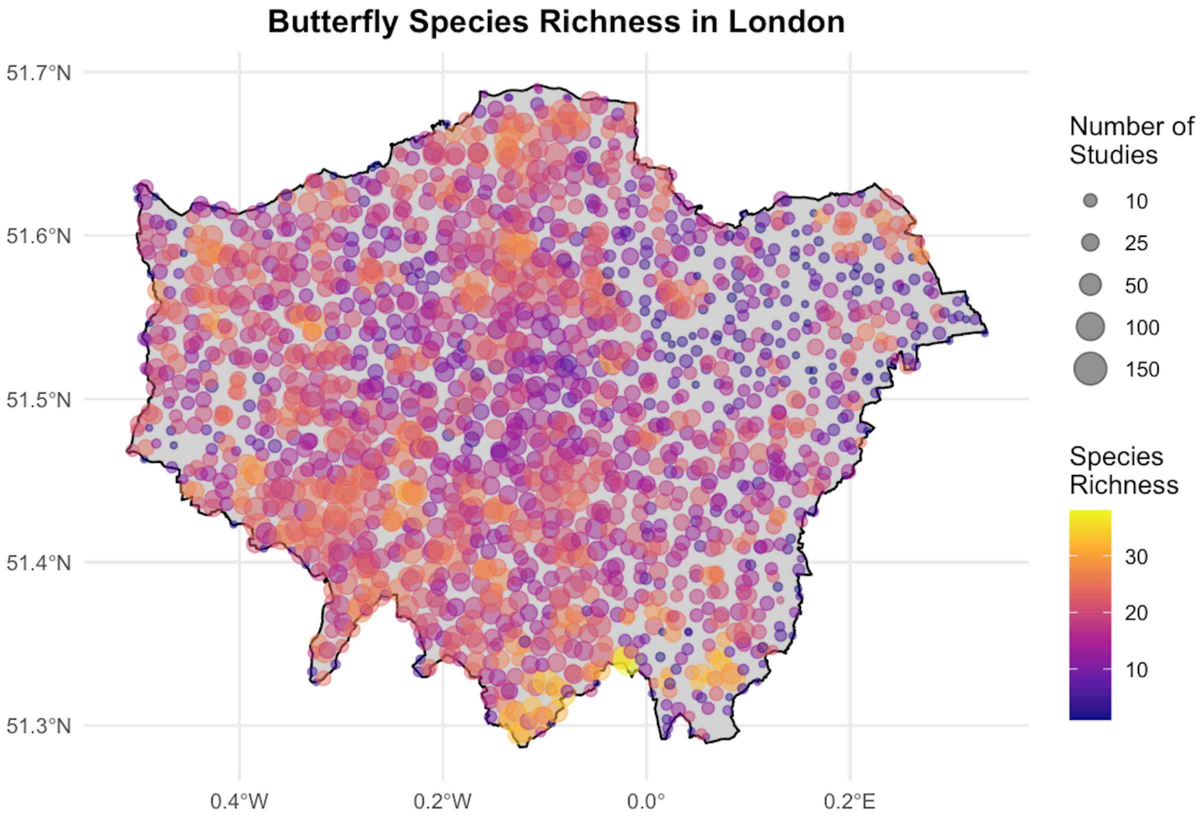


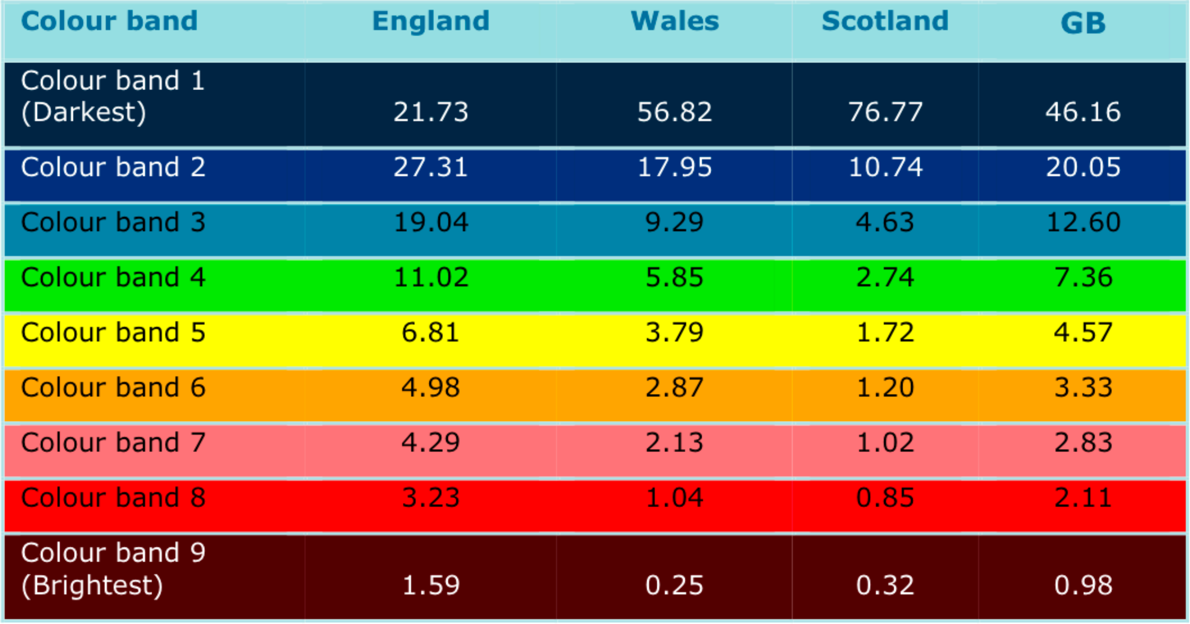
FIGURE 6: A map of Greater London with butterfly survey sites from BNM, at 1km spatial resolution. The colour of the dot represents species richness, with purple signifying sites with lower species richness, and orange and yellow signifying sites with higher species

richness. The size of the dot represents the number of studies conducted at each site over the 10-year period of the data.

3.2.2 Landscape-level data: Artificial light at night

The data used for artificial light at night (ALAN) came from Land Use Consultants (LUC, landuse.co.uk) and was commissioned by the Campaign to Protect Rural England (CPRE) in 2015, building upon CPRE's *Night Blight!* campaign from 2003, as well as other previous work to illustrate the extent of light pollution across the country. This data was generated from the Visible Infrared Imaging Radiometer Suite (VIIRS), which gathers information about the amount of light being emitted from earth, taking a picture of the same location every night at 1:30am (*England's Light Pollution and Dark Skies*, 2016). The VIIRS data is an improvement on the US Defense Meteorological Satellite Program (DMSP), which was used for the CPRE studies in 1993 and 2003. The aim of the LUC study was to produce nation-wide light pollution maps to illustrate the extent of ALAN and serve as a baseline against which to observe change over time. The LUC dataset was considered preferable to the one used for the global study because the resolution is more appropriate (400 meters) and is specific only to the UK.

The baseline data from which to create the national map comes from September 2015, which was deemed the best month from that time period due to limited cloud cover (*England's Light Pollution and Dark Skies*, 2016). The specific data used for this study is from the year 2016. Data has been rescaled from the satellite's resolution of a 742 x 742 meter-squared cell to a 400 square meter pixel across the UK. As this is a coarser resolution than the butterfly data, one light pollution value was assigned to all butterfly sites within the same 400-meter cell using the 'nearest neighbour' method. Joining the data resulted in 141 unmatched values, which were assigned the value of the next nearest point. The data comprises 9 colour bands, each representing a range of brightness values[2], with lower values indicating lower levels of light pollution and darker skies, and higher values indicating higher levels of light pollution and brighter skies. The lowest colour band comprises any value under .25, and the highest colour band comprises any value over 32. The full data set, which covers all of the United Kingdom, has values ranging from -.286 to 1,556.83, with this extremely high value coming from the Grangemouth Refinery in Scotland, suggesting a gas flare. Figure 7 shows the percent of land that falls within each colour band across England, Wales and Scotland. As the chart shows, England has significantly brighter nighttime skies than Wales or Scotland.



Colour band	England	Wales	Scotland	GB
Colour band 1 (Darkest)	21.73	56.82	76.77	46.16
Colour band 2	27.31	17.95	10.74	20.05
Colour band 3	19.04	9.29	4.63	12.60
Colour band 4	11.02	5.85	2.74	7.36
Colour band 5	6.81	3.79	1.72	4.57
Colour band 6	4.98	2.87	1.20	3.33
Colour band 7	4.29	2.13	1.02	2.83
Colour band 8	3.23	1.04	0.85	2.11
Colour band 9 (Brightest)	1.59	0.25	0.32	0.98

FIGURE 7: Percent share of land by country in each brightness colour band. Image source: Land Use Consultants (*England's Light Pollution and Dark Skies*, 2016).

ALAN values were extracted from the raster using the *terra* package in R (Hijmans *et al.*, 2024) and matched to the butterfly sites. The range of light pollution values against the butterfly site data is 0.87 to 571.54, suggesting a range of sites with vastly different levels of light pollution, as well those with some of the worst light pollution in the country. Figure 8 shows the distribution and intensity of light pollution across all of Great Britain. To create this map, ALAN values were capped at 98% to remove outliers for more seamless plotting of the UK's bright night sky.

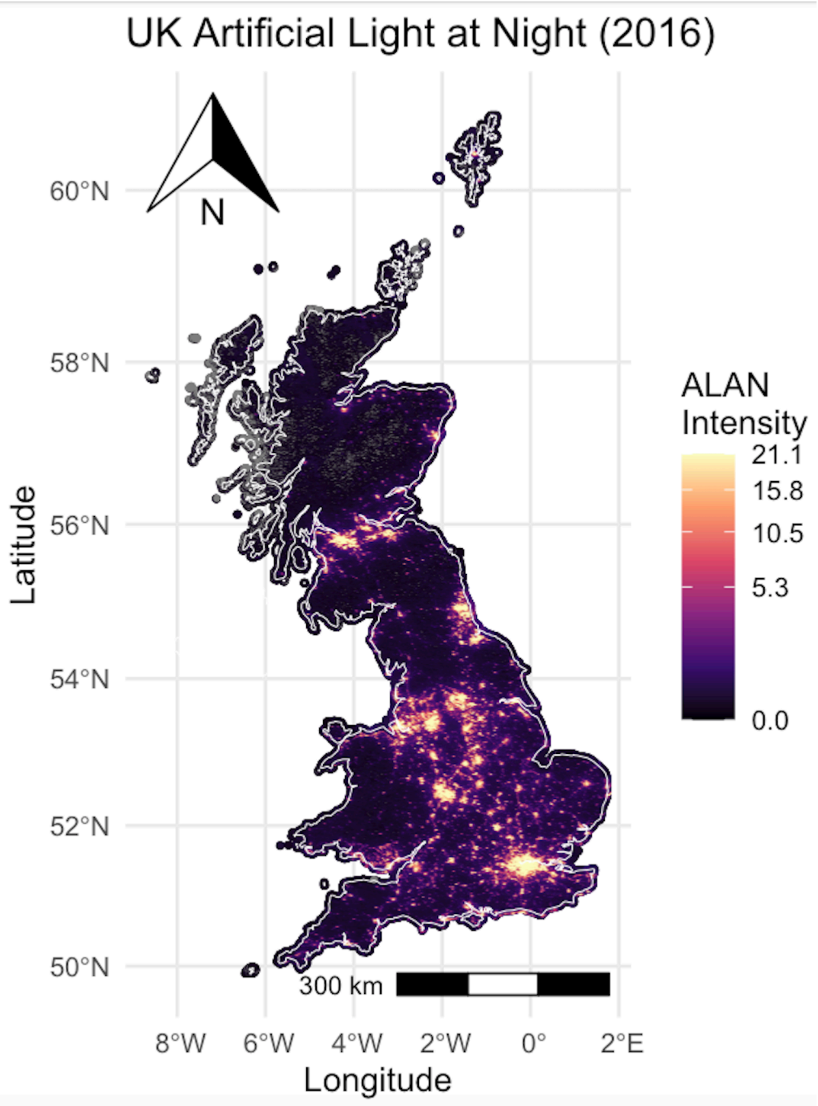


FIGURE 8: A map of Great Britain showing the areas with the most intense nighttime light pollution.

3.2.3 Landscape-level data: Impervious surface area

Impervious surface area data for the London study came from the Global Human Settlement Layer Project (GHSLP), which is the same source that was used for the global study (European Commission. Joint Research Centre., 2023). To match the temporal and spatial resolution of the butterfly data, built-up cover data for the year 2015 was downloaded, at 3-arc second—or 90 meter squared—resolution. The unit of measurement for the data set is meters, representing the number of meters within each 90-meter grid square that comprises built-up cover. At this scale, the total possible range of values is 0-8,100 meters. To cover the entire Greater London extent, two adjacent grid tiles (C18 and C19) were downloaded. These two gridded rasters were merged into one file, with a range of values from 0 to 5,629 meters. Figure 7 shows the distribution and intensity of built-up surface area throughout greater London at a 90 meter resolution, transformed into the percentage of each 90 meter grid square that is built up, defined as the 'gross surface (including the thickness of the walls) bounded by the building wall perimeter' (European Commission. Joint Research Centre., 2023).

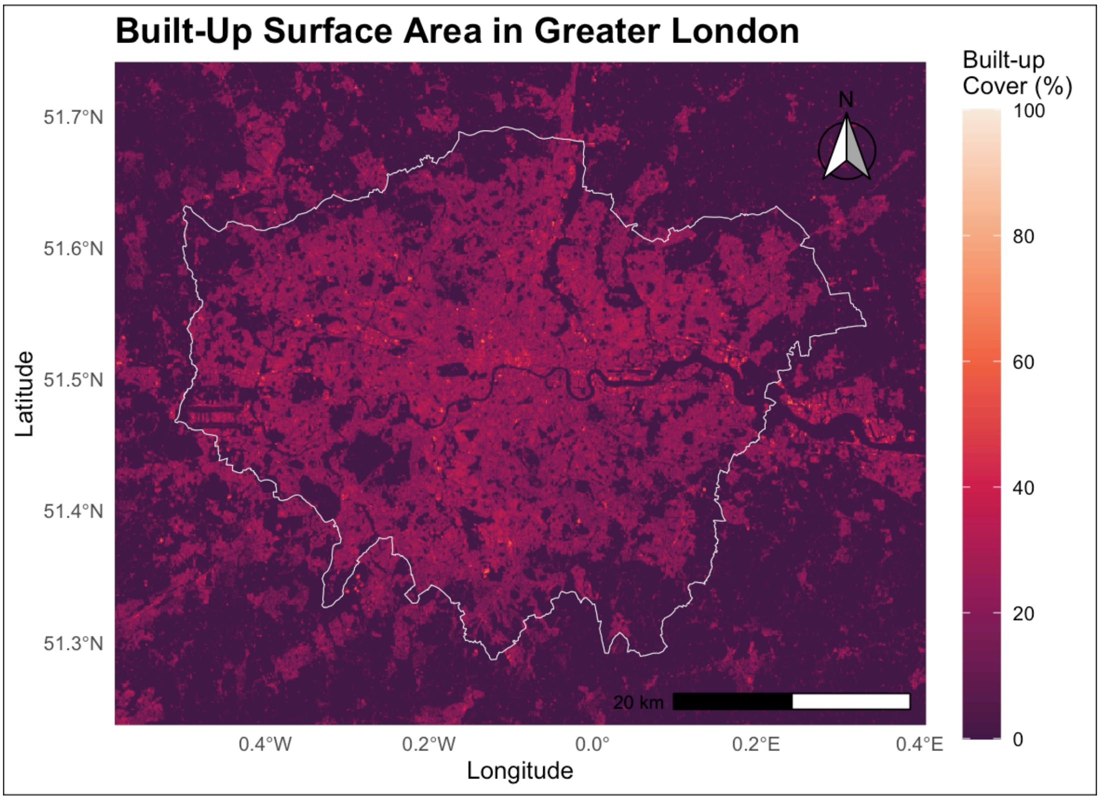


FIGURE 9: The percent of built-up surface area throughout Greater London, with lighter, brighter colours indicating a higher percentage of the area that is built up.

Spatial data points were extracted from the raster using the *terra* package in R (Hijmans *et al.*, 2024) and matched to the butterfly sites. The range of built-up surface area against the London butterfly sites is 0-5,110 meters, indicating a diversity of survey sites, including some in very built-up areas. In terms of percentages, the range of built-up cover in each 90-meter grid square is 0-63%. To explore the impact that different spatial resolutions can have on data analysis, the 1 kilometer grid square data was also matched to the butterfly sites for comparison. At this coarser resolution, the built-up surface percent changes significantly at the upper limits: for each 1 kilometer grid square, the range of built-up cover only ranges from 0-26% (0 to 259,283 meters of each km^2), highlighting the importance of scale when assessing environmental features, and recognising the diversity of urban landscapes. The 90 meter resolution was selected over the coarser spatial data for analysis, in order to more accurately capture the gradient of this urbanisation metric across London.

3.2.4 Landscape-level data: Green cover

Green cover data by the Greater London Authority (GLA) was downloaded from London Datastore (data.london.gov.uk) and used as a proxy for habitat fragmentation. The

GLA measured green cover using a combination of 4,000 data points manually labelled by humans and a machine learning model based on these data points that used infrared images, measurements of surface heights, and aerial photographs of London captured on a rolling basis between 2020 and 2022. The model used a Random Forest algorithm to classify pixels, which were given one of three categories: ‘canopy’ (individual trees or trees in a wooded area), ‘green’ (including private gardens, road verges and green roofs, and other vegetation that is not tree canopy), and ‘neither’ (everything else: roads, buildings, water, etc). The GLA model had trouble classifying ‘bare grass’ without much vegetation, but it correctly labelled areas as ‘green’ about 91% of the time (*GLA Methodology Report*, 2024).

The detailed GLA green cover map is not downloadable in a spatial format to use in analysis, but they extracted the green cover values for each of London’s 679 wards, as of 2022. The resulting data set, which is available at London Datastore (data.london.gov.uk), is an excel spreadsheet of London wards with a corresponding value representing the percent of each ward that has been classified as ‘green’. To match these values to butterfly survey sites, I uploaded London’s ward boundaries into R from ArcGIS and performed a spatial join to the butterfly data using the *sf* package in R (Pebesma *et al.*, 2024). The green cover percentage associated with each ward was then matched to the ward surrounding each site. Though the actual classification of electoral ward is not significant for this study, it presents a way to assess the spread of green cover across the capital. Wards differ greatly in size across the capital, but as they are all significantly larger than the 100m resolution of the butterfly data, every site that fell within the same ward adopted the same percent value for green cover. This could lead to some of the biodiversity indicators being skewed or masked by the value of the surrounding area, but it might also allow for analysis regarding the influence of landscape-level (in this case, ward-level) factors on local variables.

Of the 679 London wards, 638 contained butterfly survey sites. In the full data set, green cover percent values range from about 1%—for wards that fall within the City of London, like Langbourn, Aldgate and Cornhill—all the way up to 94% for the ward of Darwin, in the Sevenoaks District. The average green cover across all London wards is 38%. Figure 8 shows the Green Cover Map created by the GLA in 2024.

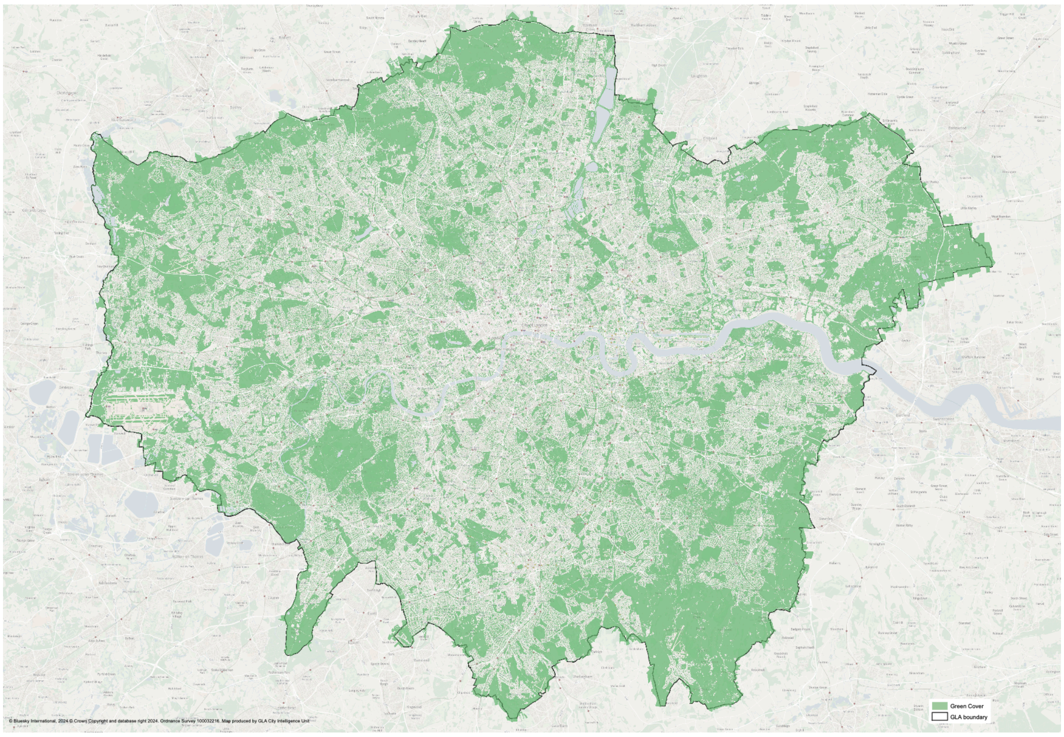


FIGURE 10: The 2024 Green Cover Map of London, produced by the Greater London Authority. Image credit: Greater London Authority (data.london.gov.uk)

3.2.5 Landscape-level data: Land cover

There are a variety of land covers blanketing the nation's capital, which can be mapped using raster data from the UK Centre for Ecology and Hydrology's Land Cover Map 2015 (ceh.ac.uk). Land Cover Map 2015 (LCM2015) was created by classifying satellite data into 21 classes, which are more granular versions of the UK Biodiversity Action Plan Broad Habitats, e.g. the 'built-up areas and gardens' category was split into two target LCM2015 classes: urban and suburban (*Land Cover Map 2015*, 2017). These classes signify land *cover*, rather than land *use,* as use could not be implied from the surface cover of the ground. The spatial resolution of LCM2015 is 25 meters, so to match the resolution of the Butterfly Conservation data, each 25-meter land parcel was aggregated to 100 meters and assigned the majority land cover across the 4 grid squares. Figure 9 shows the raw land cover data across London's entire bounding box, a 5 kilometer buffer added around the map's edges for easier viewing.

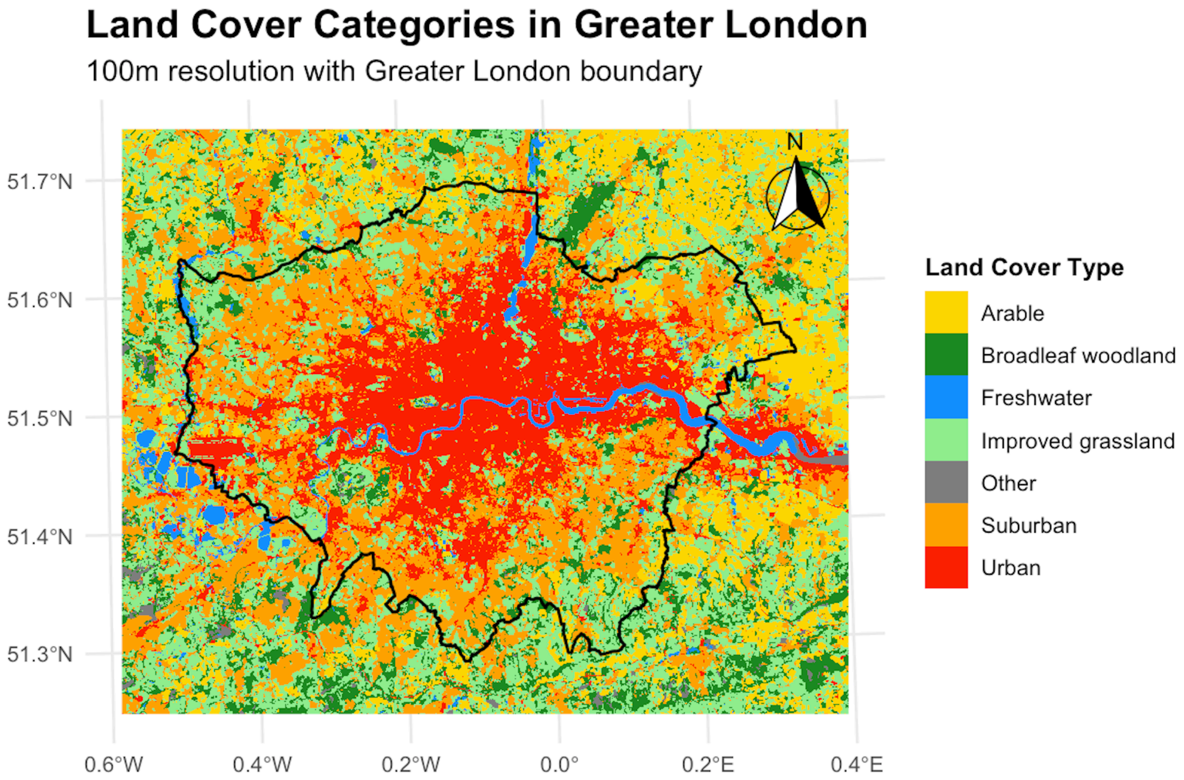


FIGURE 11: Predominant land cover for the entire greater London extent at 100 meter resolution.

Land cover values were extracted from the raster file using the *terra* package in R (Hijmans *et al.*, 2024), and then aggregated to 100 meters to be matched to the butterfly data. 94% of the sites fell within the categories of urban, suburban, improved grassland and broadleaf woodland, with a few percent each for freshwater and arable land cover. To simplify the data, just these six land covers were used, with the remaining 15 classifications aggregated and categorised as 'other'. These were then saved as factors, so they could be plotted accordingly during analysis. Table 1 lists the land cover categories of the butterfly survey sites, along with their corresponding percentage values, and Figure 10 maps the butterfly sites across London, coloured by their land cover classification.

Predominant Land Cover	Number of Sites	Percent of Total
Urban	6,442	33%
Suburban	5,672	29%
Improved Grassland	4,232	22%
Broadleaf Woodland	1,958	10%
Freshwater	504	3%
Arable	501	3%
Other	145	1%
Total	**19,454**	**100%**

Table 1: the predominant land cover categories of the Butterfly Conservation survey sites across Greater London.

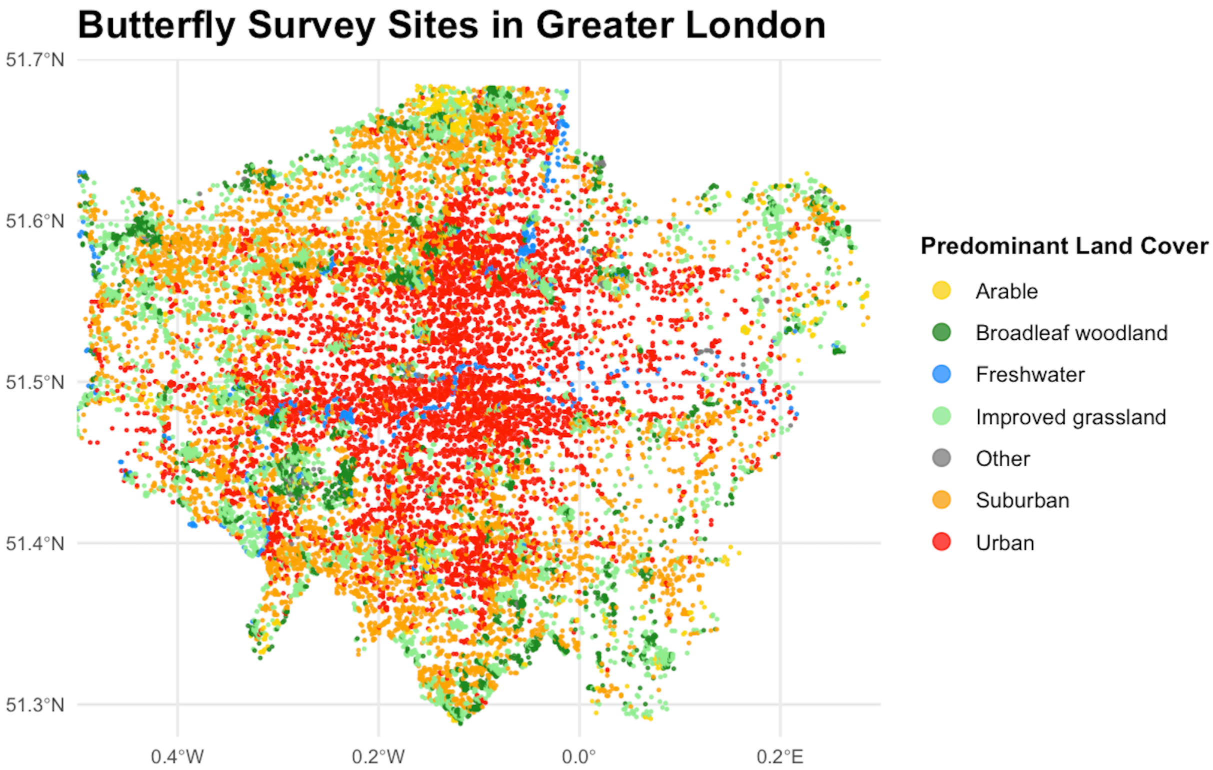


Figure 12: butterfly survey sites in greater London. The colour of the data point represents the predominant land cover category at 100 meters.

Over 50% of the land cover for the butterfly sites is classed as urban or suburban, which comprise built-up areas and private gardens. Improved grassland is a significant category, and though in more rural areas tends to represent farmland, in cities signifies for any grass-covered areas with high levels of management, dominated by few grass species and lower levels of biodiversity than natural grassland (NHBS, 2022). In London, examples of this could be many of the public parks, sports fields, larger lawns in housing estates, and areas in nature reserves that are actively managed for recreation. Pockets of broadleaf woodland grow in some of the larger parks, like Epping Forest and Richmond Park, as well as areas of the Green Belt, nature reserves, and former estate land.

3.2.6 Statistical modelling

Statistical analysis was conducted using R version 4 (‘R Core Team’, 2024). The relationship between butterfly species richness and urbanisation was modelled using a generalised linear mixed effects model, assuming Poisson-distributed errors. The levels of the land cover factor were reorganised to broadly represent levels of human disturbance, from woodland to urban. The model used the sample midpoint from the site as the random effect to correct for the large variation that could occur between years, due to factors like sampling effort, number of sites, and environmental fluctuations. Artificial light at night, impervious surface area and green cover percent were scaled and centred around zero, and these three variables, along with the predominant land cover factor variable, were fitted as fixed effects. Backwards stepwise selection using likelihood ratio tests, or Chi-squared tests (χ2), was performed to analyse the impact of each variable on the predictor variable, species richness. At the end of the selection process, all variables remained, suggesting that each one improved the fit of the model.

However, in testing the model assumptions, a few key assumptions were violated, namely that the green cover and ALAN variables failed a linearity test. Species richness appeared to exhibit a linear relationship with ALAN up to a certain point, but then curved off, while green cover showed complete non-linearity. The model checks also uncovered significant zero-inflation—most likely from the built-up surface area variable, which includes many zero values—and heteroscedasticity on the ALAN plot at higher values. Due to these issues, the Poisson error distribution was deemed inappropriate, and the data was re-modelled with a negative binomial distribution, whose variance is a quadratic rather than linear function of the mean, and can better handle non-linearity (Ver Hoef and Boveng, 2007). Polynomial terms were added to both ALAN and green cover, to specifically assess the linear vs. quadratic terms. A zero-inflation formula was tested, but in the summary of the model, the zero-intercept appeared to have no impact, so was removed. The fit of the model was improved with the negative-binomial distribution, as evidenced by the Akaike Information Criterion (AIC) test, which assigned a lower AIC value to the new model, which signifies a better fit. The ALAN variable still exhibited heteroscedasticity at upper values, but this is likely due to the few extreme values in the data set.

Backwards stepwise selection of the variables was re-run with the updated negative-binomial model, which retained all variables once again, indicating that all of the fixed terms contributed to improving the fit of the model. Because every variable was retained in the model selection process, the full and the reduced models were identical, and normal likelihood ratio tests couldn’t be performed. Instead, to analyse the significance of each predictor variable on the response variable, four additional models were created, each one removing one of the variables and allowing for the assessment of each predictor variable on its own in relation to the full model. From here, coefficients tables were generated to analyse the significance of each variable.

Both the original linear mixed effects model and the updated negative-binomial mixed effects model were from the *lme4* package in R (Bates *et al.*, 2024). The final models are presented in Appendix B.

3.3 Use of artificial intelligence

Various aspects of both the global and London study were assisted by the use of an AI language model (‘Claude 3.5 Sonnet’, 2024). This assistance involved collaboration for generating and troubleshooting code that was used for data cleaning and processing, statistical analysis, and data visualisations. All final decisions were made and implemented by the researcher.

4 | RESULTS

4.1 Global analysis of the impact of urbanisation on insect biodiversity

Impervious surface area (ISA), artificial light at night (ALAN) and land use were analysed for their impact on total insect abundance and insect species richness at the global scale. Landscape-level factors—in this case, land use—played a significantly larger role in determining insect abundance than either of the urbanisation variables used for the analysis. While species richness declined in pasture and cropland, no land use other than primary vegetation was significant in determining total insect abundance at the global level. Neither ISA nor ALAN were significant variables in determining changes in global insect biodiversity.

The statistics for the final selected models are presented here. Artificial light at night and built-up surface area each had one degree of freedom (DF), and land use had five degrees of freedom. The effects of the urbanisation variables on total abundance are: for built-up surface area $\chi2 = 0.336$ and $p = 0.562$, for artificial light at night $\chi2 = 0.245$ and $p=0.621$, and for land use $\chi2 = 11.256$ and $p = 0.047$. The effects of the urbanisation variables on species richness are: for built-up surface area $\chi2 = 0.320$ and $p = 0.0572$, for artificial light at night $\chi2 = 0.008$ and $p = 0.929$, and for land use $\chi2 = 33.967$ and $p < 0.001$.

To assess the impact of each land use type on insect biodiversity, odds ratios were calculated for each biodiversity metric, along with the p-values for each positive or negative relationship displayed. Figure 11 shows the plots of the different land use categories and their impact on both insect abundance and species richness.

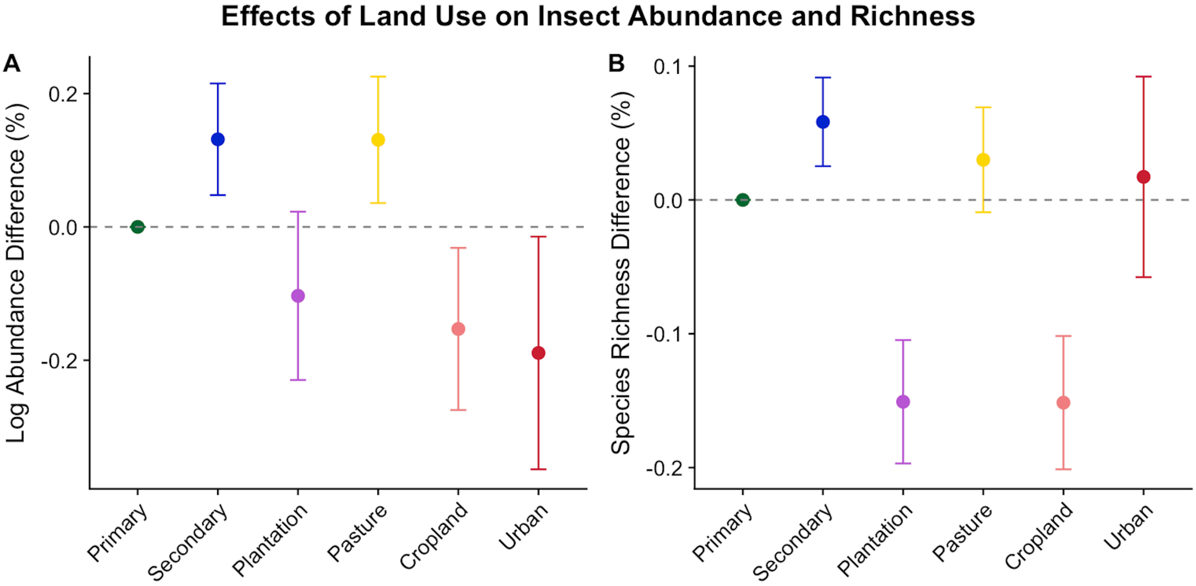


FIGURE 13: Changes in log-transformed total abundance (A) and species richness (B) across different land use categories, compared to the intercept.

The only land use that had an impact of statistical significance ($p < 0.05$) on insect abundance was the intercept, which is primary vegetation. Though plantation, cropland and urban land uses often lead to decreases in total abundance for this data set, the results were not statistically significant, with urban land displaying huge variance across the results, and a small percentage of the plantation sites exhibiting higher levels of abundance than the mean value for primary vegetation. For the species richness metric, plantation and cropland were associated with statistically significant decreases in species richness, both of about 14%, with p-values of .001 and .002, respectively. Pasture and urban land exhibited marginally positive relationships with species richness, but the results were not significant ($p = 0.447$ and $p = 0.969$, respectively), and the urban relationship in particular shows great uncertainty. Both biodiversity metrics increased in sites of secondary vegetation, though the p-values were not significant.

4.2 London: Analysing the impact of key urbanisation metrics on butterfly species richness

Impervious surface area (ISA), artificial light at night (ALAN), ward-level percent green cover, and predominant land cover were all analysed in relation to their impact on butterfly species richness across London. Every variable exhibited significant influence over changes in butterfly biodiversity for the sample data in the study. The results of the likelihood ratio test are as follows: For ALAN, DF = 2, $\chi2 = 14.634$, $p = 0.0007$; for ISA, DF = 1, $\chi2 = 16.114$, p = 5.964*e^-5; for percent green cover, DF = 2, $\chi2 = 38.074$, p = 5.388*e^-9; for land cover, DF = 6, $\chi2$ **=** 362.66**,** p <2.2*e^-16. Full coefficients tables are presented in the appendix.

Figure 12 shows the relationship between butterfly species richness in London and the four predictor variables representing urbanisation.

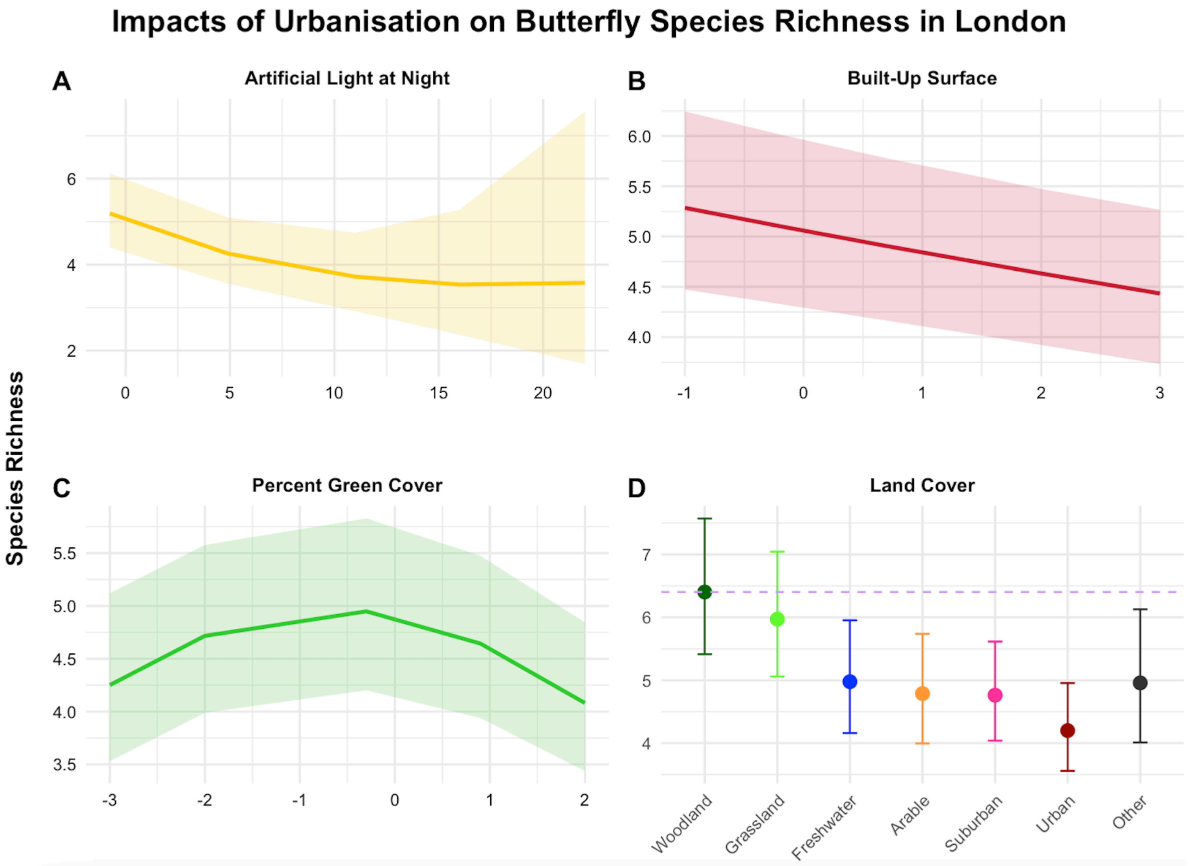


FIGURE 14. Impacts of urbanisation on butterfly species richness
A-C : Response of species richness to increasing values of each urbanisation variable. The values on the x-axis are the scaled values from the model.
D: Difference in species richness within different land covers, compared to the intercept.

Each of the 6 land covers led to lower levels of butterfly species richness than the reference land cover woodland, with every decrease associated with statistically significant p-values < 0.001. While built-up surface area exhibits an evenly distributed negative linear relationship with butterfly species richness, the relationships between species richness and both artificial light at night and percent green cover are non-linear. In these plots (A and C), the continuous plot function combines both the linear and quadratic function in the same plot. At the lower end of the range, species richness declines as artificial light increases, however, the slope of the regression line begins to decrease after the halfway point, before flattening out in the top 25% of values, where the variance becomes very broad.

The plot for green cover depicts a unimodal relationship, wherein butterfly species richness increases as the percent of the surrounding area covered in green vegetation increases, but only up to a certain point, before then decreasing. To understand what this 'ideal' level of green cover looks like in London, the vertex of the parabola was calculated using the original green cover values. Based on these calculations, butterfly species richness in London reaches its peak when the surrounding area (in this case, electoral ward), is at approximately 40% green cover.

5 | DISCUSSION

5.1 Global

Based on the data sets used in this study, changes in global insect biodiversity are very difficult to predict, and there is no clear relationship between urbanisation and either insect abundance or insect species richness. Even in the interaction model, which intended to test the hypothesis that urbanisation exerts its influence in different ways and extremes depending on the surrounding land use, no significant relationships were found. This suggests that, at the global level, there are other large-scale variables not captured by these urbanisation metrics that have significance in determining insect biodiversity.

One such predictor is climate, which is not accounted for in my models, but which has been shown to significantly influence both biodiversity and the impacts of urbanisation. In a paper analysing the response of biodiversity to different levels of land use intensity in cropland and secondary vegetation, it was found that the effects of landscape-level differences on local biodiversity varied both in size and direction based on whether the study site was located in a tropical vs. non-tropical region (Outhwaite *et al.*, 2022). Such regional differences can also influence specifically urban biodiversity. While a large majority of the studies looking at urbanisation's impact on biodiversity originate in cities with temperate climates, some interesting findings have emerged from regions with more extreme climes (Faeth, Bang and Saari, 2011). In temperate cities, species richness is generally lower than in the surrounding area, with somewhat less dramatic declines in species abundance, while in tropical cities, both biodiversity metrics suffer significant declines. However, in arid cities, species abundance tends to increase compared to the surrounding area, and species richness is just as likely to increase as it is decrease (Faeth, Bang and Saari, 2011).

While breaking the data out into tropical and non-tropical climates might help to explain urbanisation's relationship to insect biodiversity, other 'city-level' characteristics could also provide a clarifying filter for the data, such as a city's size, age and context (Norton et al., 2016). Other variables that might contextualise the data are GDP, levels of development, or geopolitics, contributing to an interrogation of the social components of socioecology. Though this kind of scrutiny was outside the scope of this study, an analysis of cities grouped by their age or their size—either by density or volume—could provide interactions that help refine this type of global study and capture more nuance than can be provided from the basic land use categories.

The significant result of this study—that insect species richness faces declines in plantations and cropland—is not a new finding (Wagner, 2020), nor, on the surface, is it related to urban expansion. However, with urban expansion in many parts of the world encroaching on agricultural land (Ustaoglu and Williams, 2017), there might in fact be a connection between cropland/plantations and urban areas. What does the biodiversity look like in urban areas developed on land converted from agricultural use? When measuring changes in biodiversity after converting land from agriculture to urban, will biodiversity increase? Would the city then act as a sanctuary, providing more diverse habitats, as well as refuge from intensive pesticide use in the surrounding area (Spotswood *et al.*, 2021)? Or would species richness remain low, after being so reduced during its agricultural use?

While the global study didn't yield specific takeaways for how to interpret urbanisation's impact on global biodiversity, it confirms the importance of landscape-level and even regional context in assessing how human pressures influence changes in biodiversity.

5.2 | London

5.2.1 Contextualising the results: Land cover

Though London in its entirety could broadly be classed as 'urban', that is a classification that would gloss over much of the nuances in land cover and use that make London such a unique habitat for both humans and wildlife. Undoubtedly a city shaped by intensive urbanisation, London is also a city with ample green space, woodlands, and even wetlands. Analysing the response of butterfly species richness to different land cover categories across the capital gives us insight into how the wider landscape might serve biodiversity. While at the global scale there was high uncertainty around the impact of many of the land uses, and even directionally it was difficult to draw conclusions, the picture for London is very clear: within this landscape that has already been significantly influenced by human pressures, each additional level of disturbance has a negative impact on butterfly species richness.

Based on these findings, how might we better manage the land for wildlife? How can we encourage the highly urban areas to behave more like the suburban areas? How can we increase the biodiversity of the green space in our suburban neighbourhoods so they might offer the support of richer grassland? Can we incorporate more blue infrastructure into the built environment to get the benefit of freshwater habitats? In a place like the City of London—blanketed as it is in concrete—it may feel like land cover is established. But could the inclusion of trees on every street provide safe passage for certain mobile species, and boost biodiversity metrics in even London's most urban neighbourhoods?

5.2.2 Contextualising the results: Artificial light at night

Because the relationship between butterfly species richness and artificial light at night produced such great variance at high values, it is uncertain how species richness responds in areas of extreme light pollution, based solely on the model. However, in mapping these extreme values, we might be able to glean some additional information about the other factors possibly influencing biodiversity under nighttime light. Figure 13 is a visualisation of butterfly survey sites near areas of high light pollution, showing that most of these very high values are clustered around central London, with its abundance of office buildings, hotels, theatres and shops. However, there a few points outside the centre generating high levels of light pollution: Heathrow airport, Kings Cross, and a few areas that have big stadiums or shopping centres, or both, like Wembley, Twickenham and Stratford.

Given that these bright spots shine in such different areas—in some of the most built-up neighbourhoods, and others with significant wild land—the responses of butterfly species richness varies greatly. While the bright lights of central London are likely to be correlated with lower levels of biodiversity, as well as interactions with other urbanisation drivers like impervious surface area, bright lights further away from the city centre might not have as negative of an effect. In this sense, the impact of artificial light at night, at least at the extremes, might be dimmed somewhat by the larger landscape: the wildflowers and brownfield sites around Olympic park, the riverside vegetation of Twickenham, and the green buffer of Regent's Park against the industrial backdrop of King's Cross.

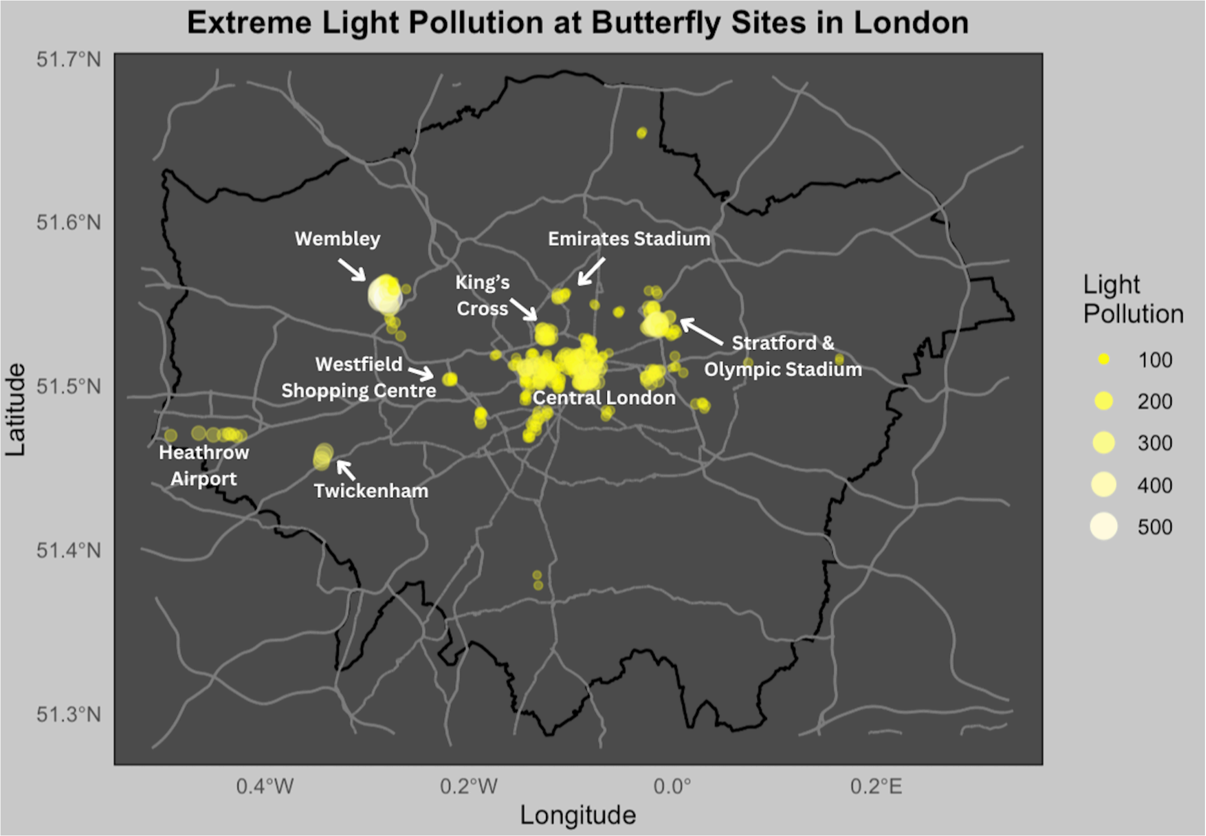


FIGURE 15: Butterfly sites with the highest levels of light pollution, falling in the top 2% of values.

5.2.3 Contextualising the results: Green cover

The ward-level green cover data set presents the opportunity to analyse the impact of landscape-level factors on local biodiversity and assess the degree to which the wider landscape influences patch-level biodiversity. I had hypothesised that butterfly species richness would exhibit a positive linear relationship with percent green cover, which is an assumption is backed up by many studies, but also one that just seems to *make sense*. In a meta-analysis of intra-urban biodiversity conducted across 75 cities, researchers found that the proportion of green surroundings has a positive influence on biodiversity, and that the two most influential characteristics that benefitted biodiversity were the size of the habitat patch, and the connectivity between green spaces (Beninde, Veith and Hochkirch, 2015). While in this study butterfly species richness increases with percent green cover at lower levels, it is far from the full picture. There are clearly other factors preventing high levels of green cover in London wards from exerting a positive influence on biodiversity.

Some London wards were measured as being as much as 90% green[1], but the type and quality of this 'greenness' was not made explicit. In this case, green cover could be short-mown amenity fields or wildflower meadows, small front gardens or species-rich nature reserves, a well-trimmed rose bush or a long line of hedgerows, all of which offer vastly different levels of biodiversity and quality of habitats. It's clear that green space is required for biodiversity to flourish; in London, however, there is a threshold above which it may be the quality, and not the quantity, of green space that determines species richness in an area.

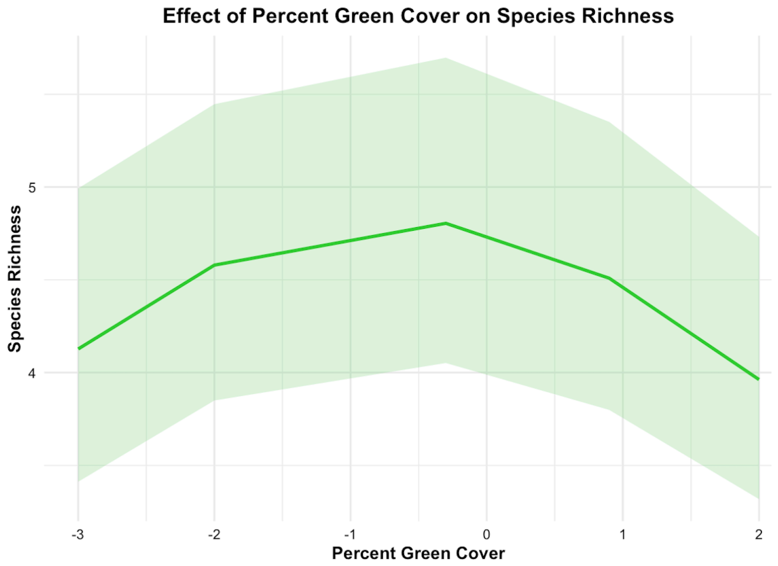


FIGURE 16: The unimodal relationship between butterfly species richness and ward-level green cover. The x-axis values are scaled and centred around zero.

This non-linear relationship, which, on average becomes negative in wards with more than 50% green cover, could also be indicative of other factors that influence species richness. Figure 15 shows a map of London's electoral wards coloured using the percent of the ward that was classified as 'green' by the Greater London Authority. The maps show many of the greenest wards on the outskirts of London, where the city abuts the Green Belt and its high proportion of agricultural land. Though most agricultural land is certainly 'green', intensive management and heavy use of pesticides makes it inhospitable for many insects. Further, pesticides don't just impact the land they are used on, but can travel great distances through the air, contaminating land further afield (Zaller *et al.*, 2022). The green belt is intended to protect the surrounding countryside from urbanisation, but, with 65% of green

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[1] Measurement classification described in the research methods section

belt land used for agriculture (CPRE, 2023), it might have the unintended consequence of harming biodiversity within the Greater London boundaries.

Something else that can be found in abundance around Greater London is motorways, bringing air and noise pollution to the area. Though under-studied, these forms of pollution have also been shown to negatively affect insect biodiversity (Fenoglio *et al.*, 2021). Though this study doesn't include a temporal analysis, further research could be done to examine the impacts of ULEZ's expansion across greater London, to assess if this regulation is better not only for humans but wildlife too.

Though the specific designation of electoral wards was not critical to this analysis, interrogating the influence—if any—of green cover on elections could open up conversation around the politics of green space. These fringe wards have pockets housing some of London's lowest income families (Leeser, 2021), and are also in the closest proximity to agricultural land; how might these and other electoral interests intersect with the provision of green space?

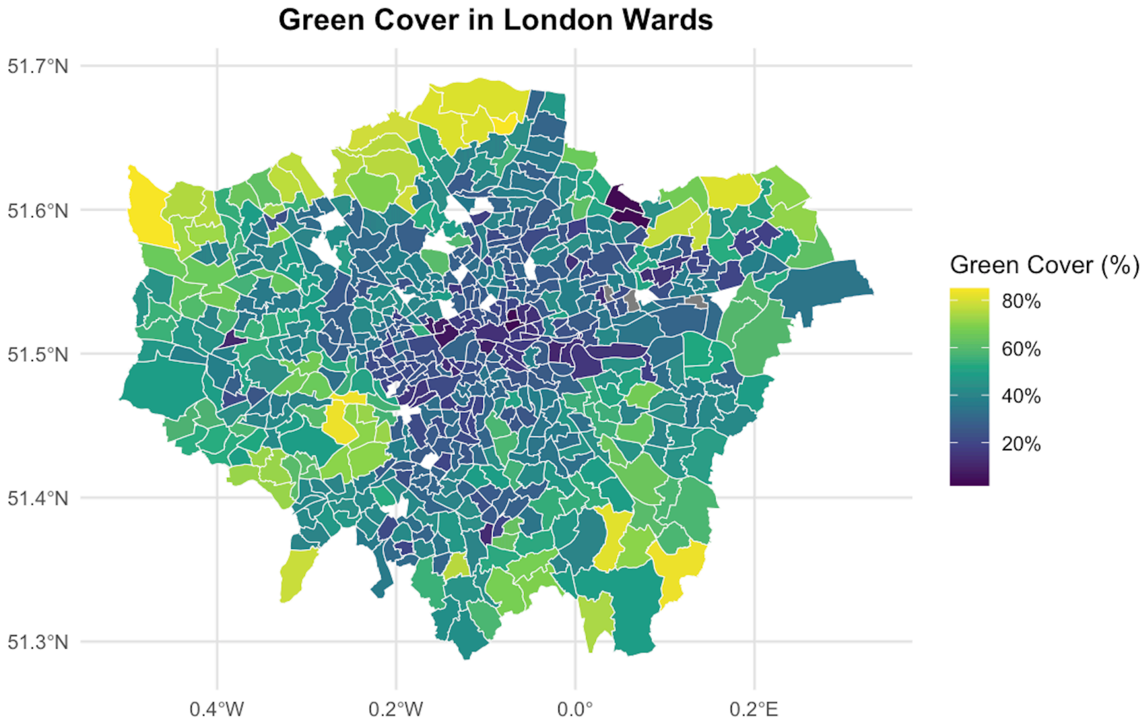


Figure 17. Ward-level green cover data. This map was created using 2022 green cover data and ward boundaries (GLA), projected onto a 2018 ward shapefile (the most recent available) using centroids from the original dataset's geometry. White spaces in the map represent wards that did not have any butterfly survey sites.

5.3 Building biodiverse cities

The effect of impervious surface area in London, estimated with 'built-up cover' data, conformed to the hypothesis that species richness decreases with increasing levels of urbanisation. Building structures are specifically erected to protect humans from their surroundings, providing shelter, and in the process, creating barriers and inhospitable environments for wildlife. Buildings and housing must necessarily convert land from its previous use—be it agriculture, woodland, or something in between—and given the projected urban expansion, the amount of built-up surface area in cities will only increase. The question then is not, how can we decrease built-up surfaces, but how can we lessen its impacts on biodiversity? What are the tools that will allow us to build biodiversity into our cities, rather than attempting to keep it out?

One of the key ways to alleviate the pressures of urbanisation is through the delivery of green infrastructure, using green walls, green roofs, wildlife corridors and sustainable drainage systems to integrate nature into the built environment (Filazzola, Shrestha and MacIvor, 2019). These kinds of features can absorb some of the impacts of urbanisation that negatively impact humans and wildlife alike, such as pollution and urban heat islands, while often directly providing wildlife with semi-natural habitats (Ying *et al.*, 2022). Especially if we are to view green infrastructure as potential habitat, its provision must be thoughtful, and not merely a box-ticking exercise. The influence of the surrounding area must be brought into planning and decision-making, as there are a plethora of external variables that can impede upon the success of GI, such as invasive species (often from gardens), soil erosion from construction, and the amount and type of impervious surface in the nearby area (Hostetler, Allen and Meurk, 2011). Biodiversity must also be explicitly prioritised in the planning and provision of green infrastructure, and not viewed as a secondary or even tertiary goal, as is often the case (Filazzola, Shrestha and MacIvor, 2019). The results from this study support the evidence that building nature into our cities, and realising the full potential of urban spaces to provide habitat for wildlife can greatly benefit biodiversity and lessen the negative impacts of urbanisation for all species.

There is evidence that London has acknwledged the value of green infrastructure and biodiversity for the city. The 2021 London Plan contains significant information on green infrastructure and its benefits to people, wildlife, and the built environment, and the Mayor of London has set a target for 50% of London to be ‘green’ by 2050 (*Green Infrastructure*, 2024). Further, statutory Biodiversity Net Gain went into effect in 2024, requiring all new developments to deliver a 10% increase in biodiversity (*Understanding biodiversity net gain*, 2024). While in theory this is an excellent way to protect and foster biodiversity in the city, off-site biodiversity credits are part of the mitigation hierarchy, which could lead to developers simply pushing these gains elsewhere. Some private developers, like the Grosvenor Estate, have created far more ambitious goals, targeting anywhere from 12 to 100% biodiversity net gain by 2030 (Grosvenor Estate, 2022).

A world with greener, more biodiverse cities will benefits not just wildlife, but people too. In multiple studies, biodiversity has been positively correlated with human wellbeing (Fuller *et al.*, 2007; Sandifer, Sutton-Grier and Ward, 2015), and more biodiverse green spaces have been associated with greater ‘restorative effects’ on people regardless of their age, gender or ethnicity (Wood *et al.*, 2018). These studies highlight the socioecology of urban biodiversity studies, and make the case for holistic approaches to both human and planetary health. We must leave behind the nature-culture dualism once and for all, and embrace our connection to nature, no matter the landscape we see through our window. Cities may never be as biodiverse as nature reserves, but with foresight, planning and coordination, we can develop cities that act as habitats for all living species, deserving of conservation action for wildlife in just the same way as hedgerows, woodlands and orchards.

5.4 Limitations and Considerations

Data limitations—including both availability and useability—influenced analysis and results at both the local and global levels. Firstly, finding appropriate urbanisation datasets, especially at the global scale, presented significant challenges. Many data sets were at very fine scales, which, when applied on a global level, required the merging of hundreds of tiff files and massive amounts of computing power. For example, the data set for impervious surface area (ISA) created by Huang and Li (2021) was collected at 30 meters, generating a large amount of heavy files that R was unable to process. Further, 30 meters is probably not an appropriate spatial resolution for a global data set, where landscape-level variables are potentially more influential. In its place, the built-up cover data from the Global Human Settlement Layer Project was selected as a proxy for impervious surface area. However, what is not made explicit in the metadata is whether paved-over surfaces other than buildings have been classed as built-up surface area. As cities are so much more than just their buildings, and as impervious surfaces abound in the form of paths, parking lots and town squares, this data may not fully capture the extent of impervious surfaces and their impact on biodiversity. Based on the upper limits of the raw London data—which was only 61% at a 100 meter resolution—this data does not include *all* impervious surface area, rather, only that bounded by a building wall perimeter. In this way, the data reflects only surfaces that are truly built *up*, rather than all surfaces where soil has been covered by impermeable materials, likely creating an incomplete picture of the impact of this feature commonly associated with decreased biodiversity.

Though I originally set out to analyse the impact of urban heat island effect (UHI) on biodiversity, analysis against this metric was not available in a meaningful way due to significant gaps in the data that stem from the way it was collected and categorised. UHI and ISA are correlated, so it is likely that some of this impact is captured by the built-up surface data. However, again, because the built-up data is potentially not as robust as true ISA data, this study may not be capturing that correlation either.

There is the potential for significant bias in both biodiversity data sets due to a species' conservation status or detectability, the focus of the researcher, or the geographical bias and/or data-rich or -poor areas (Boakes *et al.*, 2010). For the Butterfly Conservation data, there is an additional layer of inherent bias due to the nature of the data, which was predominantly collected through citizen science surveys. Though this method is increasingly gaining recognition as a form of high-quality primary data collection, and all the butterfly records in the data set have been verified, observations can still be biased by the person surveying, in terms of species observed and recognised, locations surveyed, and sampling effort (Callaghan *et al.*, 2021)

For the London data set, only species richness was analysed because abundance numbers cannot be inferred from presence-only data. This greatly limits the analysis of butterfly biodiversity in London, as it only tells one part of the story, especially as abundance and species richness do not always react the same way to urbanisation (Faeth, Bang and Saari, 2011). It is often habitat specialists that are the most sensitive to environmental change, while generalist species can usually adapt more easily (Vickery, 2008).

Because both of these studies examined differences in biodiversity across space, I was unable to analyse changes in biodiversity over time, though that would have added significantly to the study, especially as the world rapidly urbanises.

The decision to select or exclude certain data sets inherently precludes the use of other data sets in this analysis. All results are specific to the data used for these studies and must be considered in that context. Multi-city studies with varying levels of urbanisation or other unique characteristics would produce interesting data for comparison and help contextualise some of these findings.

6 | Conclusion

This study pulls together biodiversity and urbanisation data at global and local scales to better understand the impact of urbanisation on insect biodiversity. For centuries, cities have provided people with economic opportunities, cultural exploration, and refuge from discrimination. Home to some of the largest universities and institutions, they are hubs of intellectual curiosity, interrogation and discovery. Cities have shaped, stretched and strengthened the human experience. But they have also been at the heart of the biodiversity crisis, demanding outsize energy and natural resources, releasing pollution into the sky and the sea, and snatching up wild habitat to satiate the hunger of urban expansion. We have sacrificed the safety of countless other species to pursue our own ambition and comfort. But the wellbeing of humans and wildlife are not mutually exclusive, and we can still live good lives while providing adequate habitat for the many species we share our cities with.

If we understand how urbanisation influences biodiversity and how we might reduce its negative impacts, as well as what the interplay looks like between landscape- and patch-level variables, we can develop more wildlife-friendly cities and towns. This study showed that the extent of built-up surfaces in an area is negatively correlated with butterfly species richness in almost all cases across London, suggesting that this variable is a useful indicator of urbanisation's impact on biodiversity. Decreasing the magnitude of the effect of built-up areas can benefit butterfly species richness, and likely biodiversity more generally. Incorporating nature into the built environment through the provision of green infrastructure that explicitly prioritises biodiversity is one of the best ways to protect biodiversity in built-up areas. As the green cover data showed, quantity cannot always be substituted for quality, and thoughtful consideration of biodiversity in urban green space management is necessary for it to thrive. City-wide coordination of green spaces and green infrastructure is recommended so that both landscape and local variables are accounted for.

Larger-scale biodiversity patterns related to urban expansion need further consideration, and future studies might benefit from breaking down global biodiversity into its constituent pieces. Though drawing conclusions about biodiversity’s response to urbanisation at the global scale is appealing, single- or multi-city studies may be more appropriate, given the broad range of factors that influence the composition and behaviour of urban systems. Future urban biodiversity studies should focus on Asia, Africa and South America, to fill the existing knowledge gap and concentrate resources on the areas that will experience the biggest increases in urban development in the coming years.

The cities of tomorrow could be hotter, greyer and more devoid of life, or they could be colourful, vibrant places pulsing with the movement and sounds of wildlife. The decision to summon the compassion and will to make our cities better for all living things, or focus solely on short-term human interests, lies with all of us.

Conflict of Interest

The author has no conflict of interest to declare.

Bibliography

Adams, W.M. (2013) *Against Extinction: The Story of Conservation*. Routledge.

Alho, C.J.R. (2008) 'The value of biodiversity', *Brazilian Journal of Biology*, 68, pp. 1115–1118. Available at: https://doi.org/10.1590/S1519-69842008000500018.

Angold, P.G. *et al.* (2006) 'Biodiversity in urban habitat patches', *Science of The Total Environment*, 360(1), pp. 196–204. Available at: https://doi.org/10.1016/j.scitotenv.2005.08.035.

Aronson, M.F. *et al.* (2017) 'Biodiversity in the city: key challenges for urban green space management', *Frontiers in Ecology and the Environment*, 15(4), pp. 189–196. Available at: https://doi.org/10.1002/fee.1480.

Bates, D. *et al.* (2024) 'lme4: Linear Mixed-Effects Models using "Eigen" and S4'. Available at: https://cran.r-project.org/web/packages/lme4/index.html (Accessed: 21 August 2024).

Beninde, J., Veith, M. and Hochkirch, A. (2015) 'Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation', *Ecology Letters*, 18(6), pp. 581–592. Available at: https://doi.org/10.1111/ele.12427.

Blood, E. (1994) 'Prospects for the Development of Integrated Regional Models', in P.M. Groffman and G.E. Likens (eds) *Integrated Regional Models: Interactions between Humans and their Environment*. Boston, MA: Springer US, pp. 145–153. Available at: https://doi.org/10.1007/978-1-4684-6447-4_9.

Boakes, E.H. *et al.* (2010) 'Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data', *PLOS Biology*, 8(6), p. e1000385. Available at: https://doi.org/10.1371/journal.pbio.1000385.

Bonthoux, S. *et al.* (2014) 'How can wastelands promote biodiversity in cities? A review', *Landscape and Urban Planning*, 132, pp. 79–88. Available at: https://doi.org/10.1016/j.landurbplan.2014.08.010.

Breuste, J., Niemelä, J. and Snep, R.P.H. (2008) 'Applying landscape ecological principles in urban environments', *Landscape Ecology*, 23(10), pp. 1139–1142. Available at: https://doi.org/10.1007/s10980-008-9273-0.

Butterfly Conservation (2024) *Butterfly Conservation*. Available at: https://butterfly-conservation.org/ (Accessed: 21 August 2024).

Callaghan, C.T. *et al.* (2021) 'Three Frontiers for the Future of Biodiversity Research Using Citizen Science Data', *BioScience*, 71(1), pp. 55–63. Available at: https://doi.org/10.1093/biosci/biaa131.

Ceballos, G. *et al.* (2015) 'Accelerated Modern Human-Induced Species Losses: Entering the Sixth Mass Extinction.', *Science Advances*, 1, p. e1400253. Available at: https://doi.org/10.1126/sciadv.1400253.

Chakraborty, T. and Lee, X. (2023) ‘Yale Center for Earth Observation (YCEO) Surface Urban Heat Islands, Version 4, 2003-2018’. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). Available at: https://doi.org/10.7927/S5M5-ZK14.

‘Claude 3.5 Sonnet’ (2024). Anthropic.

Collins, M.K., Magle, S.B. and Gallo, T. (2021) ‘Global trends in urban wildlife ecology and conservation’, *Biological Conservation*, 261, p. 109236. Available at: https://doi.org/10.1016/j.biocon.2021.109236.

Cooper, J.E.J. *et al.* (2024) ‘Using butterfly survey data to model habitat associations in urban developments’, *Journal of Applied Ecology*, 61(4), pp. 773–783. Available at: https://doi.org/10.1111/1365-2664.14583.

Couch, C. and Dennemann, A. (2000) ‘Urban regeneration and sustainable development in Britain’, *Cities*, 17(2), pp. 137–147. Available at: https://doi.org/10.1016/S0264-2751(00)00008-1.

CPRE (2023) *All you need to know about the Green Belt*, *CPRE*. Available at: https://www.cpre.org.uk/explainer/all-you-need-to-know-about-the-green-belt/ (Accessed: 28 August 2024).

Dale, A. and Newman, L.L. (2009) ‘Sustainable development for some: green urban development and affordability’, *Local Environment*, 14(7), pp. 669–681. Available at: https://doi.org/10.1080/13549830903089283.

Davis, A.M. and Glick, T.F. (1978) ‘Urban Ecosystems and Island Biogeography’, *Environmental Conservation*, 5(4), pp. 299–304. Available at: https://doi.org/10.1017/S037689290000638X.

Dixon, T. (2007) ‘The Property Development Industry and Sustainable Urban Brownfield Regeneration in England: An Analysis of Case Studies in Thames Gateway and Greater Manchester’, *Urban Studies*, 44(12), pp. 2379–2400. Available at: https://doi.org/10.1080/00420980701540887.

England’s Light Pollution and Dark Skies (2016). Land Use Consultants. Available at: https://www.cpre.org.uk/wp-content/uploads/2023/05/Englands-Light-Pollution-and-Dark-Skies-LUC-Report-2016.pdf (Accessed: 6 August 2024).

Environment, U.N. (2017) *Cities and climate change | UNEP - UN Environment Programme*. Available at: https://www.unep.org/explore-topics/resource-efficiency/what-we-do/cities-and-climate-change (Accessed: 21 August 2024).

zu Ermgassen, S.O.S.E. *et al.* (2022) ‘A home for all within planetary boundaries: Pathways for meeting England’s housing needs without transgressing national climate and biodiversity goals’, *Ecological Economics*, 201, p. 107562. Available at: https://doi.org/10.1016/j.ecolecon.2022.107562.

European Commission. Joint Research Centre. (2023) *GHSL data package 2023.* LU: Publications Office. Available at: https://data.europa.eu/doi/10.2760/098587 (Accessed: 4 July 2024).

Faeth, S.H., Bang, C. and Saari, S. (2011) ‘Urban biodiversity: patterns and mechanisms’, *Annals of the New York Academy of Sciences*, 1223(1), pp. 69–81. Available at: https://doi.org/10.1111/j.1749-6632.2010.05925.x.

Faeth, S.H. and Kane, T.C. (1978) ‘Urban biogeography’, *Oecologia*, 32(1), pp. 127–133. Available at: https://doi.org/10.1007/BF00344697.

Fahrig, L. (2003) ‘Effects of Habitat Fragmentation on Biodiversity’, *Annual Review of Ecology, Evolution, and Systematics*, 34(Volume 34, 2003), pp. 487–515. Available at: https://doi.org/10.1146/annurev.ecolsys.34.011802.132419.

Fenoglio, M.S. *et al.* (2021) ‘Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities’, *Ecological Entomology*, 46(4), pp. 757–771. Available at: https://doi.org/10.1111/een.13041.

Filazzola, A., Shrestha, N. and MacIvor, J.S. (2019) ‘The contribution of constructed green infrastructure to urban biodiversity: A synthesis and meta-analysis’, *Journal of Applied Ecology*, 56(9), pp. 2131–2143. Available at: https://doi.org/10.1111/1365-2664.13475.

Fox, J. *et al.* (2023) ‘car: Companion to Applied Regression’. Available at: https://cran.r-project.org/web/packages/car/index.html (Accessed: 21 August 2024).

Fuller, R.A. *et al.* (2007) ‘Psychological benefits of greenspace increase with biodiversity’, *Biology Letters*, 3(4), pp. 390–394. Available at: https://doi.org/10.1098/rsbl.2007.0149.

Gaston, K.J. and Miguel, A.S. de (2022) ‘Environmental Impacts of Artificial Light at Night’, *Annual Review of Environment and Resources*, 47(Volume 47, 2022), pp. 373–398. Available at: https://doi.org/10.1146/annurev-environ-112420-014438.

GLA Methodology Report (2024). Methodology Report. Greater London Authority.

Green Infrastructure (2024) *London City Hall*. Available at: https://www.london.gov.uk/programmes-and-strategies/environment-and-climate-change/parks-green-spaces-and-biodiversity/green-infrastructure (Accessed: 27 August 2024).

Grosvenor Estate (2022) *Valuing Nature*. Grosvenor Estate UK. Available at: https://www.grosvenor.com/getattachment/9e734d09-6566-47c7-89f6-f0ec11114b8b/Valuing-Nature_GPUK-Biodiversity-Strategy_v9.pdf (Accessed: 27 August 2024).

Haila, Y. (2000) ‘Beyond the Nature-Culture Dualism’, *Biology and Philosophy*, 15(2), pp. 155–175. Available at: https://doi.org/10.1023/A:1006625830102.

Hanski, I. (2011) ‘Habitat Loss, the Dynamics of Biodiversity, and a Perspective on Conservation’, *AMBIO*, 40(3), pp. 248–255. Available at: https://doi.org/10.1007/s13280-011-0147-3.

Harrison, C. and Davies, G. (2002) ‘Conserving biodiversity that matters: practitioners’ perspectives on brownfield development and urban nature conservation in London’, *Journal of Environmental Management*, 65(1), pp. 95–108. Available at: https://doi.org/10.1006/jema.2002.0539.

Hijmans, R.J. *et al.* (2024) ‘terra: Spatial Data Analysis’. Available at: https://cran.r-project.org/web/packages/terra/index.html (Accessed: 21 August 2024).

Hostetler, M., Allen, W. and Meurk, C. (2011) ‘Conserving urban biodiversity? Creating green infrastructure is only the first step’, *Landscape and Urban Planning*, 100(4), pp. 369–371. Available at: https://doi.org/10.1016/j.landurbplan.2011.01.011.

Hudson, L. *et al.* (2023) ‘The 2016 release of the PREDICTS database V1.1’. Natural History Museum. Available at: https://doi.org/10.5519/j4sh7e0w.

Hudson, L.N. *et al.* (2014) ‘The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts’, *Ecology and Evolution*, 4(24), pp. 4701–4735. Available at: https://doi.org/10.1002/ece3.1303.

Hudson, L.N. *et al.* (2017) ‘The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project’, *Ecology and Evolution*, 7(1), pp. 145–188. Available at: https://doi.org/10.1002/ece3.2579.

Jerome, G. *et al.* (2019) ‘A framework for assessing the quality of green infrastructure in the built environment in the UK’, *Urban Forestry & Urban Greening*, 40. Available at: https://doi.org/10.1016/j.ufug.2019.04.001.

Keesing, F. *et al.* (2010) ‘Impacts of biodiversity on the emergence and transmission of infectious diseases’, *Nature*, 468(7324), pp. 647–652. Available at: https://doi.org/10.1038/nature09575.

‘Kunming-Montreal Global Biodiversity Framework’ (2022) in. *CONFERENCE OF THE PARTIES TO THE CONVENTION ON BIOLOGICAL DIVERSITY*, Montreal, Canada: UN Environment Programme.

Lampinen, J. *et al.* (2021) ‘Acceptance of near-natural greenspace management relates to ecological and socio-cultural assigned values among European urbanites’, *Basic and Applied Ecology*, 50, pp. 119–131. Available at: https://doi.org/10.1016/j.baae.2020.10.006.

Land Cover Map 2015 (2017). Dataset Documentation. Centre for Ecology & Hydrology.

Lee, E. (2016) ‘Protected Areas, Country and Value: The Nature–Culture Tyranny of the IUCN’s Protected Area Guidelines for Indigenous Australians’, *Antipode*, 48(2), pp. 355–374. Available at: https://doi.org/10.1111/anti.12180.

Leeser, R. (2021) ‘Poverty in London 2019/20’, *London Datastore*, 28 March. Available at: https://data.london.gov.uk/blog/poverty-in-london-2019-20/ (Accessed: 28 August 2024).

Lepczyk, C.A. *et al.* (2017) ‘Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation’, *BioScience*, 67(9), pp. 799–807. Available at: https://doi.org/10.1093/biosci/bix079.

Lepczyk, C.A., Aronson, M.F. and La Sorte, F.A. (2023) ‘Cities as sanctuaries’, *Frontiers in Ecology and the Environment*, 21(5), pp. 251–259. Available at: https://doi.org/10.1002/fee.2637.

Li, X. and Zhou, Y. (2017) ‘A Stepwise Calibration of Global DMSP/OLS Stable Nighttime Light Data (1992–2013)’, *Remote Sensing*, 9(6), p. 637. Available at: https://doi.org/10.3390/rs9060637.

Lorimer, J. (2008) ‘Living Roofs and Brownfield Wildlife: Towards a Fluid Biogeography of UK Nature Conservation’, *Environment and Planning A: Economy and Space*, 40(9), pp. 2042–2060. Available at: https://doi.org/10.1068/a39261.

Losey, J.E. and Vaughan, M. (2006) ‘The Economic Value of Ecological Services Provided by Insects’, *BioScience*, 56(4), pp. 311–323. Available at: https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2.

Magle, S.B. *et al.* (2012) ‘Urban wildlife research: Past, present, and future’, *Biological Conservation*, 155, pp. 23–32. Available at: https://doi.org/10.1016/j.biocon.2012.06.018.

Maslow, A.H. (1943) *A Theory of Human Motivation*, *Classics in the History of Psychology*. Available at: https://psychclassics.yorku.ca/Maslow/motivation.htm (Accessed: 22 July 2024).

Murkin, K. *et al.* (2023) ‘Biodiversity and the Recreational Value of Green Infrastructure in England’, *Sustainability*, 15(4), p. 2915. Available at: https://doi.org/10.3390/su15042915.

Newbold, T. *et al.* (2015) ‘Global effects of land use on local terrestrial biodiversity’, *Nature*, 520(7545), pp. 45–50. Available at: https://doi.org/10.1038/nature14324.

NHBS (2022) *The NHBS Introduction to Habitats: Grassland*. Available at: https://www.nhbs.com/blog/the-nhbs-introduction-to-habitats-grassland (Accessed: 16 August 2024).

Niemelä, J. (1999a) ‘Ecology and urban planning’, *Biodiversity & Conservation*, 8(1), pp. 119–131. Available at: https://doi.org/10.1023/A:1008817325994.

Niemelä, J. (1999b) ‘Is there a need for a theory of urban ecology?’, *Urban Ecosystems*, 3, pp. 57–65. Available at: https://doi-org.libproxy.ucl.ac.uk/10.1023/A:1009595932440.

Norton, B.A., Evans, K.L. and Warren, P.H. (2016) ‘Urban Biodiversity and Landscape Ecology: Patterns, Processes and Planning’, *Current Landscape Ecology Reports*, 1(4), pp. 178–192. Available at: https://doi.org/10.1007/s40823-016-0018-5.

Otero, I. *et al.* (2020) ‘Biodiversity policy beyond economic growth’, *Conservation Letters*, 13(4), p. e12713. Available at: https://doi.org/10.1111/conl.12713.

Outhwaite, C.L. *et al.* (2022) ‘Availability and proximity of natural habitat influence cropland biodiversity in forest biomes globally’, *Global Ecology and Biogeography*, 31(8), pp. 1589–1602. Available at: https://doi.org/10.1111/geb.13532.

Parikh, G., Rawtani, D. and Khatri, N. (2021) ‘“Insects as an Indicator for Environmental Pollution”’, *Environmental Claims Journal*, 33(2), pp. 161–181. Available at: https://doi.org/10.1080/10406026.2020.1780698.

Pebesma, E. *et al.* (2024) ‘sf: Simple Features for R’. Available at: https://cran.r-project.org/web/packages/sf/index.html (Accessed: 28 August 2024).

Pickett, S.T.A. *et al.* (1997) ‘Integrated urban ecosystem research’, *Urban Ecosystems*, 1(4), pp. 183–184. Available at: https://doi.org/10.1023/A:1018579628818.

‘R Core Team’ (2024).

Richardson, K. *et al.* (2023) ‘Earth beyond six of nine planetary boundaries’, *Science Advances*, 9(37), p. eadh2458. Available at: https://doi.org/10.1126/sciadv.adh2458.

Roe, M. and Mell, I. (2013) ‘Negotiating value and priorities: evaluating the demands of green infrastructure development’, *Journal of Environmental Planning and Management*, 56(5), pp. 650–673. Available at: https://doi.org/10.1080/09640568.2012.693454.

Sánchez-Bayo, F. and Wyckhuys, K.A.G. (2019) ‘Worldwide decline of the entomofauna: A review of its drivers’, *Biological Conservation*, 232, pp. 8–27. Available at: https://doi.org/10.1016/j.biocon.2019.01.020.

Sandifer, P.A., Sutton-Grier, A.E. and Ward, B.P. (2015) ‘Exploring connections among nature, biodiversity, ecosystem services, and human health and well-being: Opportunities to enhance health and biodiversity conservation’, *Ecosystem Services*, 12, pp. 1–15. Available at: https://doi.org/10.1016/j.ecoser.2014.12.007.

Saunders, D. (2011) *Arrival City: How the Largest Migration in History is Reshaping Our World*. Windmill Books.

Scudder, G.G.E. (2017) ‘The Importance of Insects’, in *Insect Biodiversity*. John Wiley & Sons, Ltd, pp. 9–43. Available at: https://doi.org/10.1002/9781118945568.ch2.

Shabani, Farzin *et al.* (2020) ‘Invasive weed species’ threats to global biodiversity: Future scenarios of changes in the number of invasive species in a changing climate’, *Ecological Indicators*, 116, p. 106436. Available at: https://doi.org/10.1016/j.ecolind.2020.106436.

Sinnett, D. (2015) ‘Chapter 5: Green infrastructure and biodiversity in the city: principles and design’, in. Available at: https://www.elgaronline.com/edcollchap/edcoll/9781783473991/9781783473991.00011.xml (Accessed: 26 July 2024).

van der Sluijs, J.P. (2020) ‘Insect decline, an emerging global environmental risk’, *Current Opinion in Environmental Sustainability*, 46, pp. 39–42. Available at: https://doi.org/10.1016/j.cosust.2020.08.012.

Soanes, K. *et al.* (2019) ‘Correcting common misconceptions to inspire conservation action in urban environments’, *Conservation Biology*, 33(2), pp. 300–306. Available at: https://doi.org/10.1111/cobi.13193.

Spence, M.D. (1999) *Dispossessing the Wilderness: Indian Removal and the Making of the National Parks*. Oxford University Press.

Spotswood, E.N. *et al.* (2021) ‘The Biological Deserts Fallacy: Cities in Their Landscapes Contribute More than We Think to Regional Biodiversity’, *BioScience*, 71(2), pp. 148–160. Available at: https://doi.org/10.1093/biosci/biaa155.

State of Nature (2023). United Kingdom. Available at: https://stateofnature.org.uk/wp-content/uploads/2023/09/TP25999-State-of-Nature-main-report_2023_FULL-DOC-v12.pdf (Accessed: 21 August 2024).

Sultana, M., Corlatti, L. and Storch, I. (2023) ‘Are the same factors determining biodiversity in cities across different regions? Comparing drivers of urban bird richness patterns in Southern Asia vs. Western Europe’, *Urban Ecosystems*, 26(6), pp. 1545–1557. Available at: https://doi.org/10.1007/s11252-023-01404-1.

S.V. Chithra *et al.* (2015) ‘Impacts of Impervious Surfaces on the Environment’, *International Journal of Engineering Science Invention*, 4(5), pp. 27–31.

The IUCN Red List of Threatened Species (2024) *IUCN Red List of Threatened Species*. Available at: https://www.iucnredlist.org/en (Accessed: 25 April 2024).

‘Towards an Urban Renaissance’ (1999). Depatment of the Environment, Transport and the Regions.

Troudet, J. *et al.* (2017) ‘Taxonomic bias in biodiversity data and societal preferences’, *Scientific Reports*, 7(1), p. 9132. Available at: https://doi.org/10.1038/s41598-017-09084-6.

Understanding biodiversity net gain (2024) *GOV.UK*. Available at: https://www.gov.uk/guidance/understanding-biodiversity-net-gain (Accessed: 19 April 2024).

Ustaoglu, E. and Williams, B. (2017) ‘Determinants of Urban Expansion and Agricultural Land Conversion in 25 EU Countries’, *Environmental Management*, 60. Available at: https://doi.org/10.1007/s00267-017-0908-2.

Ver Hoef, J.M. and Boveng, P.L. (2007) ‘Quasi-Poisson Vs. Negative Binomial Regression: How Should We Model Overdispersed Count Data?’, *Ecology*, 88(11), pp. 2766–2772. Available at: https://doi.org/10.1890/07-0043.1.

Vickery, M. (2008) ‘Butterflies as Indicators of Climate Change’, *Science Progress*, 91(2), pp. 193–201. Available at: https://doi.org/10.3184/003685008X327927.

Wagner, D.L. (2020) ‘Insect Declines in the Anthropocene’, *Annual Review of Entomology*, 65(Volume 65, 2020), pp. 457–480. Available at: https://doi.org/10.1146/annurev-ento-011019-025151.

Werner, P. (2011) ‘The ecology of urban areas and their functions for species diversity’, *Landscape and Ecological Engineering*, 7(2), pp. 231–240. Available at: https://doi.org/10.1007/s11355-011-0153-4.

Wood, E. *et al.* (2018) ‘Not All Green Space Is Created Equal: Biodiversity Predicts Psychological Restorative Benefits From Urban Green Space’, *Frontiers in Psychology*, 9. Available at: https://www.frontiersin.org/articles/10.3389/fpsyg.2018.02320 (Accessed: 7 February 2024).

World Bank (2024) *Urban Development*, *World Bank*. Available at: https://www.worldbank.org/en/topic/urbandevelopment/overview (Accessed: 25 April 2024).

Wu, J. (2008) ‘Toward a Landscape Ecology of Cities: Beyond Buildings, Trees, and Urban Forests’, in M.M. Carreiro, Y.-C. Song, and J. Wu (eds) *Ecology, Planning, and Management of Urban Forests*. New York, NY: Springer New York, pp. 10–28. Available at: https://doi.org/10.1007/978-0-387-71425-7_2.

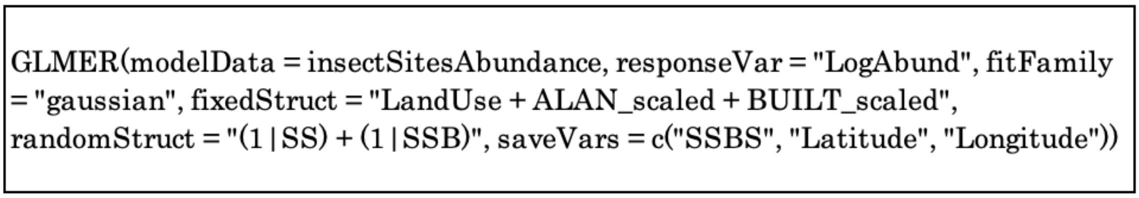
Ying, J. *et al.* (2022) ‘Green infrastructure: systematic literature review’, *Economic Research-Ekonomska Istraživanja*, 35(1), pp. 343–366. Available at: https://doi.org/10.1080/1331677X.2021.1893202.

Zaller, J.G. *et al.* (2022) ‘Pesticides in ambient air, influenced by surrounding land use and weather, pose a potential threat to biodiversity and humans’, *Science of The Total Environment*, 838, p. 156012. Available at: https://doi.org/10.1016/j.scitotenv.2022.156012.

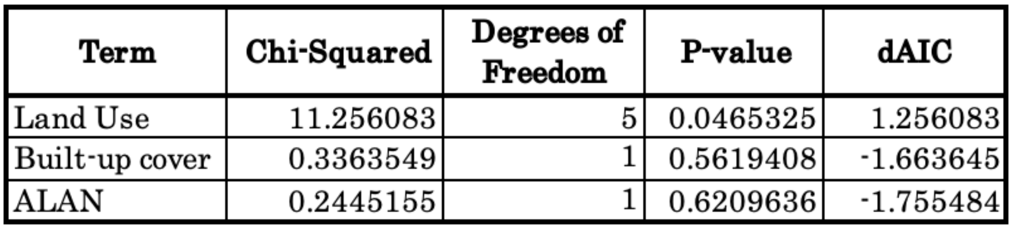
Appendix A

Final Stats: global study

Final abundance model

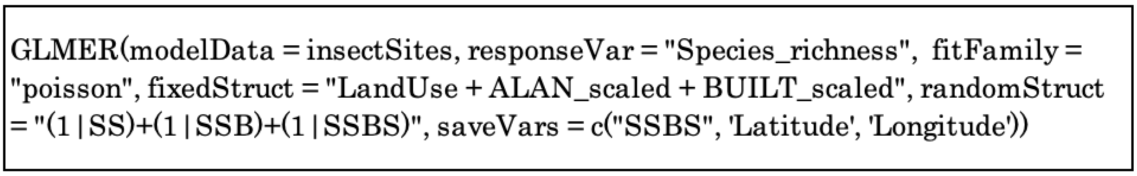


```
GLMER(modelData = insectSitesAbundance, responseVar = "LogAbund", fitFamily
= "gaussian", fixedStruct = "LandUse + ALAN_scaled + BUILT_scaled",
randomStruct = "(1 | SS) + (1 | SSB)", saveVars = c("SSBS", "Latitude", "Longitude"))
```

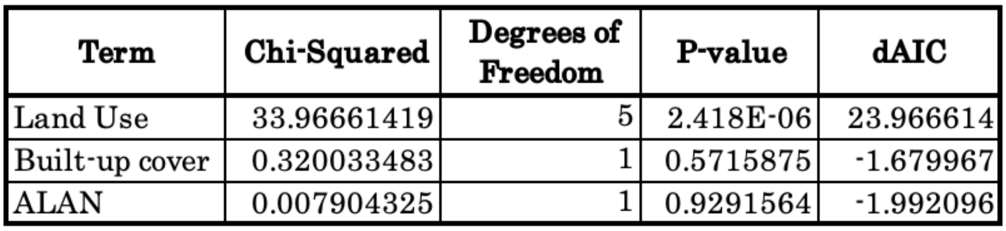


Term	Chi-Squared	Degrees of Freedom	P-value	dAIC
Land Use	11.256083	5	0.0465325	1.256083
Built-up cover	0.3363549	1	0.5619408	-1.663645
ALAN	0.2445155	1	0.6209636	-1.755484

Final species richness model



```
GLMER(modelData = insectSites, responseVar = "Species_richness",  fitFamily =
"poisson", fixedStruct = "LandUse + ALAN_scaled + BUILT_scaled", randomStruct
= "(1 | SS)+(1 | SSB)+(1 | SSBS)", saveVars = c("SSBS", 'Latitude', 'Longitude'))
```

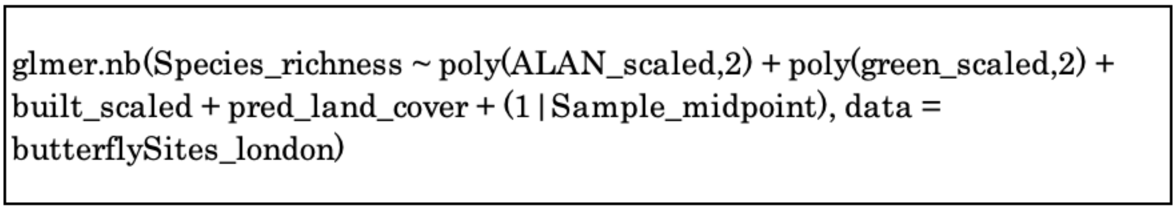


Term	Chi-Squared	Degrees of Freedom	P-value	dAIC
Land Use	33.96661419	5	2.418E-06	23.966614
Built-up cover	0.320033483	1	0.5715875	-1.679967
ALAN	0.007904325	1	0.9291564	-1.992096

Appendix B

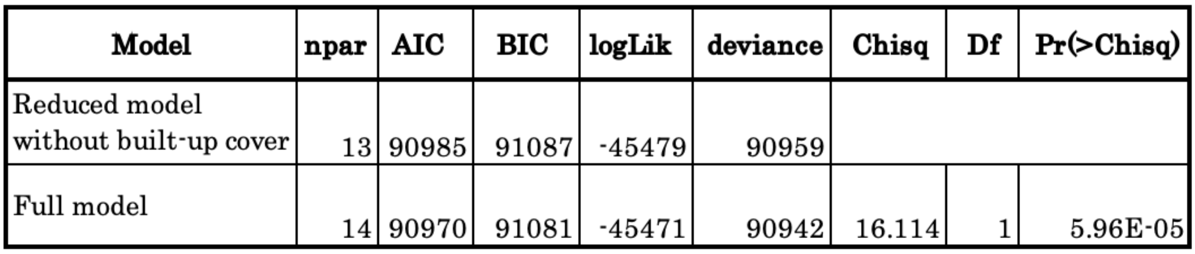
Final Stats: London study

Final model

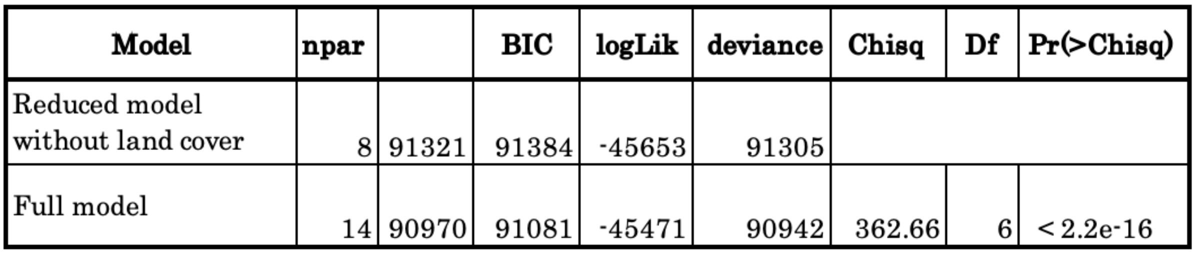


```
glmer.nb(Species_richness ~ poly(ALAN_scaled,2) + poly(green_scaled,2) +
built_scaled + pred_land_cover + (1 | Sample_midpoint), data =
butterflySites_london)
```

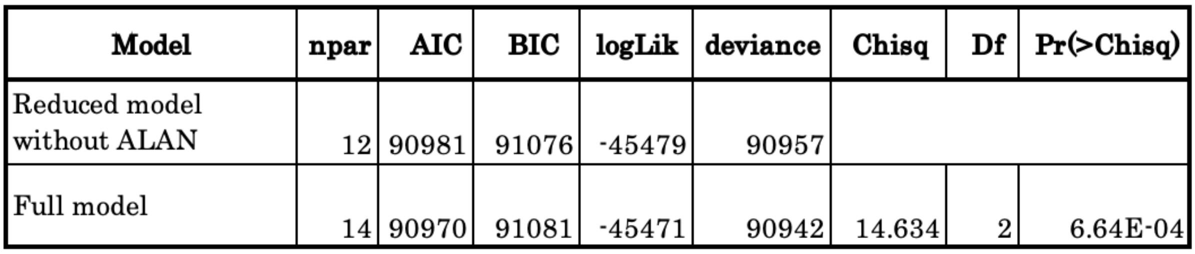
Likelihood ratio tests



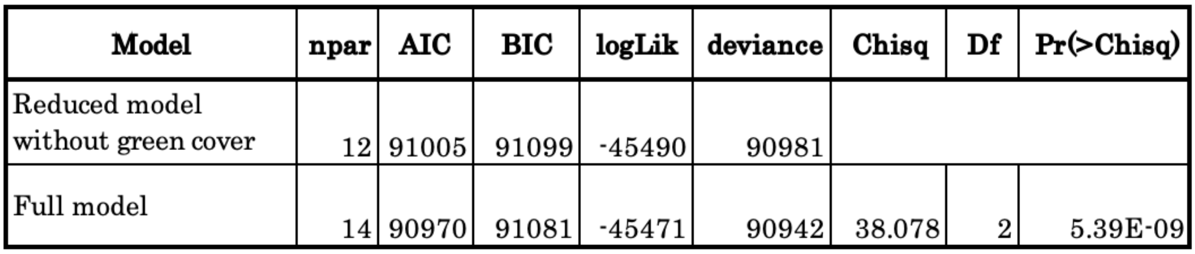
Model	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
Reduced model without built-up cover	13	90985	91087	-45479	90959			
Full model	14	90970	91081	-45471	90942	16.114	1	5.96E-05



Model	npar		BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
Reduced model without land cover	8	91321	91384	-45653	91305			
Full model	14	90970	91081	-45471	90942	362.66	6	< 2.2e-16



Model	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
Reduced model without ALAN	12	90981	91076	-45479	90957			
Full model	14	90970	91081	-45471	90942	14.634	2	6.64E-04



Model	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
Reduced model without green cover	12	91005	91099	-45490	90981			
Full model	14	90970	91081	-45471	90942	38.078	2	5.39E-09