Urbanisation and its implications for tropical urban ecosystems in Bangkok, Thailand

Phakhawat Thaweepworadej

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Abstract

Southeast Asian cities have been growing rapidly since entering the 21st century, including Bangkok where their urban agglomeration increased from 6.4 million in 2000 to 10.5 million in 2020. The regional urban growth creates marked landscape transformations, most of which are within the region's biodiversity hotspot. The consequent loss of vegetation cover tends to reduce biodiversity and ecosystem services, and thus well-being benefits. Most people live and work in urban areas, and there is growing interest in improving the quality of urban ecosystems. However, relatively limited urban ecological research has been conducted in rapidly urbanising tropical regions that can inform planning and management for biodiversity conservation and sustainable urban development. This thesis uses Bangkok as a case study of a rapidly urbanising tropical mega-city and investigates i) landscape transformation and vegetation dynamics arising from the recent urban development ii) biodiversity consequences of environmental change due to increasing urbanisation intensity, and iii) possible mitigation via nature-based solutions to improve the quality of the urban environment. The study region was defined as a 70 km × 80 km area (5,600 km^2) centred on Metropolitan Bangkok and surrounding provinces. Using classification of high resolution aerial imagery, landcover maps were generated for two recent time points (i.e. ~2004 and ~2018) to assess landscape transformation and temporal changes in vegetation dynamics along an urbanisation gradient, and distinguishing impacts of urban expansion and densification. A subset of this region was delimited as 2 km × 2 km grid cells with ≥25% impervious surface cover. Random stratification was then used to select 150 1 km × 1 km sampling grid cells along the gradient of urbanisation intensity in the urban Bangkok region. Biodiversity surveys were conducted for trees, birds, and small arboreal mammals using 50 m fixed radius survey plots located at the centre of the randomly selected cells. Equivalent surveys were conducted in the largest patches of woodland or areas of trees within each cell. Comparing biodiversity patterns along the urbanisation gradient at these different types of locations enables us to assess how retaining or creating wooded patches can help mitigate urbanisation impacts on biodiversity and ecosystem services. The Bangkok region has undergone intense urban development, resulting in a considerable loss of vegetation cover. Urban expansion and densification shows similar effects on the loss of total vegetation at the grid cell resolution, but urban growth has primarily arisen through the expansion which thus has greater impacts on vegetation dynamics. Notably, however, infill densification has substantially reduced tree cover contrasting with increasing tree cover in the rest of the region including that undergoing urban expansion. 162 tree, 142 bird, 3 squirrels, and 1 tree-shrew species were recorded across all survey sites during March to July 2018, with literature based comparisons suggesting urbanisation has substantially reduced species richness of the focal taxa relative to nearby natural settings. There is interspecific-variation in population responses of squirrels and tree-shrews to urbanisation intensity, with *Callosciurus finlaysonii* becoming more abundant in highly urbanised locations whilst other species exhibited negative responses. Species richness and ecosystem services of tree assemblages appear to be maintained across the urbanisation gradient. Avian biodiversity declines linearly along the urbanisation gradient contrasting with the unimodal patterns typically observed in temperate regions, with the rate of the decline being reduced in the woodland locations. My results highlight the differences in biodiversity responses to urbanisation arising in tropical systems compared to the much more documented temperate regions. Results from woodland survey points also highlight the potential of woodland retention to enhance biodiversity and ecosystem service provision — even in highly urbanised locations. Although further urbanisation in Bangkok will adversely impact vegetation dynamics and biodiversity, policy interventions could mitigate some of these impacts by increasing urban tree cover to benefit biodiversity and ecosystem service provision.

Keywords: urbanisation gradient, landscape transformation, tropical mega-city, urban biodiversity, ecosystem services, urban woodland

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Declaration

I, the author, confirm that the Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not been previously being presented for an award at this, or any other, university.

CHAPTER ONE

General introduction

Urbanisation is a rapid and devastating process of landscape alteration that converts natural and semi-natural areas to town and cities (Bren D'Amour, 2016; Deng *et al.*, 2015; Parris, 2016). This process drives numerous environmental changes such as air pollutions (Di Sabatino *et al.*, 2018; Silver *et al.*, 2018) and urban heat island effects (Estoque *et al.*, 2017; Lee *et al.*, 2020). Despite its economic importance and links to employment and education opportunities, the stressful urban environment adversely influences people's health and well-being (Dye, 2008; Eckert and Kohler, 2014). As most people either live or work in urban areas, there is increasing interest in mitigating these adverse impacts and improving quality of urban life, most of which focus on nature-based solutions such as availability of urban greenspace (Bertram and Rehdanz, 2015a; Krekel *et al.*, 2016; Vujcic *et al.*, 2017).

Cities are, however, not just home for people but also a wide range of other species. The environmental changes along gradients from rural to highly urbanised areas generate selection pressures on wildlife — with taxonomic groups and species exhibiting much variation in their abilities to cope with or adjust to these pressures (McKinney, 2002; Schochet *et al.*, 2016). This leads to the winner-loser situation in which large numbers of species are eliminated from urban environments (McKinney and Lockwood, 1999). Urbanisation thus drives biodiversity loss (McKinney, 2002; McKinney, 2006; Shochat *et al.*, 2010). Future urbanisation is predicted to occur disproportionately in biodiversity hotspots, especially those in tropical regions, further increasing extinction risk (Seto *et al.*, 2012; Sodhi *et al.*, 2004). Urbanisation can also reduce human-nature engagement which influences willingness to conserve nature, especially among younger people (Coldwell and Evans, 2017; Hosaka *et al.*, 2017; Soga *et al.*, 2016).

This thesis introduction first describes urbanisation trends globally and southeast Asia (the region in which my case study (Bangkok) is located). I then discuss the environmental consequences of urbanisation with a focus on wildlife responses to urban selection pressures. I then discuss mitigating these impacts by changing the management of urban greenspace and thus promoting the development of more sustainable city. Finally, I present the thesis objectives and an outline of each data chapter.

1.1 Urbanisation

This section considers the recent trends in urbanisation.

1.1.1 Global trends

Globally, more people now reside in urban areas than rural ones (United Nations, 2018). In 2007 half of the world's human population lived in urban areas for the first time and the proportion living in urban areas is predicted to reached 68.4% by 2050 (Fig. 1.1a). There is a great variation across continents in the extent to which the human population is urbanised (United Nations, 2018), with only 49.9% of the Asian and 42.5% being urbanised in Africa (Fig. 1.1b). More developed regions, such as Europe, Northern America, and Japan have had highly urbanised populations since, at least, 1950 (United Nations, 2018), whilst most less developed regions have just recently become urban urbanised (Fig. 1.1c). Income level is closely associated with the proportion of the population that is urbanised (Fig. 1.1d).

Rising urban populations is partly due to the natural growth of the existing urban population and partly to the migration of people from rural to urban areas (United Nations, 2014). In the first decade of the 21st century these two processes contributed almost equally to global urban population growth (Tacoli *et al.*, 2015). Cities tend to provide more shelter, services, transportation, and employment opportunities than rural ones (Moore *et al.*, 2003), generating an attractive force that encourages rural-to-urban migration (Annez and Buckley, 2009). Although not all migrants to cities benefit from moving to urban areas (Moore *et al.*, 2003; Zhao *et al.*, 2006), this migration is one of the factors that helps to promote innovation and creativity (Annez and Buckley, 2009), and, at the national scale, urbanisation is vital for economic growth especially in the middle-income countries (Chen *et al.*, 2014).

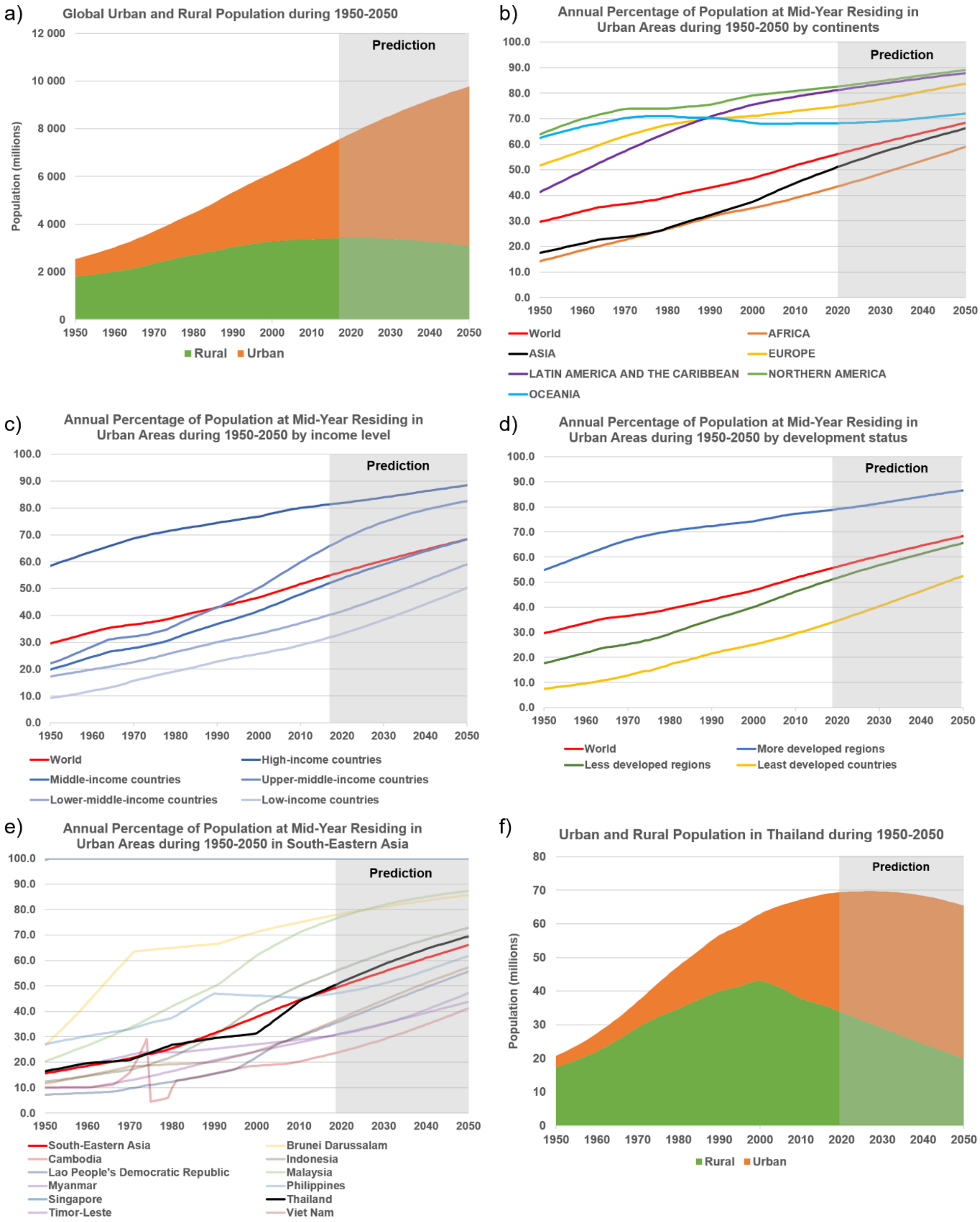


Figure 1.1: Graphic summaries of urban population during 1950 to 2018 and predicted data for 2019 to 2050 using statistics from World Urbanisation Prospects (United Nations, 2018); a) global urban and rural population, b) percentage of population residing in urban areas by continents, c) percentage of population residing in urban areas by development status, d) percentage of population residing in urban areas by income level, e) percentage of population residing in urban areas in Southeast Asia, and f) urban and rural population in Thailand.

Although migration of people from rural to the urban areas is related to the economic success of cities, the resultant urbanisation is associated with social (e.g. overcrowding, congestion, crime, etc.) and environmental problems (i.e. pollution, urban heat islands, etc.), especially in the low-income countries (Tacoli *et al.*, 2015). Conversion of rural areas to towns and cities produces numerous environmental changes within the urbanised areas, and resource consumption by urban dwellers creates a wide range of environmental impacts outside the boundaries of the urban area (Lambin *et al.*, 2001).

From 1970 to 2000 urban areas expanded twice as fast as the urban human population (Seto *et al.*, 2011). It was predicted that by 2030 more than one million km^2 of lands will potentially be transformed into urban areas, threatening approximately 9% of the area of global biodiversity hotspots (Seto *et al.*, 2012). Although urban areas are estimated merely around 3% of the global surface area, they are centres of environmental problems, including pollution and biodiversity loss (Di Sabatino *et al.*, 2018; Grimm *et al.*, 2008; Zhao *et al.*, 2006).

1.1.2 Urbanisation in developing countries and southeast Asia

Urbanisation in developing countries poses great challenges. The recent urbanisation rate in developing countries is four times higher than that experienced in developed countries (Fig. 1.2; Angel *et al.*, 2011; Chen *et al.*, 2014; Henderson, 2002; United Nation, 2014). Nearly half of global urban expansion in the first part of the 21st century is predicted to occur in Asia, the largest region in terms of land area and human population size (Seto *et al.*, 2012). Rapid economic growth, industrialisation, and globalisation are key factors driving urban growth in Asia (Schneider *et al.*, 2015). Even though Asia only reached the point where half its human population lies in cities in 2018 (United Nation, 2018), the continent contains 16 mega-cities, defined as those with over 10 million inhabitants (United Nation, 2014).

Southeast Asia is increasingly urbanised, as urban human population shifted from 198.8 million (37.9% urban) in 2000 to 320.4 million (48.9% urban) in 2018 (Fig. 1.1e, United Nations, 2018). These shifts are occurring despite a general decline in human population growth rate (United Nations, 2019). For example, total human population in Thailand is predicted to gradually decrease after reaching 70 million in 2030 (Fig. 1.1f, United Nations, 2018; United Nations, 2019). This increase in urbanisation is mainly driven by the shift from primary economic sectors (i.e. agriculture) to secondary economic sector (i.e. industry)

(ASEAN, 2017), which generated forces promoting labour migration towards cities and resultant urbanisation (Dahiya, 2014).

Rapid urbanisation in Southeast Asia is considerably influencing biodiversity loss (Sodhi *et al*., 2004; Sodhi *et al*., 2010). During 1990 to 2010, urbanisation contribute to a conversion of over 30 million hectares of natural forests in Southeast Asia (Stibig, 2014). In 2000, over 27,000 km^2 of urban area, accounting for 88% of the region's total urban land cover, were situated in biodiversity hotspots (Fig. 1.3; Güneralp and Seto, 2013), and the area of urban land occurring in hotspot is predicted to double by 2030 (Seto *et al*., 2012). Additionally, urban development in this region can interrupt avian migration along the Asian-Australasian flyway which potentially adversely affects the nearly 500 migratory bird species that use this pathway (Fig. 1.4; BirdLife, 2015). As southeast Asia has a high level of species endemism (Sodhi *et al*., 2004), urbanisation in this region may significantly increase biodiversity loss at the global scale.

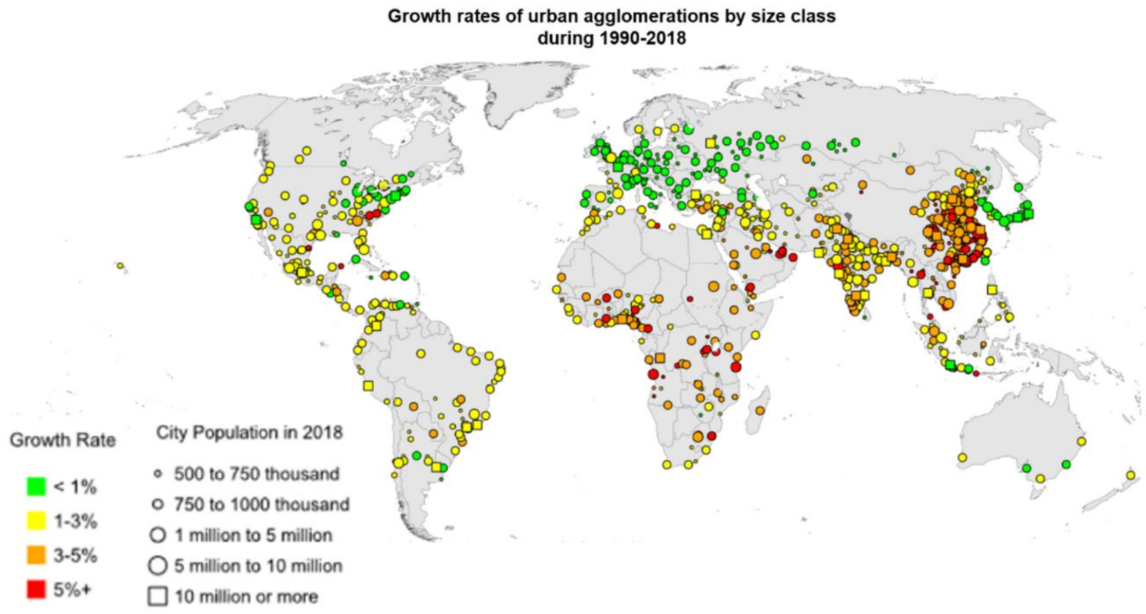


Figure 1.2: World map shows growth rates of urban agglomerations during 1990–2018 among cities in developing regions, especially in Asia and Africa, were higher than those in more developed regions in Europe and North America (taken from United Nations (2018)). Circles represent cities with a human population of 0.5 to 10 million, with circle size varying by population size, and squares represent cities with ≥10 million human population. Colours represent % growth rate (green represent the lowest growth rate (<1%) and red represents highest growth rate of ≥5%).

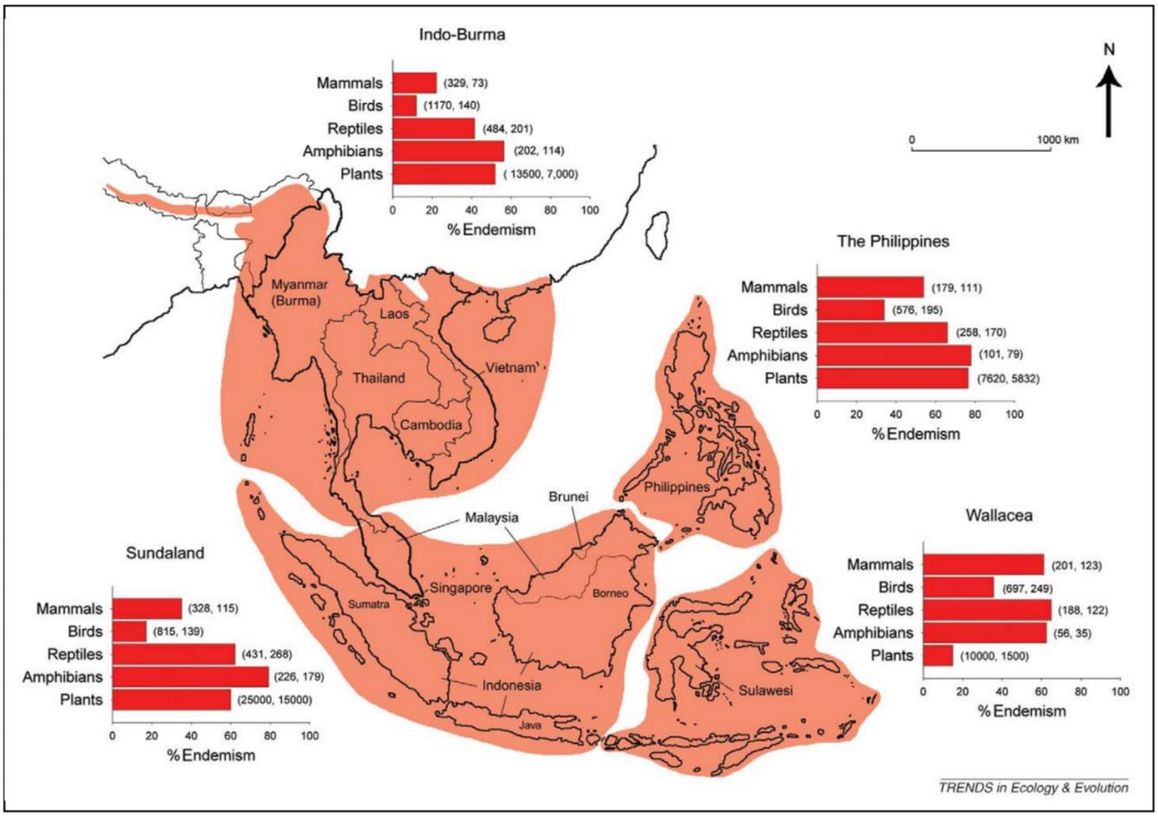
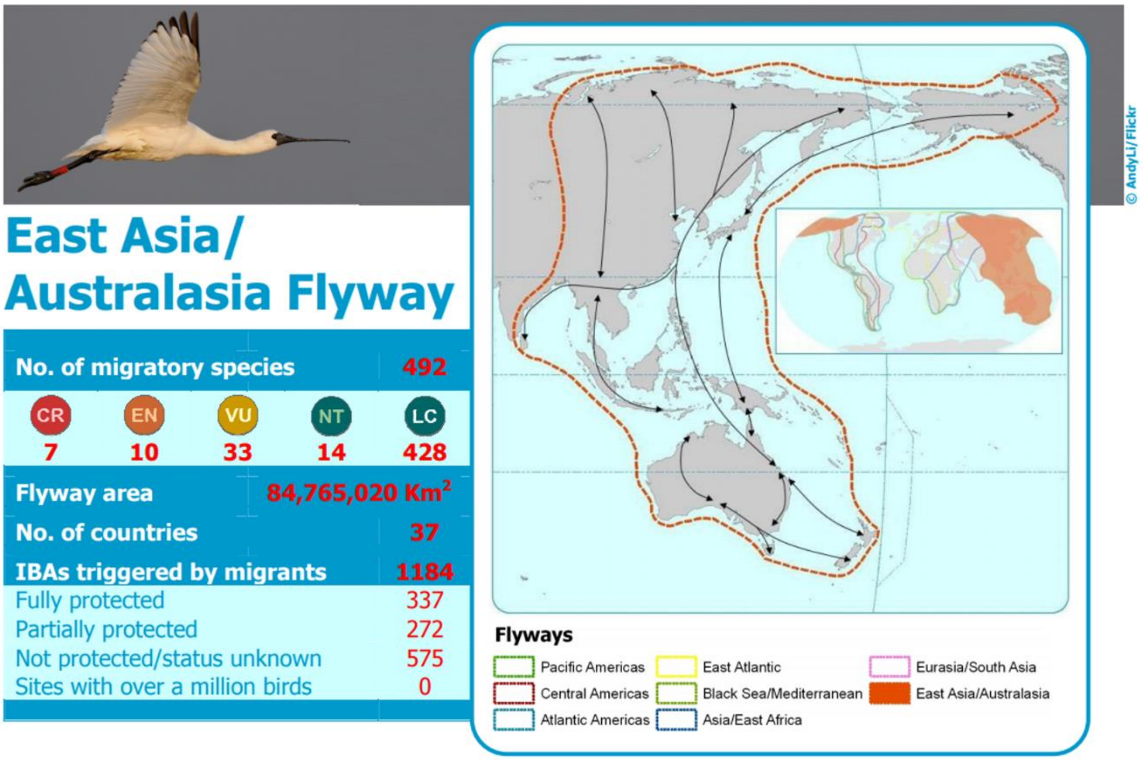


Figure 1.3: Southeast Asia map (taken from Sodhi *et al*. (2004)) shows the region's four biodiversity hotspots with bar charts indicates high proportion of species endemism.



No. of migratory species	492
CR 7	EN 10
VU 33	NT 14
LC 428	
Flyway area	84,765,020 Km^2
No. of countries	37
IBAs triggered by migrants	1184
Fully protected	337
Partially protected	272
Not protected/status unknown	575
Sites with over a million birds	0

Figure 1.4: Map illustrates bird migratory route along the East Asia/Australasian flyway with general information on number of species and International's Important Bird Area (IBA). Figure was reproduced from BirdLife (2015).

1.2 Environmental changes and selection pressures along the urbanisation gradient

Urbanisation intensity is often defined by the proportion of impervious surface cover, i.e. building, road, paved ground (Arnold Jr and Gibbons, 1996; Moll *et al.*, 2019; Parris, 2016), which is particularly concentrated in commercial and industrial areas (Alberti, 2005; Moll *et al.*, 2019; Parris, 2016). By definition, impervious surface prevents infiltration of water into soil and thus influences storm water runoff (Arnold Jr and Gibbons, 2016; Fig. 1.5). Physical properties of impervious surface also considerably contribute to numerous climatic changes in the urban areas, such as absorbing and reflecting solar radiation, reflecting noise, interrupting nutrient cycle, etc. (Grimm *et al.*, 2008; Parris, 2016; Raciti *et al.*, 2012). Moreover, impervious surface also directly impacts urban vegetation by preventing root penetration and interrupting belowground biological activities (Bartens *et al.*, 2009; Viswaqnathan *et al.*, 2011). Consequently, environmental conditions at high levels of urbanisation intensity are heavily impacted by extensive coverage of impervious surfaces. This section discusses the selection pressures due to environmental changes along the urbanisation gradient, with the emphasis on their implications for urban wildlife.

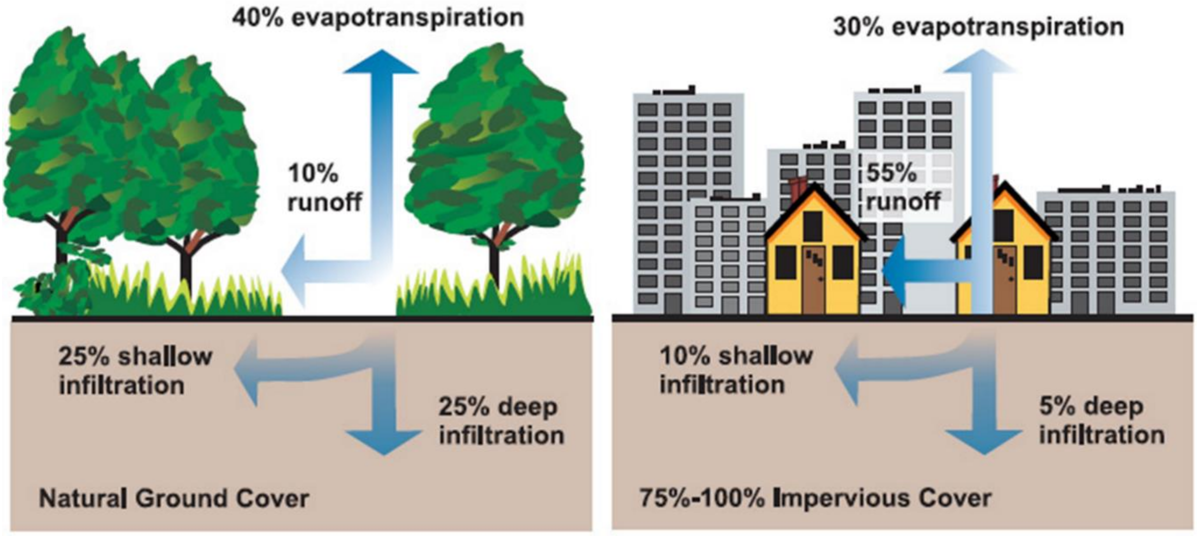


Figure 1.5: Impacts of impervious surface on surface water runoff, infiltration, and evapotranspiration comparing between natural process and urban environment. Figure taken from Federal Interagency Stream Restoration Working Group (1998).

1.2.1 Habitat loss, alteration, and fragmentation

When cities grow, most of the original habitats are degraded and transformed into urban land, whilst remained areas are mostly isolated as small habitat patches (McDonald *et al.*, 2009) — these impacts increase with the magnitude of urbanisation intensity (Du *et al.*, 2019; Yao *et al.*, 2019). Loss of original habitat directly threatens 33% of species of global conservation concern (i.e. IUCN red list), profoundly driving species extinction risk (Bright and Morris; 1995; Gurevitch and Padilla, 2004; Markovchick-Nicholls et al., 2008; Shanahan *et al.*, 2014). For example, loss of almost the entire original forest covers in Singapore has contributed to an estimated loss of approximately 28% of native plant species originally present (Duncan *et al.*, 2011).

However, in some locations, the loss of original vegetation is partially compensated by newly created urban greenspace (Pincetl *et al.*, 2013; Wolch *et al.*, 2014), such habitat can have high plant diversity of plant due to selection and introduction by people (Porter *et al.*, 2001; Whitney and Adams, 1980). This creates novel ecosystems that typically contain a high proportion of non-native species (Morgenroth *et al.*, 2016; Schlaepfer *et al.*, 2020). Urban systems are thus often viewed as highly managed, complex and novel ecosystems (Savard *et al.*, 2000).

Habitat fragmentation, as a consequence of habitat loss, is the process of breaking continuous original habitat into several small habitat patches separating by different types of landscape matrix. The magnitude of habitat fragmentation varies with urbanisation intensity, ranging from highly fragmented in the urban core to more continuous patches in largely rural areas with negligible amounts of human settlement (Tian *et al.*, 2011). Habitat fragmentation has profound negative impacts on wildlife. Habitat specialists, such as forest-dependent species, are more sensitive to the impacts of habitat fragmentation as they are less able to disperse through the matrix generating functional isolation of populations in small patches that are often smaller than required for long-term viability (Watson *et al.*, 2005).

Populations confined to fragmented habitat patches are influenced by isolation, with movements between islands of suitable habitats adversely impacted by human transportation infrastructures, especially roads which are highly associated with the magnitude of urbanisation intensity (Kent *et al.*, 2021). Roadkill causes approximately up to

340 million bird mortalities annually in the USA (Loss *et al*., 2014). Habitat fragmentation and isolation reduce effective population size and disrupt connectivity between population, leading to a loss of genetic diversity (Dixo *et al*., 2009). Furthermore, impaired animal movement across the isolated habitats affects plant-animal interaction, such as pollination (Fortel *et al*., 2014; Hermansen *et al*., 2017) and seed dispersal (Gelmi-Candusso and Hämäläinen, 2019; Niu *et al*., 2018).

1.2.2 Pollution

Cities are centres for pollution and environmental problems which are generally lowering the quality of urban life (Grimm *et al*., 2008; He *et al*., 2017; van Kamp *et al*., 2003). This section provides examples of these major types of urban pollution (i.e. urban heat island, air pollution, noise pollution, and light pollution), and its implications for urban dwellers, human and wildlife. To mitigate urban pollution, urban planners, policy makers, and researchers have been assessing potential approaches to improve urban greenspace management as potential nature-based solutions (see section 1.5.1).

Urban heat island

Urban heat island effect, the event that ambient temperature in the city is higher than the outer surrounding areas, is considered as thermal pollution (Memon *et al*., 2009; Oke, 1982). Rising temperature in the urban areas is mainly characterised by the conversion of permeable surface to impervious surface (e.g. roads, building, paved ground, etc.) which absorb solar radiation and subsequently release heat into the urban environment (Morabito *et al*., 2021). In addition to solar radiation, heat generated by human activities (e.g. automobiles, air-conditioners, etc.) also greatly contributes to urban heat island effects (Parris, 2016; Phelan *et al*., 2015). Globally there is growing concern on the effects of urban heat island, as part of global climate change crisis, particularly across the Asian megacities (Chayapong and Dasananda, 2013; Estoque *et al*., 2017; Lee *et al*., 2020; Yue *et al*., 2019)

Urban heat island effects critically impact human health by enhancing heat waves within cities in which can potentially increase mortality rate (Basu, 2009; Tan *et al*., 2010). They also strongly impact the ecology of urban environment. In temperate regions vegetation phenology is shifted by urban heat islands, with extended growing seasons and shifting flowering periods (Abu-Asab *et al*., 2001; Bechtel and Schmidt, 2011; Primack *et al*., 2009;

Zhenghong *et al*., 2009; Zipper *et al*., 2016). Conversely, urban heat island effect in the tropical city tend to shorten plant growing seasons (Kabano *et al*., 2021). These phenological shifts could disrupt biotic interactions between plants and their invertebrate consumers, generating impacts on higher order consumers (e.g. avian insectivores) through trophic mismatches (Chick *et al*., 2019), although this is not a universal pattern (Seress *et al*., 2018).

Migratory birds adjust to urban heat island effect by advancing their first arrival date in the urban habitat (Tryjanowski *et al*., 2013) or not migrating (Bonnet-Lebrun *et al*., 2020). Thermal stress adversely impacts to reproductive success and survival of species in the urban environment (Diamond *et al*., 2018; Hall and Warner, 2018), in which tolerance to thermal stress vary by species (Battles and Kolbe, 2018; Diamond *et al*., 2018; Hall and Warner, 2019; Kaiser *et al*., 2016; Martin *et al*., 2019). Animals, especially ectotherms such as invertebrates, in the warm environment (i.e. urban environment) may adapt and subsequently evolve to tolerate high temperature, causing variation in thermal tolerance along the urbanisation gradient (Angilletta *et al*., 2007). Species having less ability to tolerate thermal stress are thus likely to be eliminated from the urban environment, leading to a local extinction (Baur and Buar, 1993).

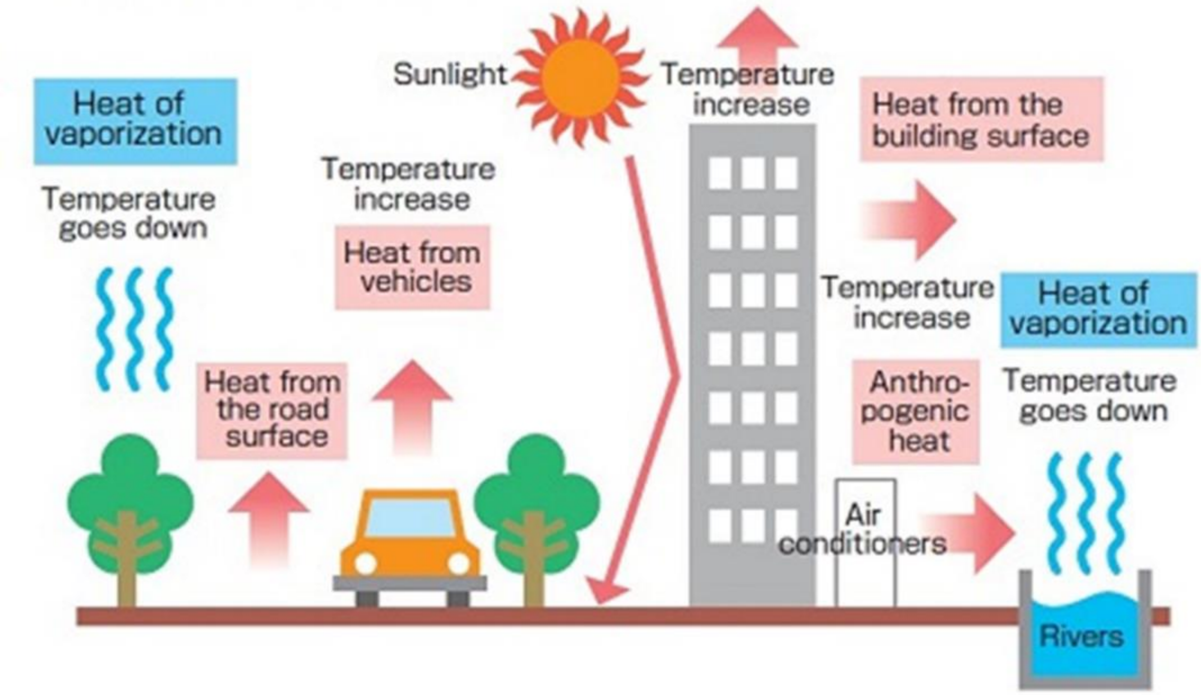


Figure 1.6: Sources of urban heat island and cooling effects from blue (i.e. water surface) and green (i.e. vegetation) structures. Figure was taken from Osaka City Environment Bureau.

Air pollution

Globally, air pollution is one of the most marked urban environmental problems (He *et al.*, 2002; Hopke *et al.*, 2008; Wakamatsu *et al.*, 2013). Air pollution comprises a diversity of pollutants including ozone (O_3), carbon monoxide (CO), carbon dioxide (CO_2), nitrogen oxides (NO_x), sulphur dioxide (SO_2), particulate matters (i.e. $PM_{2.5}$ and PM_{10}), and heavy metals (McDonald, 2012). The key sources if these pollutants are burning fossil and other fuels for transportation, industrial and domestic purposes — although construction and transportation are important additional sources of particulate matter (McDonald, 2012; Parris, 2016; Stone, 2008). Whilst urban air quality in more developed regions such as Europe has been substantially improved (Guerreiro *et al.*, 2014), air pollution has been increasing rapidly in developing Asian countries (Vadrevu *et al.*, 2017; Zhang and Day, 2015), for example, the annual average of $PM_{2.5}$ in Bangkok (Thailand) increased from 33 $\mu g/m^3$ in 2011 to 36 $\mu g/m^3$ in 2014 which were consistently much higher than the annual average standard of 10 $\mu g/m^3$ by the WHO (Langkulsen *et al.*, 2017).

Urban air pollution is a major threat to human health (Guan *et al.*, 2016; Kampa and Castanas, 2008; Kim et al., 2018; Yang *et al.*, 2020) and can generate with significant economic loss (Maji *et al.*, 2018; Xie *et al.*, 2019; Yin *et al.*, 2021). There is also clear evidence indicating the adverse impacts of air pollution on birds (North *et al.*, 2017; Salmón *et al.*, 2018; Sanderfoot and Holloway, 2017), in which it may vary by species and mode of foraging (Eeva and Lehikoinen, 1995; Sepp *et al.*, 2019). Several studies also indicated the direct impacts of urban air pollution on respiratory systems or reproductive success such as reducing quality of eggshell and nestling body condition in birds (Eeva and Lehikoinen, 1995; Eeva *et al.*, 1998; Morrissey *et al.*, 2014). Moreover, indirect impacts, such as altering habitat conditions and reducing food resources, were also documented (Liang *et al.*, 2020). Consequently, adverse impacts of air pollution may also negatively influence density and diversity of urban wildlife (Sanderfoot and Holloway, 2017), in which it may plays significant role in driving urban biodiversity loss (Lovett *et al.*, 2009).

Noise pollution

Noisy environments impact people and wildlife. Birds begin to respond to noise pollution at the levels of approximately 40dB (Shannon *et al.*, 2016) and noise levels above 53dB will begin to have adverse human health impacts (WHO, 2018). There are various sources of noise pollution occurring in the urban environment, but it is mainly associated with transportation, especially road traffic (Slabbekoorn, 2013; Shannon *et al*., 2016). Noise created from human activities changes the acoustic environment and affects wildlife mainly by interrupting their communication, such as, defending territory, mate attraction, alarm call, etc. Noisy areas may increase perceived predation risk by interfering with the detection of predators which results in an increasing vigilance rates and reduced feeding rates (Merrall and Evans, 2020). Low pitched anthropogenic noise tends to overlaps in frequency range with avian vocalisations (Nemeth *et al*., 2013). Song birds thus adjust to the presence of noise by levelling pitch frequency, amplitude, or avoiding the peak period of noise (Buxton *et al*., 2020; Cardoso and Atwell, 2011; Fuller *et al*., 2007; Parris and Schneider, 2009), whilst tolerance to anthropogenic noise varies among species (Buxton *et al*., 2020; Patón *et al*., 2012), in which some species appear to be insensitive to noise pollution (Angelier *et al*., 2016). Inter-specific variation in the sensitivity to anthropogenic noise may negatively influence abundance and species richness of urban birds (Barbosa *et al*., 2020; Perillo *et al*., 2017). However, some studies in the temperate cities have found a lack of such inter-specific variation in urban avian communities (e.g. Merrall and Evans, 2020).

Light pollution

At night, towns and cities are characterised by the presence of artificial light, such as building lights and streetlights (Longcore and Rich, 2004). Artificial light in the cities drives phenological changes in urban plants (Škvareninová *et al*., 2017; Ffrench-Constant *et al*., 2016), and consequently influences plant-insect interaction (Bennie *et al*., 2015). Artificial light at night considerably influences circadian rhythms, physiology, and behaviour of nocturnal insects, driving population declines (Boyes *et al*., 2021; Owens *et al*., 2020). Conversely, artificial light also provides additional foraging time for diurnal species, especially predators thus potentially shifting trophic interactions (Gaston *et al*. 2013; Longcore and Rich 2004; Schoeman, 2015).

Light pollution can also interrupt orientation in migratory species (La Sorte *et al*., 2017). Migratory birds are attracted to the night-time lights which tends to deplete more energy and migrating time (La Sorte *et al*., 2017). Disorient causing by artificial light at night during the migration is critical to life primarily from being exhausting (Loss *et al*., 2015; Spoelstra and

Visser, 2014). Moreover, whilst artificial light at night from urban buildings tends to attract migratory bird and lower their altitude (Watson *et al.*, 2016), it also induces high chance of building collisions, in which it contributes to high avian mortality rates in the United States (Loss *et al.*, 2014).

1.2.3 Biotic interactions

Urbanisation drives changes in the way species interact with each other. This section underlines changes in interspecific interactions in urban ecosystems including resource competition, predation pressures, and diseases transmission. Additionally, the impacts of invasive species are also described in this section as biological invasion.

Interspecific competition

Interspecific competition plays a significant role in shaping diversity and community structures in urban areas (Kath *et al.*, 2009; Martin and Bonier, 2018). Whilst competition between species often occurs when species with similar niche are living in the same area (Di Santo *et al.*, 2017), predictable availability of fundamental resources in the urban environment could increase competition between species by favouring generalist species that exploit the same niche as each other (Marzluff, 2001; Shochat, 2004; Shochat *et al.*, 2010).

Whilst in urban areas there is generally higher competition for resources, such as foods (Bonnington *et al.*, 2014; Galbraith *et al.*, 2015), nesting sites (Broughton, 2020; Charter *et al.*, 2016), and territory (Minias and Janiszewski, 2016) compared to other non-urban habitats (Shochat *et al.*, 2010), competitive abilities, such as size, aggression, boldness, are species-specific (Galbraith *et al.*, 2017; Shochat, 2004). Moreover, in the human-dominated urban environment, superior competitive species are often restricted to a small number of species that are more tolerant of human disturbance and well adapted to the use human subsidised resources (McKinney, 2002). Species dominating at resources competition in the urban habitats are often non-native species (Borden and Flory, 2021; Galbraith *et al.*, 2017; Shochat *et al.*, 2010), there are, however, evidences that native species could also dominate in an urban area (Haythorpe et al., 2004). Only a few number of dominant species tends to displace other subordinate species, mostly native species, through competitive exclusion (Martin and Bonier, 2018), for example, dominance of non-native house sparrow *Passer domesticus* and spotted dove *Streptopelia chinensis* at bird feeders in New Zealand potentially reduce diversity of native urban avifauna (Galbraith *et al.*, 2017). Consequently, interspecific competition can thus lead to biotic homogenisation and local extinction (Crooks *et al*., 2004; Marzluff, 2001; McKinney and Lockwood, 1999).

Predation

Native predators tend to occur at lower densities in urbanised landscapes than more urbanised ones (Møller, 2012), leading to increased densities of some urban species (McKinney, 2002; Chace and Walsh, 2006). However, urban environments also have high densities of human commensal predators, such as cats *Felis canis* (see Loss and Marra, 2017) and dogs *Canis lupus familiaris* (see Doherty *et al*., 2017), that can greatly impact urban biodiversity. Cats are one of the most common companion animals and can cause profound loss of urban biodiversity. In China free-ranging cats are estimated to predate annually between 2.7–5.5 million birds and 3.6–9.89 million mammals (Li *et al*., 2021), and whilst most of the evidence is focused on westernised temperate regions some still regard the evidence for large scale population impacts to be equivocal (Baker *et al*., 2005; Baker *et al*., 2008; Loss and Marra, 2017; Santiago-Alarcon and Delgado, 2017; Woods *et al*., 2003). Similarly, despite far less attention than the impacts from domestic cats, domestic dogs contribute to extinctions of 11 vertebrate species and potentially threatened to nearly 200 threatened vertebrate species (Doherty *et al*., 2017).

Disease transmission

Changes in physical and biological attributes of the urban environment can increase transmission of infectious diseases to both people and wildlife (Bradley and Altizer, 2006; Mackenstedt *et al*., 2015; Young *et al*., 2017). This is partly due to higher densities of a smaller number of species in urban areas, as predicted by the 'dilution effect hypothesis' (Dictchkoff *et al*., 2006; Schmidt and Ostfeld, 2001; Shochat *et al*., 2006). High densities are compounded by concentration of individuals at spatially clustered resources, such as birds concentrating at supplementary feeding stations and bird baths (Parson *et al*., 2006, Cleary *et al*., 2016). Non-native hosts that are highly abundant in the urban environment can introduce novel pathogens and transmitted to the native species (Tompkins *et al*., 2002). Moreover, increasing human-wildlife contact within the urban areas, particularly for some urban exploiter species, tend to increase pathogen transmission to human and diseases outbreak

(Blasdell *et al*., 2019; Desvars-Larrive *et al*., 2020; Rothenburger *et al*., 2017). Conversely, risks of disease and parasitic infections can also be reduced in the urbanised habitats due to lower density and diversity of insect vectors of pathogens (Evans *et al*., 2009; Santiago-Alarcon *et al*., 2020).

Invasive species

Biological invasion is one of the most critical anthropogenic impacts on biodiversity (Shochat *et al*., 2010). Humans deliberately and accidentally facilitate the transport, introduction, and establishment of non-native species to urban environment (Bossenbroek *et al*., 2001; Lockwood *et al*., 2005; McKinney, 2008). Consequently, urban flora and fauna are typically considered as hotspot for non-native invasive species (Aronson *et al*, 2015; Borden and Flory, 2021; Francis and Chadwick, 2015).

Globally, invasive species are one of the major drivers of native biodiversity loss and species extinction risks (Clavero and Garcia-Berthou, 2005; Mollot *et al*., 2017), threatening over 900 species of conservation concern on the IUCN red lists (Gurevitch and Padilla, 2004). The adverse impacts of invasive species can occur in various forms of species interaction, such as, competition (e.g. Davis, 2003; Kath *et al*., 2009), invasive predator (e.g. Davis, 2003; Loss *et al*., 2015), and diseases transmission (e.g. Blanvillain *et al*., 2021; Gozzi *et al*., 2013; Wells *et al*., 2014). However, it is worth noting that not all non-native species become invasive and have a significant adverse impacts (Davis *et al*., 2011), and biological invasion can have wide-ranging impacts on urban ecosystem including supporting native biodiversity (Davis, 2011; Hitchmough, 2011; Rodriguez, 2006; Schlaepfer *et al*., 2020). There is growing evidence suggesting that non-native trees can provide substantial ecosystem services (Almas and Conway, 2016; Castro-Díez *et al*., 2019) which challenge urban planning decision that have traditionally prioritised native vegetation.

1.2.4 Human activities

Without doubt, presence of humans greatly impacts all other species (Gaston *et al*., 2003), especially in the urban areas where they are designed, created, and dominated by humans (Parris, 2016). Generally, animals consider human beings as potential predators and respond by avoiding people or increasing vigilance when close to people (Gill *et al*., 1996; Shanahan *et al*., 2011). There is however much inter-specific variation in these responses (Fernandez-

Juricic and Jokimaki, 2001; McGiffin *et al*., 2013), with some species likely to avoid even a very low level of human disturbance, whilst others may tolerate extremely close response. Due to this inter-specific variation human disturbance can alter how species interact with each other in urban environment, e.g. human disturbance along roads may reduce rates of avian nest predation as nest predators are more sensitive to disturbance than their prey (Gering and Blair, 1999; Pescador and Peris, 2007). Some previous work has used spatial variation in human disturbance to conduct observational studies suggesting that this disturbance is an important determinant of the composition of urban bird assemblages (Ortega-Álvarez and MacGregor-Fors, 2009; MacGregor-Fors and Schondube; 2011). Reduction of human activities during COVID-19 pandemic lockdowns have enabled these suggestions to be confirmed experimentally (Driessen, 2021; Manenti *et al*., 2020).

Human resource provision can alter wildlife behaviour and community structure. Supplementary food resources in urban areas are provided intentionally (wildlife feeding: Evans *et al*., 2011; Fuller *et al*., 2008) and accidentally (e.g. rubbish and food waste: Contesse *et al*., 2004; Smith an Carlile, 1993). Human planting decisions in domestic gardens, parks and along roads also determines food resources for wildlife (Corlett, 2005; Frankie *et al*., 2019; Parris, 2016). Feeding birds in parks and gardens is one of the most common recreational practises that bring human together with nature (Cox and Gaston, 2016; Fuller *et al*., 2008) further delivering educational benefits (Beck *et al*., 2001).

Supplementary feedings in the urban areas can support an increase in bird abundance (Evans *et al*., 2011; Fuller *et al*., 2008; Jones and Reynolds, 2008) and enhance survival during the winter season which natural food resources are shorten (Robb *et al*., 2008). However, in relation to a high level of competition and low diversity of food type, species benefiting from supplementary feeding in urban areas tend to be species that have high levels of boldness, aggression, and tolerance of human disturbance (Evans *et al*., 2010; Lowry *et al*., 2013), potentially leading to human-wildlife conflicts (Savard *et al*., 2000). In contrary, resource provision by human can also have adverse impacts on wildlife by increasing predation risks (Hanmer *et al*., 2017), enhancing inter-specific competition (Bonnington *et al*., 2014), increasing diseases infection risks (Moyers *et al*., 2018; Schaper *et al*., 2021), and provision of low quality supplementary foods that adversely impacts reproductive success (Plummer *et al*., 2013).

1.3 Wildlife responses to the effects of urbanisation

In general, urban selection pressures drive biological changes in wildlife, including their behaviour (Lowry *et al*., 2013; McGiffin *et al*., 2013; Miranda, 2017; Uchida *et al*., 2019), morphology (Banaszak-Cibicka *et al*., 2018; Liker *et al*., 2008), and physiology (Costantini *et al*., 2014; Hall and Warner, 2018)**.** Ultimately these changes determine how population structure varies with urbanisation (Prange *et al*., 2003; Rodewald and Gehrt, 2014), with marked inter-specific variation in these responses (Gomes *et al*., 2011; McKinney, 2002).

Species that are cope well with the urban environment are often termed as 'synurbic' or 'synanthropic' species (Francis and Chadwick, 2012; Johnston, 2001; Luniak, 2004; Parker and Nilon, 2012; Shochat *et al*., 2010), or 'urban exploiter' (Blair, 1996; McKinney, 2002). Such species, contrast with 'urban avoiders' and 'urban adapters'.

Urban avoiders are sensitive to the presence of human and habitat disturbance (McKinney, 2002), and tend to avoid human disturbed habitats (i.e. urban areas). Large mammals and predators, especially those that are in the higher trophic levels, are more likely to be urban avoider (McKinney, 2002; Møller, 2012). Most of these are also specialist species that tend to rely on specific natural resources and habitats (Johnston, 2001), and the abundance and diversity of urban avoider tend to decrease when urbanisation intensity increases (Fig. 1.7).

Urban adapters are species that tend to find insufficient resources in highly urbanised locations but that also find relatively low abundance of their preferred resources in very rural areas. This may be due to adverse ecological impacts of agricultural intensification or because the species are adapted to edge habitats and thus their preferred resources are scarce in highly forested landscape (Fischer *et al*., 2014; Bateman and Fleming, 2012). Urban adapters thus have highest population densities in suburban areas or at the interface between urbanised and natural habitats, where levels of human disturbance are moderated (Fig. 1.7), human subsidised resources are provided, and natural predators are scarcer (Callaghan *et al*., 2020; McKinney, 2002; McKinney, 2006; Møller, 2012).

Urban exploiters are species that adapt well to utilise human subsidies, but they differ from urban adapters as they are almost completely rely on it (McKinney, 2002). These species are highly tolerant of human disturbance and the extreme environmental conditions present in cities (Banks and Smith, 2015). Mechanisms underlining this adaptation may include behavioural traits (Evans *et al.*, 2011; Møller, 2009), such as boldness (Gravolin *et al.*, 2014; Vines and Lill, 2016), and degree of sociality (Kark *et al.*, 2006) and wide range of dietary niches (Palacio, 2020). The population densities of urban exploiters thus peak at very high urbanisation intensities (Fig 1.7; Blair, 1996; McKinney, 2002). Consequently, urban exploiters can become pests in urban areas, examples include feral pigeon *Columba livia* (Gendall *et al.*, 2015) and brown rat *Rattus norvegicus* (Desvars-Larrive *et al.*, 2020; Rothenburger *et al.*, 2017). Even urban exploiters may, however, be vulnerable to declining environmental conditions in urban areas as evidenced by marked declines in urban house sparrow *Passer domesticus* populations in Europe (Angelier *et al.*, 2016; Mohring *et al.*, 2021). Globally, only a very small proportion of species are urban exploiter, many of which are invasive non-natives in many of the urban areas in which they occur. Such distributions arise as across the globe cities tend to have very similar environmental condition (McKinney, 2006), and these species contribute to the biotic homogenisation in the urban habitats (McKinney and Lockwood, 1999).

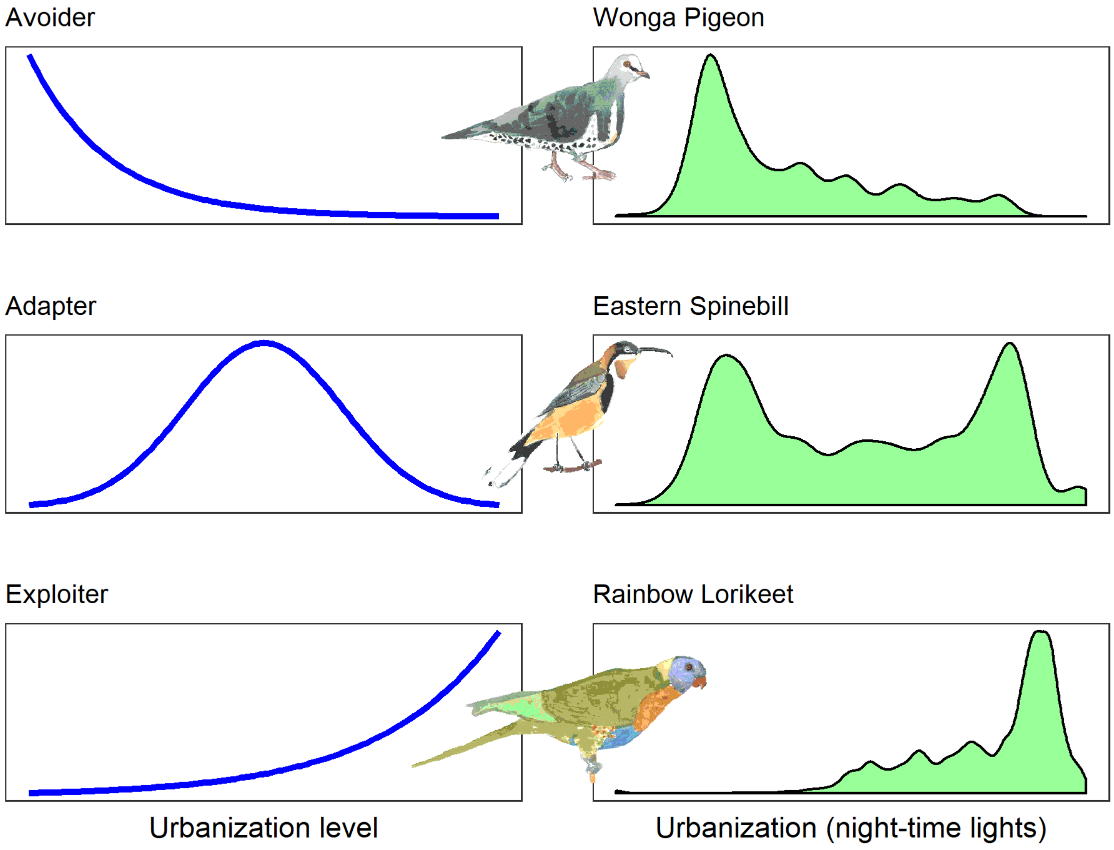


Figure 1.7: Population response of urban avoider, urban adapter, and urban exploiter along the urbanisation gradient using examples from the Australian avifauna (taken from Callaghan *et al.* (2020)).

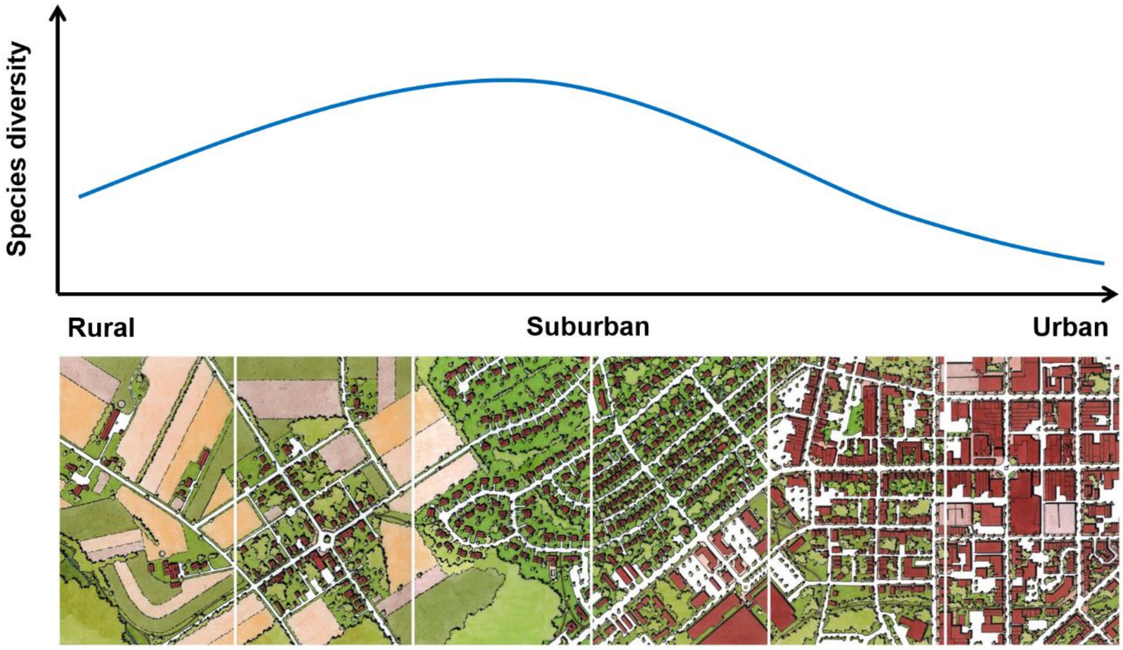


Figure 1.8: Species diversity tends to peak at the intermediate levels of urbanisation intensity, but most such studies have been conducted in temperate regions (modified from Luck and Smallbone (2010) and Lancaster county planning commission (December 13, 2012)).

Along the rural-to-urban gradient, it is clear that highly urbanised areas have the lowest number of species (Lee *et al*., 2021; McKinney, 2006), but the intensity of urbanisation at which species richness peaks is still somewhat unclear. Many studies from temperate regions often report a unimodal pattern of species richness along the urbanisation gradient (Fig. 1.8), with the peak occurring at intermediate level of urbanisation intensity — although this varies with taxonomic group and the spatial scale at which urbanisation is defined (Crooks *et al*., 2004; Porter *et al*., 2001; Vignoli *et al*., 2013). These patterns are probably partially generated by high habitat diversity that enables relatively large numbers of generalist urban adapter species to co-occur, and compensates (in terms of number of locally occurring species) for the exclusion of urban avoiders (Blair & Johnson, 2008; Mckinney, 2002; Tratalos *et al*., 2007). However, it is still unclear if such patterns also arise in the tropical region. They may not do so if tropical assemblages comprise a greater proportion of specialists (which is sometimes thought to be the case — although this is debated), which are less likely to be able to tolerate even moderate levels of urbanisation. Human planting and other management decisions may also generate divergent patterns in habitat diversity along the urban-rural gradient in tropical and temperate regions. Given the current rapid urbanisation of tropical region (Seto *et al*.,

2012) and the much greater biodiversity in such regions understanding the exact pattern of species richness along tropical urbanisation gradients is essential.

1.4 Biotic homogenisation

Urbanisation has been viewed as the major cause of biotic homogenisation (McKinney, 2006; Blair and Johnson, 2008; Ferenc *et al*., 2014). Biotic homogenisation is the process of increasing similarity between ecological communities due to biological invasion and local extinction of native species occurring at the same time (McKinney and Lockwood, 1999; Olden, 2006; Tabarelli *et al*., 2012). Cities are very homogenised habitats as they are built and functioned in according to human preference. Consequently, similarity in environmental conditions among cities thus favours towards similar group of species that have abilities to adapt to the urban environment, which narrow down to a few numbers of non-native synanthropic species (McKinney, 2006), and at the same time selectively removed large number of native urban avoider species (Blair and Launer, 1997). However, whilst several studies have focused on the role of non-native 'Winner' on driving biotic homogenisation (i.e. through biological invasion), there is evidence that native 'Winner' could also drive biotic homogenisation (Tabarelli *et al*., 2012). Biotic homogenisation is now considered as critical threat to global biodiversity, and conservation strategies for urban biodiversity should give attention on retaining native biodiversity and enhancing habitat heterogeneity to mitigate the impacts of biotic homogenisation (McKinney, 2006).

1.5 Urban greenspace and ecosystem services

The quality of the urban environment from a human perspective is strongly influenced by the abundance of urban greenspace and its accessibility for urban residents (Cox *et al*., 2018; Kabisch *et al*., 2016; Gianfredi *et al*., 2021; Schipperijn *et al*., 2010; Verheij *et al*., 2008). Although in highly urbanised locations greenspace tends to be small (Qian et al., 2015; Wolch *et al*., 2014; Sun and Chen, 2017), these locations provide numerous beneficial impacts for people as well as biodiversity (Bolund and Hunhammar, 1999). Whilst there is growing interest in mitigating adverse environmental impacts and promoting sustainable development and the quality of life in town and cities (Aronson *et al*., 2017; Kleinschroth and Kowarik, 2020), such goals are compromised by the lack of appropriate greenspace management in cities and limited financial resources (Song *et al*., 2021; Richards *et al*., 2017).

This section highlights the ecological benefits of urban greenspace and considers urban greenspace as a nature-based solution to mitigate urban environmental problems. This section focuses on urban trees as one of the key components of urban green infrastructure (Livesley *et al*., 2016; Ordóñez and Duinker, 2012).

1.5.1 Ecosystem services of urban greenspace

Ecosystem services are defined as the benefits that human derive, directly and indirectly, from ecosystem functions (Costanza *et al*., 1997) and there are many ways to classify ecosystem services. In this section ecosystem services of urban greenspace are discussed in four major categories; i.e. cultural services, regulating services, provisioning services, and supporting services (MEA, 2005).

Cultural services

The cultural services of urban greenspace are key for human well-being in the cities (Dickinson and Hobbs, 2017; Ko and Son, 2018; Scopelliti *et al*., 2016). Most of the urban greenspace is designed, created, and managed primarily for human purposes; e.g. public parks (Lin *et al*., 2014), botanical gardens (Hu *et al*., 2017; Ward *et al*., 2010), and street trees (Thaiutsa *et al*., 2008). This wide range of urban greenspace types provides opportunities for recreational and exercise activities, outdoor education, spiritual services (Ngulani and Shackleton, 2019), historic values, and enhancing urban aesthetics (Dickinson and Hobbs, 2017).

Urban areas are typically stressful environments that adversely impact mental and physical health of their urban residents (Arena *et al*., 2017; Sandifer *et al*., 2015). It is well demonstrated, however, that engaging with nature in urban greenspaces can help mitigate stress and provide health, behavioural, and social benefits by increasing physical activities, social engagement, and attention restoration (Berto, 2005; Jennings and Bamkole, 2019; Shan, 2014; Zhou and Rana, 2012).

Additionally, urban greenspace, especially those within or nearby schools or university, can offer great opportunities for outdoor education (Hutcheson *et al*., 2018), which not only provide a platform to support knowledge, especially but not just environmental education (Loures *et al*., 2007), it can also raise environmental awareness initiate a willingness to support conservation (Hosaka *et al*., 2017).

Regulating services

Vegetation plays an important role in climate regulation and pollution reduction (van Ryswyk *et al*., 2019). The effectiveness of urban greenspace in cooling urban air temperature is primarily determined by features such as its size and type of vegetation (Aram *et al*., 2019), with trees being particularly important (Fowler *et al*., 2004). Trees can mitigate urban heat island effects by canopy evapotranspiration (Chen *et al*., 2019; Konarska *et al*., 2016; Meili *et al*., 2021) and shading effects (Armson *et al*., 2012; Lin and Lin, 2010). Trees further contribute to climate regulating by absorbing atmospheric CO_2 and storing carbon in the form of biomass (Nowak *et al*., 1993; Nowak, 2013), with tree planting being one of the most cost-effective solutions to regulate global CO_2 concentrations (Jayasooriya *et al*., 2017; McHale *et al*., 2007). Moreover, cooling effects of urban greenery can also indirectly reduce CO_2 emission via reducing energy uses in urban buildings (Jayasooriya *et al*., 2017; Nowak *et al*., 2017; Wang *et al*., 2019), thus also contributes to economic benefits through reduced energy bills (Isaifan and Baldauf, 2020; Nowak *et al*., 2017). Urban vegetation helps to mitigate air pollution by absorbing air pollutants through leaf stomata and through dry deposition of particulate matter on leaf surface (de Jalón *et al*., 2019; Nowak *et al*., 2006). Capacity to remove air pollutants is highest in trees due to a substantially higher biomass and surface areas than herbaceous vegetation, for example, a study in UK shows PM_{10} captured by trees was three time higher than grasslands (Fowler *et al*., 2004). In Beijing (China), over 1,200 tons of annual air pollutant removed by trees in 2002, most of which was PM_{10} (61% of the total; 2005). Dense vegetation in urban greenspace can reduce noise pollution (Ow and Ghosh, 2017; Van Renterghem *et al*., 2012).

Plant species vary in their ability to generate regulating ecosystem services (Lin and Lin, 2010; Mo *et al*., 2015; Salmond *et al*., 2016), with traits such as canopy density, foliage longevity, water-use strategy, and emission of reactive compounds being associate with air pollution reduction efficiency (Grote *et al*., 2016). Study in China shows species with high density of pubescene and rougher leaves can intercept more particulate pollutants (Mo *et al*., 2015). Species with high foliage density and thick and rough leaves tend to have a greater cooling effect (Lin and Lin, 2010). Appropriate species selection is thus key maximising the ability of vegetation, especially to maintain service provision in the future in the face of long-term environmental change (Hewitt *et al*., 2020; Morani *et al*., 2011; Tallis *et al*., 2011).

Provisioning services

Food production is one of the most well-known provisioning services (Richardson, 2010). Whilst urban food security is of increasing global concern (Prosekov and Ivanova, 2018; Rahaman *et al*., 2021), urban greenspace can contribute to urban food security through food production from its edible vegetation components (Çelik, 2017; Russo *et al*., 2017). Planting edible plants in urban greenspace can provide important food sources for local, especially impoverished, residents (Dimitri *et al*., 2016; Meenar and Hoover, 2012). There are various types of greenspace that can contribute to urban agriculture (see Lin *et al*., 2015) including, community/allotment gardens (Dobson *et al*., 2020; Edmondson *et al*., 2020a), home gardens (Galhena *et al*., 2013), easement gardens (Hunter ad Brown, 2012), rooftop gardens (Calheiros and Stefanakis, 2021), orchards (Horák *et al*., 2018; Vahidi *et al*., 2018), and peri-urban agriculture or the original agricultural lands that often exist at the edge of the urban areas (Opitz *et al*., 2016; Thebo *et al*., 2014). Despite limited greenspace in urban areas it has been suggested that there is still sufficient space to grow food in urban locations, albeit with some trade-off with alternative land-uses, and that public engagement and technology are often greater challenges (Edmondson *et al*., 2020b). The importance of urban, especially domestic, food production was highlighted in much of the world during the COVID-19 pandemic lockdowns when fresh food supplies were limited and increasing risk of infection from crowds at market places reduced access to food for some urban residents (Khan *et al*., 2020; Loker and Francis, 2020; Nicola *et al*., 2020; O'Hara and Toussaint, 2021).

Supporting services

Productions of all other ecosystem services (described above) depends on supporting services, such as soil formation and nutrient cycle, that determine capacity of natural processes and productivity (Deutsch *et al*., 2013). In the urban setting, soils are often covered by impervious surface (i.e. soil sealing) and are modified by, for example, filling of artificial substrates, addition of soils from outside the city, excavation of urban soils, soil compaction, and contamination of chemical compounds (Byrne, 2007; Lorenz and Kandeler, 2005; Sauerwein, 2011). These modifications alter nutrient and hydrological cycles in the urban systems, which consequently influences other ecosystem service provisioning. Despite a generally low quality of urban soils (e.g. Herrmann *et* al., 2017; Zhao *et al*., 2013), organic matters and nitrogen contents in soils in some urban greenspace, such as parks and allotments, can be found higher than arable lands in non-urban areas (e.g. Edmondson *et al*., 2014; Schindelbeck *et al*., 2018). Provision of supporting services, alongside with regulating services, in the urban setting is thus considered most important in urban parks (Bertram and Rehdanz, 2015b).

1.5.2 Challenges in managing urban greenspace

It is clear that urban greenspace is crucial for sustainable urban development. Moreover, within cities the distribution of urban greenspace is often unequal, with disadvantaged groups having far less access to green-space and its associated ecosystem services especially in developing countries (Rigolon *et al*., 2018). The opportunities and willingness to increase urban greenspace is, however, limited by the availability of land that can be converted to greenspace and the high cost of doing so (Richards *et al*., 2017). Although the increasing wealth of many economics in southeast Asia may enable a small number of flagship projects creation of new urban greenspace is unlikely to be a universal or sufficient solution in solution. One thus needs to consider how to maximise the benefits delivered by existing greenspace which is often poorly managed in terms of biodiversity and ecosystem services (Aronson *et al*., 2017). One potential leverage point for enhancing management of privately owned space is the link between the amount and quality of greenspace and property prices (Pandit *et al*., 2014; Sander *et al*., 2010). This could be used to encourage urban residents to maintain tree cover and increase tree planting on their lands, which can also increase people's engagement with nature and willingness to support conservation (Coldwell and Evans, 2017). Greenspace management to improve urban environment could start from enhancing capacity to support urban biodiversity of existing urban greenspaces (Aronson et al., 2017), for example, replacing heavily managed grassland to high biodiverse urban meadows (Norton *et al*., 2019).

Conversely, although ecosystem services of urban greenspace its well supported and increasing urban greenspace in towns and cities is widely suggested, urban greenspace is not always desirable. Urban greenspace with poor landscape design and many hidden areas can induce crimes, especially during the night (Boessen and Hipp, 2018; Ceccato, 2014; Groff and McCord, 2012; Lyytimäki *et al*., 2008; Sreetheran and Van Den Bosch, 2014; Taylor *et al*., 2019; but also see Bogar and Bayer, 2015; Escobedo *et al*., 2018). Trees, particularly those with poor maintenance, can damage building structures and falling branches can damage on property (van Haaften *et al*., 2016) and death or injury risks (Brookes, 2007; Forbes-Laird, 2009). This is a major factor in decisions to remove urban trees (Conway and Yip, 2016). Further, urban greenspace can also promote human-wildlife conflicts by supporting habitats for nuisance wildlife (Lyytimäki *et al.*, 2008; Soulsbury and White, 2016). Taking the views of balancing ecosystem services and disservices of urban greenspace is crucial for urban planning and management to support beneficial impacts of urban greenspace whilst mitigating ecosystem disservices and reducing human-wildlife conflicts (Hosaka and Numata, 2016; Lyytimäki and Sipilä, 2009).

Several studies have addressed the adverse impacts of human density on wildlife in urban greenspace and reduction of human disturbance in urban greenspace has been suggested (Gaynor *et al.*, 2018; Kang *et al.*, 2015). Exposure of people to nature in the urban environment is critically important, however, for maintaining human well-being and the benefits of human-nature engagement on initiating willingness to support conservation. This poses a great challenge in optimising human-nature interactions in urban planning and management (Rega-Brodsky *et al.*, 2018). There is thus a growing need to integrate ecological and biodiversity concepts into the planning and management of urban environment, potentially with zoning areas according to the levels of human-wildlife interactions that are facilitated, to sustain and enhance both human well-being and ecological fertility of the urban environment (Aronson *et al.*, 2017; Snep and Opdam, 2010; Tan and bin Abdul Hamid, 2014).

1.6 The Bangkok region — a case study of a rapidly urbanising tropical mega-city

Bangkok, the capital city and the only mega-city in Thailand, provides a good example of a rapidly urbanising tropical mega-city in southeast Asia (see section 1.1.2). The urban human population size has increased from 4.7 million in 1980 to 6.4 million in 2000 and 10.5 million in 2020, and has been predicted to exceed 12 million by 2030 (United Nations, 2018). The flat topography of Bangkok has facilitated this expansion, although expansion in the southern region is limited by the inner gulf of Thailand (Estoque and Murayama, 2015; Fig. 1.9).

Bangkok is located in the Indo-Burma biodiversity hotspot (Myers *et al.*, 2000) and has a tropical monsoon climate. The city is separated into eastern and western sections by the Chao-Praya river that runs through the central plains of Thailand and flows into the Gulf of Thailand. In this thesis, the Bangkok region is delimited by a 70 km × 80 km rectangle (5,600 km^2) covering Metropolitan Bangkok and parts of the surrounding provinces (Fig. 1.9). This broader extend covers the lower part of the Chao-Praya lowland — the country's largest river basin, comprising various types of natural and semi-natural habitats such as wetlands, freshwater meadows, mangrove forests, and agricultural lands such as rice paddies and fruit orchards (Thaitakoo *et al*., 2013). This region harbours substantial biodiversity as, for example, 412 bird species and 127 tree species have previously been reported (Round and Gardner, 2008; Thaiutsa *et al*., 2008). Changes in vegetation dynamics due to unplanned urban development in Bangkok will profoundly contribute to biodiversity loss and environmental degradation (Song *et al*., 2021; Srivanit *et al*., 2012). Ecological research in this region will thus provide useful information on the impacts of rapid urbanisation on the tropical urban ecosystems.

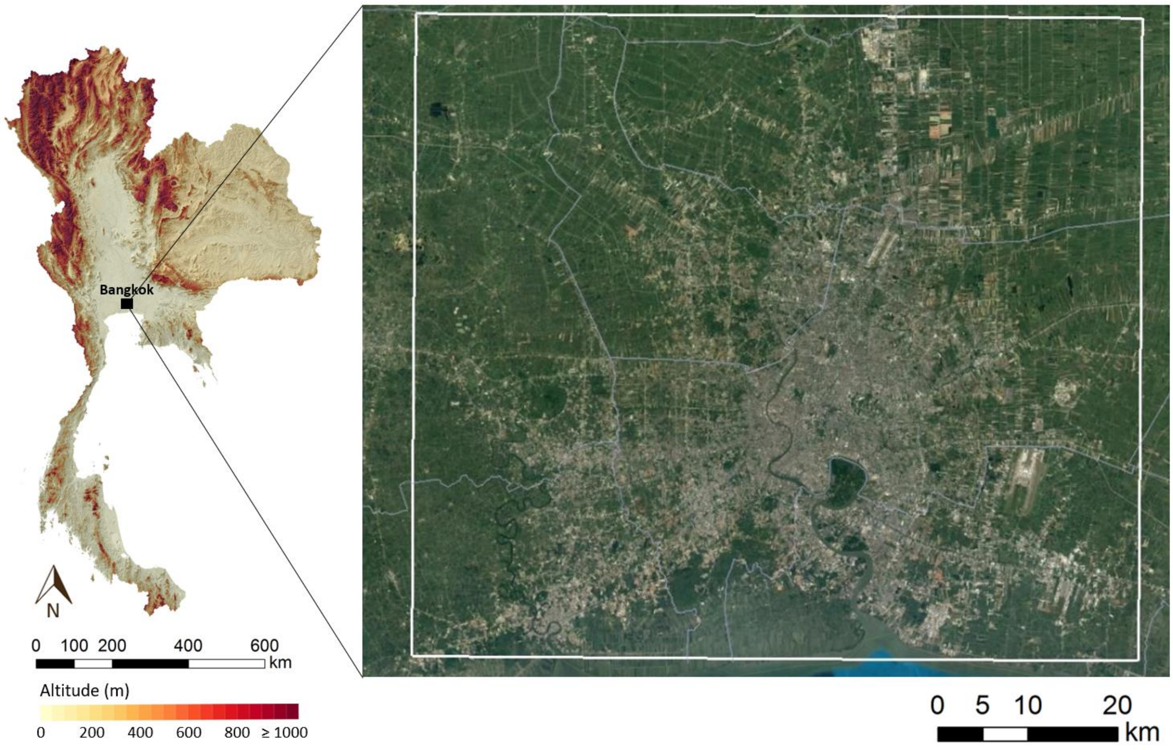


Figure 1.9: Map of Thailand with colours representing altitude (m) and the location of Bangkok (modified from www.mitrearth.org). An inset map shows the Google Earth's satellite image of the Bangkok region taken in 2018 with a 70 km × 80 km grey rectangle border delimiting the focal study region.

1.7 Aims of thesis

Whilst the importance of healthy urban environments for sustaining and promoting quality of life is beyond question, understanding of urbanisation impacts on biodiversity and its related ecosystem services are rather limited. Moreover, urban ecological research is geographically biased towards more developed countries in the temperate regions, with less attention being given to developing tropical countries which are experiencing the highest rates of urbanisation. Research into urbanisation and its implication for urban ecosystems in developing tropical cities is therefore crucial for informing effective management and conservation of biodiversity. To provide a case study of a rapidly urbanising tropical mega-city, the thesis work investigates urbanisation in Bangkok (Thailand) and its implications for urban ecosystems including biodiversity (i.e. trees, birds, squirrels and tree-shrews), and ecosystem services (Fig. 1.9). Objectives for each chapter of this thesis are:

Chapter 2: To construct landcover maps of Bangkok region comparing between two recent time points using high resolution aerial imagery from Google Earth and assess spatiotemporal pattern in vegetation dynamics along the gradient of urbanisation intensity.

Chapter 3: To investigate how assemblages of squirrels and tree shrews respond to urbanisation intensity and urban selection pressures and assess if urbanisation promotes hybridisation between two allopatric squirrel species by increasing the permeability of an ecological barrier.

Chapter 4: To assess how species richness and ecosystem services potential of tree assemblages vary along the gradient of urbanisation intensity and assess if provision of ecosystem services is greatest in areas with higher tree diversity.

Chapter 5: To assess the avian species richness-urbanisation intensity relationship in a tropical urban ecosystem and to assess how these relationships are altered by retaining woodland cover along the gradient. This thus provides insights into potential mitigation strategies for urban avian conservation.

Chapter 6: To discuss recent pattern in urbanisation in the Bangkok region, biodiversity consequences, and possible mitigation solutions for a rapidly urbanising tropical mega-city. This generate further research questions to explore urban ecology and implications for management and conservation in this region.

All data chapters within this thesis (i.e. Chapter 2–5) are presented as the exact version that were submitted to the scientific journal, in which the plural terms (i.e. ‘We’ and ‘Our’) are used, and in all other chapters (i.e. Chapter 1 and 6) the singular terms (i.e. ‘I’ and ‘My’) are used. Furthermore, all spellings in chapter 5 are in American spelling to meet the guidelines for the journal Ecological Applications.

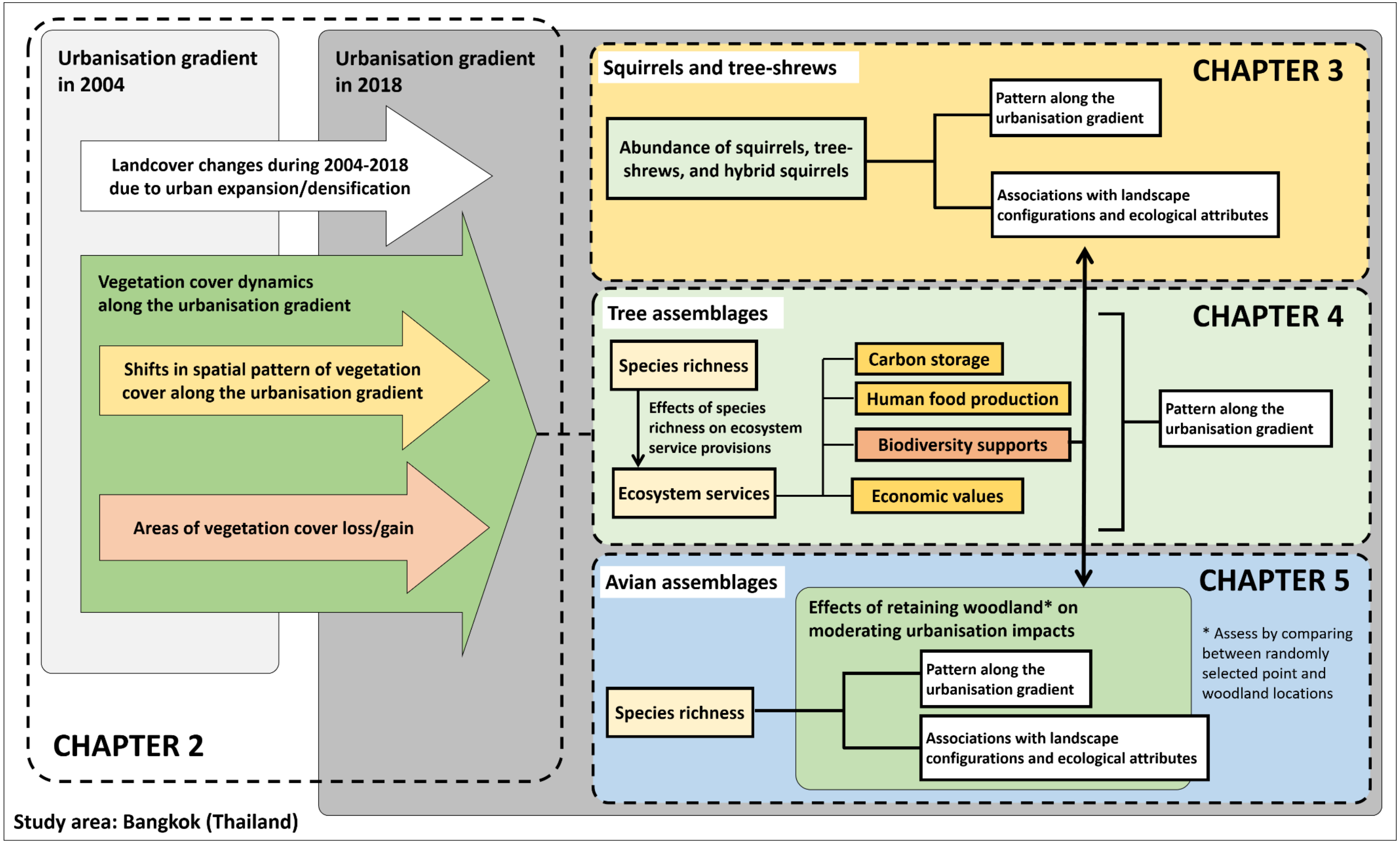


Figure 1.10: Conceptual diagram summarising thesis framework based on four data chapters.

1.7 References

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CHAPTER TWO

Urbanisation of a growing tropical mega-city during the 21st century — landscape transformation and vegetation dynamics (in preparation for the journal Landscape and Urban Planning)

Abstract

The world is becoming increasingly urban and the resultant marked landscape transformation drives marked vegetation loss and shifts in the abundance of different vegetation types, major consequences for ecosystem services and biodiversity. The fine scale spatial and temporal dynamics of these vegetation changes is, however, insufficiently understood — especially in tropical megacities which are often located in biodiversity hotspots and are amongst the most rapidly growing urban areas. Most Southeast Asian cities have for example been growing rapidly throughout the 21st century, for example, Bangkok's (Thailand) human population increased by over a million inhabitants from 2000 to 2020. Here we quantify recent changes (from ~2004 to ~2018) in landcover across the greater Bangkok region using high resolution aerial imagery. Specifically, we first contrast landcover dynamics in newly urbanised areas (created by urban expansion) with those occurring in existing urban areas that are experiencing increasing urbanisation intensity (created by densification). We then assess how total vegetation cover and coverage of specific vegetation types vary along the urbanisation gradient and assess if landcover changes have generated temporal shifts in the vegetation cover-urbanisation intensity relationship. We then quantify how temporal changes in landcover vary with magnitude of urbanisation intensity. Finally, we quantify how temporal changes in vegetation cover due to conversion between impervious surface cover vary along the urbanisation gradient. Our results indicate the Bangkok region has undergone intensive urban development, resulting in a considerable loss of vegetation cover. The lack of a temporal shift in the form of vegetation cover-urbanisation intensity relationships indicates the ability of space-for-time substitution approaches to predict future vegetation dynamics. Expansion and densification have similar affects at local spatial scales on the loss of total vegetation and grassland, but urban growth has primarily arisen through expansion, which thus contributes significantly more to loss of these vegetation types than densification. Rice field loss is relatively limited, and has arisen primarily from expansion. Policies that promote densification may thus appear to be advantageous in protecting vegetation cover and agricultural production. Yet, infill densification has generated substantial local loss of tree cover, contrasting with increasing tree cover elsewhere — including in areas experiencing urban expansion. There is an urgent need for actions to implement effective tree protection and planting schemes in highly urbanised locations to avoid detrimental impacts of densification on people and biodiversity.

Keywords: space-for-time substitution, tropical city, urban woodland, urban greenspace, densification, expansion, compact city

2.1 Introduction

The global human population is growing rapidly, with more people now residing in urban areas than rural ones (United Nations, 2019). The spatial extent of urban areas is, however, expanding even more rapidly than the growth rate of human urban populations (based on global data from 1970 to 2000; Seto *et al.*, 2011). This increase in urban land-cover arises from densification within urban areas (i.e. conversion of urban greenspace to impervious surfaces) and expansion (i.e. conversion of rural areas to impervious surfaces). Growth of global land cover is set to continue with approximately 0.6–1.3 million km^2 of rural land having a high probability of being converted into urban areas between 2015 and 2050 (Huang *et al.*, 2019). Nearly half of this growth is predicted to occur in Asia (Huang *et al.*, 2019), a region which already contains significant urban regions (e.g. 16 megacities, defined as cities with over 10 million inhabitants) even though most of the Asian human population still resides in rural areas (United Nation, 2019).

Within Asia, southeast Asia has experienced one of the fastest rates of urbanisation during the 21st century (ASEAN, 2017; Hughes, 2017), and this rate is notably higher than those in developed regions, i.e. Europe, North America and Oceania (Seto *et al.*, 2011). Southeast Asia's human population is predicted to continue urbanising rapidly, growing from 37.9% in urban areas in 2000 to 50% by 2020 and 66% by 2050 (United Nation, 2019).

Urbanisation is a major factor driving biodiversity loss in Southeast Asia (Sodhi *et al.*, 2004; Sodhi *et al.*, 2010), with almost all of the region's urban areas overlapping with its four biodiversity hotspots (Güneralp and Seto, 2013). The impact of urbanisation on biodiversity hotspots in Southeast Asia is predicted to increase significantly, with the urbanised area of these hotspots growing from approximately 27,000 km^2 in 2000 to nearly 100,000 km^2 in 2030 (Seto *et al.*, 2012). The adverse impacts of increased urban landcover within these hotspots may be particularly marked as Southeast Asian cities tend to have a lower proportion of green-space than cities in other regions (Richards *et al.*, 2017), and thus less capacity to support biodiversity (Aronson *et al.*, 2017; Karuppannan *et al.*, 2014). These adverse impacts on biodiversity will be particularly marked in those Southeast Asian cities with high population densities and large spatial extents (Richards *et al.*, 2017), i.e. megacities which often have some of the highest rates of urban expansion (Estoque and Murayama, 2015; Xu *et al.*, 2019).

Environmental impacts of urban expansion can arise directly through conversion of natural habitat of high biodiversity value, such as forest and wetland, or indirectly through loss of agricultural land — which is then replaced by clearance and conversion of natural vegetation types to create new farmland. These indirect impacts are often much greater than direct impacts (Song *et al*., 2015; van Vliet, 2019). In southeast Asia, around 2.5 Mha of agricultural land was converted to urban areas during 1992 to 2015, accounting for approximately 80% of the region's urban land expansion (Barbier, 2004; Kummer and Turner, 1994; van Vliet, 2019). Urbanisation thus contributes significantly to the impact of agricultural expansion on tropical deforestation (Geist and Lambin, 2002). Conversely, urban expansion can lead to gains in tree cover when the original landscape has limited tree cover, and urban management policies encourages urban forestry and planting of street trees (Díaz-Porras *et al*., 2014; Nowak *et al*., 2001; Parris, 2016).

There is a clear need to understand landscape dynamics arising from urbanisation which are frequently spatially and temporally variable (Estoque and Murayama, 2015; Schneider *et al*., 2015; Seto *et al*., 2011; Song *et al*., 2021). Studies to date have quantified how topography and proximity to currently urbanised areas and transport networks influence the probability of urban expansion (e.g. Song *et al*., 2015; Xu *et al*., 2019), and how urbanisation can proceed along a gradual transition of increasing anthropogenic alteration of landscapes, i.e. from forest, to agriculture to urban land (e.g. Lemoine-Rodriguez *et al*., 2019). Adverse impacts of urban growth can be reduced by effective planning regulations that limit urban expansion and instead promote increasing urban intensity in already urbanised areas, i.e. urban densification (Broitman and Koomen, 2015). Such regulations are lacking, however, in much of the global south, including southeast Asian cities resulting in marked degradation of surrounding agricultural and semi-natural land as cities expand (Chandan *et al*., 2014; Srivanit *et al*., 2012; Song *et al*., 2021).

Despite much interest and progress in understanding urban landscape dynamics there is limited understanding of fine-scale spatial patterns of urban expansion, including which habitat types are converted to urban land-covers, and how landscape dynamics vary depending on base-line levels of urbanisation. This is especially the case in rapidly urbanising regions. Here, as a case study, we focus on Bangkok, Thailand, which is located within the Indo-Burma biodiversity hotspot (Myers *et al*., 2000). Bangkok is one of southeast Asian's rapidly growing mega-cities with population estimates of 63 million in 2000, increasing to 67.2 million in 2010 and 69.8 million in 2020 (United Nations, 2019).

Our overall objective is to quantify recent changes in landcover across the greater Bangkok region via landcover classification from high resolution aerial imagery. We quantify temporal changes in landcover from ~2004 to ~2018. We contrast the impacts of urban densification and expansion on vegetation cover by assessing if newly urbanised areas (created by urban expansion) have different landcover change dynamics compared to areas that are already urbanised and experiencing increasing urbanisation intensity (created by densification). We then assess the spatial pattern of landcover across the rural to urban gradient, assessing if landcover changes have generated temporal shifts in the relationship between urbanisation intensity and coverage of specific vegetation types. We then quantify how temporal changes in landcover vary with the magnitude of urbanisation intensity. Finally, we quantify how changes in vegetation cover arising from conversion to impervious surfaces, and from impervious surfaces to vegetation vary along the urbanisation gradient. The resultant data inform understanding of environmental impacts of urban development in this region and help develop recommendations for minimizing adverse impacts of urban development.

2.2 Methods

Defining the study area

Our study area was delimited by a 70 km × 80 km rectangle (5,600 km^2) centred approximately on the centre of Bangkok; it covers Metropolitan Bangkok and neighbouring provinces, i.e. Samuth-Prakarn, Samuth-Sakorn, Nakorn-Pathom, Nontaburi and Pathumthani (Fig. S2.1). The size and location of this grid captures the substantial amount of urban land-cover within the region that extends beyond the official administrative city limits, whilst also incorporating parts of the rural landscape surrounding Bangkok. This thus enables us to contrast land-cover change in urbanised and more rural locations whilst providing a suitable baseline for assessing further future impacts of urbanisation.

Land cover classification

The sampling region was divided into 5,600 1 km × 1 km cells and a grid of 140,000 evenly spaced sampling points (25 per cell, i.e. one sampling point every 200 m) in ArcGIS using the

UTM co-ordinate system. The habitat type at each sampling point was determined from high resolution aerial imagery obtained via Google Earth (following Evans *et al*. 2009). High resolution cloud free google earth images were selected that were centred on two time periods i) 2004 and ii) 2018. Due to a lack of cloud free images for some parts of the sampling region in these years we used the cloud free image that was closet in time to our target year. Images used for the most recent time period were either from 2017 (56.1% of grid cells) or 2018 (43.9% of grid cells). For the 2004 sampling date 94% of grid cells were assessed using images taken within three years of the target year (Table S2.1). The remaining 6% of grid cells were all located far from the centre of Bangkok in mainly rural areas and the images available for these cells were from 2008–2013. These grid cells typically had small and very similar amounts of urban land cover in both time periods (1st time period: 6.7% ± 0.4 (range 0–33.3%); 2nd time period (i.e. 2017/2018): 6.8% ± 0.4 (range 0–43.5%). There was no significant difference in urban land cover in these grid cells between the two time periods (matched pair t-test: $P = 0.137$; n = 272) and inclusion of these grid cells thus has negligible influence on our estimates of how urbanisation influences land-cover change.

Land cover type at each sampling point was classified into one of nine categories. These categories were selected to enable us to distinguish grey-space (i.e. urban land cover), green-space (i.e. vegetation) and blue-space (i.e. areas of water) whilst obtaining as much information as is feasible given image quality regarding the precise nature of landcover within these categories. We classified each sampling point as one of the following: i) impervious surface (i.e. buildings, roads, pavements etc.; which is one of the most frequently used urbanisation intensity metrics (Moll *et al*., 2019), ii) trees (including shrubs), iii) grasslands (aerial imagery did not enable us to consistently distinguish managed and unmanaged grasslands), iv) rice fields (the dominant form of agriculture in the Bangkok region (Song *et al*., 2021)), v) salt pans, vi) green roofs, vii) bare ground, viii) construction sites and ix) water bodies.

Images clearly enabled grassland to be distinguished from areas of trees and shrubs as the later exhibited distinct canopy shapes and often areas of shade. Vegetated rice fields were distinguished from grassland by the lattice network of fields, and uniform lighter green colour compared to other areas of vegetation. Flooded rice fields were distinguished from areas of permanent open water by checking images taken at different points within the same focal year together with the lattice network of fields. Rice fields were distinguished from salt pans as the later are restricted to locations immediately next to the sea and are smaller than rice fields and never fully vegetated. Construction sites were distinguished from other areas of bare ground by the presence of building equipment or partially constructed infrastructure. Other land-cover types (impervious surface, water bodies, and green roofs) were straightforward to classify.

The accuracy of our classifications was confirmed by comparing landcover classifications obtained from aerial imagery taken during our second time period (2017 or 2018) with ground-truth landcover classifications for 1,355 sampling points that were visited during March or April 2018. These ground truthing points comprised 150 points located at the centre of 150 1 km × 1 km cells that were selected using random stratification across the rural to urban gradient, and an additional 1,255 sampling points that were selected haphazardly due to their location close to travel routes between the randomly selected cells. These comparisons provide worst case scenarios for assessing the accuracy of landcover classifications from aerial imagery due to the potential for genuine landcover change to occur between the dates at which imagery was taken and the date of the ground-truthing visit, but revealed that classifications had at least 90% accuracy for almost all landcover types (Table S2.2). The exceptions were bare ground (62.50% accuracy) and construction sites (77.8% accuracy). These landcover types are particularly likely to exhibit rapid genuine change (as bare ground becomes vegetated due to succession or conversion to a construction site; and as construction sites are turned to impervious surfaces). We thus assessed if changes at these sampling points were due to classification error or genuine change by assessing all available aerial imagery between the date of the original image and the date at which ground-truthing occurred. All discrepancies were due to genuine landcover change implying that there was 100% classification accuracy for bare ground and construction sites.

Data analyses

All analyses were performed in R studio version 3.4.2 (Rstudio Team, 2015). We excluded grid-cells with over 80% surface water cover as such cells contain an insufficient number of land-based sampling points with which to estimate changes in land-cover; all analyses are thus based on 5,482 (97.9%) of our original 5,600 grid cells. We start by quantifying changes between our two time points (i.e. ∼2004 and ∼2018) in the percentage cover of each of the nine landcover types (impervious surface, trees, grasslands, rice fields, salt pans, green roof, bare ground, construction sites, and water bodies) and change in total green area (i.e. combining grasslands, rice fields and trees) using matched paired t-test. Note that only one sampling point (<0.001 %) was a green roof, and this habitat type was excluded from the calculation of total green area cover as the ecology of green roofs is very different to other green-spaces occurring at ground level (MacIvor, 2016). We used the false discovery rate (FDR) method of Benjamini and Hochberg (1995) to correct for multiple testing and report the FDR corrected P values.

There is likely to be substantial heterogeneity in the nature of landcover change within the Bangkok region, especially regarding changes in vegetation types, depending on the original intensity of urbanisation. Areas that have recently become urbanised due to urban expansion will, for example, tend to have different vegetation dynamics than areas which were originally urbanised but are experiencing densification, i.e. becoming more urbanised (Parris, 2016). We define grid cells with over 25% impervious surface cover as urbanised grid cells (following Bonnington *et al*. (2013)). We then conduct three sets of matched paired t-tests that compare changes in vegetation cover, in total and for each vegetation type, across our two time periods for i) grid cells that became urbanised between our two focal time periods (termed "Urban expansion"; 973 grid cells), ii) grid cells that were already urbanised in ~2004 and in which the proportion of impervious surface cover increases by less than 10% (termed "Remain urban"; 910 grid cells), iii) grid cells that were already urbanised in ~2004 with the proportion of impervious surface cover increasing by over 10% (termed "Urban densification"; 761 grid cells), and iv) grid cells that remained rural (i.e. impervious surface ≤25%) during ~2004 to ~2018 (termed "Remain rural"; 2,756 grid cells). In each case, differences between paired values were normally distributed thus validating the test's assumption. Comparing the results of these analyses enables us to assess how urban expansion and urban densification differentially influence vegetation dynamics, by contrasting rural sites that are converted to urban areas with those that remain rural, and contrasting urban sites that experience densification with those that do not. These analyses exclude a small proportion of grid cells (n = 82; 1.5%) that were urban in 2004 but which loose some impervious surface and became rural in 2018. Equivalent analyses conducted using 40% impervious surface as a threshold to define urbanised grid cells (rather than 25%) generated very similar results (see Fig. S2.2; Table S2.3). The FDR method (p.adjust function in R) was applied for multiple comparison and corrected P values are reported.

We then assess if landscape dynamics have generated temporal shifts in the relationship between urbanisation intensity and total vegetation cover and each of the most widespread types of vegetation cover (trees, grassland, and rice fields). We modelled the relationship between total vegetation cover and urbanisation intensity (i.e. percentage impervious surface cover) as these two variables are not simple the inverse of each other as three of our landcover classifications are neither greenspace or impervious surface (i.e. bare ground, construction sites, and salt pans). We modelled the focal vegetation cover response variable as a function of the proportion of impervious surface (including linear, quadratic, and cubic terms to detect simple non-linear relationships) constructing separate models using data from each of our two time periods. We took this appraoh rather than fitting all data in the same model with additional predictors of time period and interaction terms between time period and urbanisation intensity due to the complexity of fitting and interpreting multiple interaction terms (in the same model) with the linear, quadratic, and cubic functions of impervious surface cover. Moran's I test (ape package) detected significant spatial autocorrelation for all our response variable/year combinations (Table S2.4). We thus constructed generalised least squared models (gls function in nlme package) using three different spatial correlation structure (i.e. exponential, spherical, or gaussian), selecting the optimal structure based on Akaike Information Criterion (AIC) values (Table S2.5). We selected between linear, quadratic, cubic models using AIC values, i.e. selecting models with higher power predictors only when their AIC values were ≥2 point values lower than alternative models, and when parameter estimates of the higher power predictors had 95% confidence intervals that did not overlap zero.

Finally, we calculated three measures of vegetation dynamics between our two time periods for each grid cell: i) total net loss/gain of total vegetation cover and each vegetation type, ii) loss of total vegetation cover and of each vegetation type arising from conversion to impervious surface cover, and iii) gain in total vegetation cover and each vegetation type arising from conversion of impervious surface cover to vegetation. This third type of vegetation dynamic is rare but can occur, for example, when an urban area is abandoned or when tree canopies expand. We then assess how vegetation dynamics change along the urbanisation gradient by modelling each type of vegetation dynamic as a function of impervious surface cover in our first time period whilst also taking into account the number of years between the two sets of images. We used linear, quadratic, and cubic terms of proportion of impervious surface, and again used AIC values, in combination with considering if 95% confidence intervals of parameter estimates overlap zero, to assess model fit. Moran's I tests (ape package) revealed positive spatial autocorrelation in our initial models' residuals (Table S2.6, S2.7), so we used generalised least squared model (gls function in nlme package) with three different spatial covariance structure (i.e. exponential, spherical, or gaussian) to taking spatial correlation into account. The optimal structure was again selected based on AIC values (Table S2.8).

2.2 Results

Summary of landcover transformations at the regional scale

Impervious surface cover increased significantly across the study region between the study's two time periods (∼2004 and ∼2018) with fewer cells having less than 25% impervious surface cover, and more cells in all other impervious surface categories (Fig. 2.1). There was a significant decline in total vegetation cover and that of grassland and rice fields; whilst tree

Table 2.1: Median, mean (± standard error) percentage cover of each landcover type in our two time periods ~2004 and ~2018, in 1 km × 1 km grid cells (n = 5,482). *P*-values of matched paired t-tests assessing the statistical significance of these changes were corrected using the false discovery rate (FDR) method (p.adjust function in R). Note that green roofs were only detect at one sampling point (<0.001% of the total).

Landcover type	∼2004		∼2018		Matched paired t-test results	
	Median	Mean ± s.e.	Median	Mean ± s.e.	*t*	*P*
Impervious surface	12.50	20.50 ± 0.30	23.53	29.16 ± 0.33	51.16	$<2.2e^{-16}$
Green areas (total)	84.41	76.82 ± 0.31	71.43	66.96 ± 0.33	-51.34	$<2.2e^{-16}$
Trees	16.00	18.86 ± 0.20	20.00	21.35 ± 0.21	13.50	$<2.2e^{-16}$
Grasslands	33.33	35.74 ± 0.31	20.83	25.11 ± 0.25	-41.95	$<2.2e^{-16}$
Rice fields	4.00	22.22 ± 0.39	0	20.5 ± 0.38	-9.35	$<2.2e^{-16}$
Salt pans	0	0.05 ± 0.02	0	0.04 ± 0.16	-2.23	0.029
Green roof	0	0.00 ± 0.00	0	$1.1e^{-3} \pm 1.1e^{-3}$	1.00	0.317
Bare ground	0	1.63 ± 0.07	0	3.31 ± 0.09	17.46	$<2.2e^{-16}$
Construction sites	0	1.00 ± 0.06	0	0.53 ± 0.03	-7.46	$1.4e^{-13}$
Water bodies	4	9.82 ± 0.20	4	10.37 ± 0.20	4.77	$2.4e^{-6}$

cover increased (Table 2.1; Fig. 2.2, Fig. 2.3). There was a slight but significant decline in salt pans (Table 2.1), and whilst bare ground is consistently rare its cover doubled between our focal time periods, whilst the area of construction sites fell by nearly a half (Table 2.1).

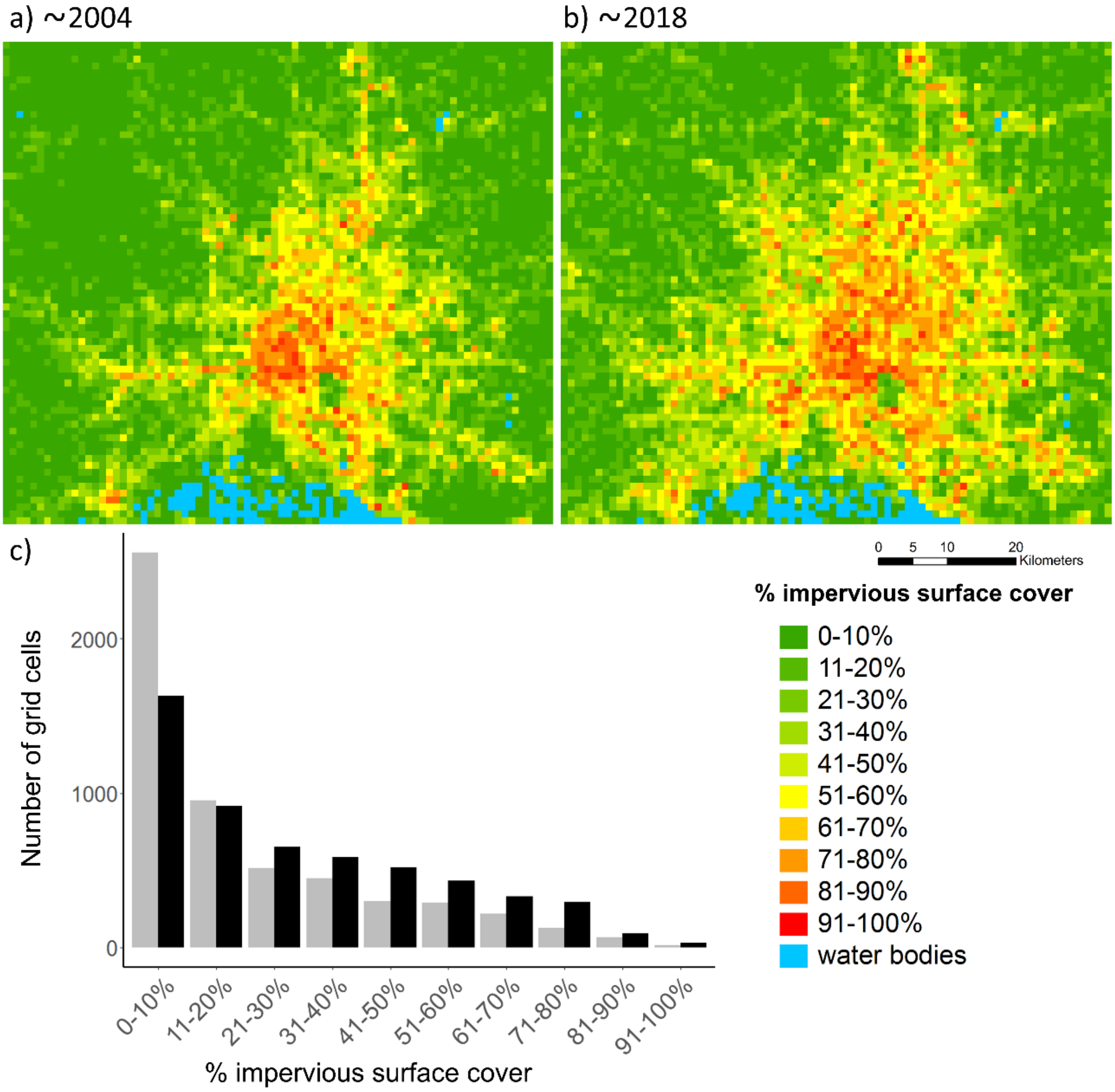

Figure 2.1: Impervious surface cover across the Bangkok study region in a) ~2004 and b) ~2018 and c) number of 1 km × 1 km grid cells in each of the impervious surface categories in ~2004 (grey) and ~2018 (black).

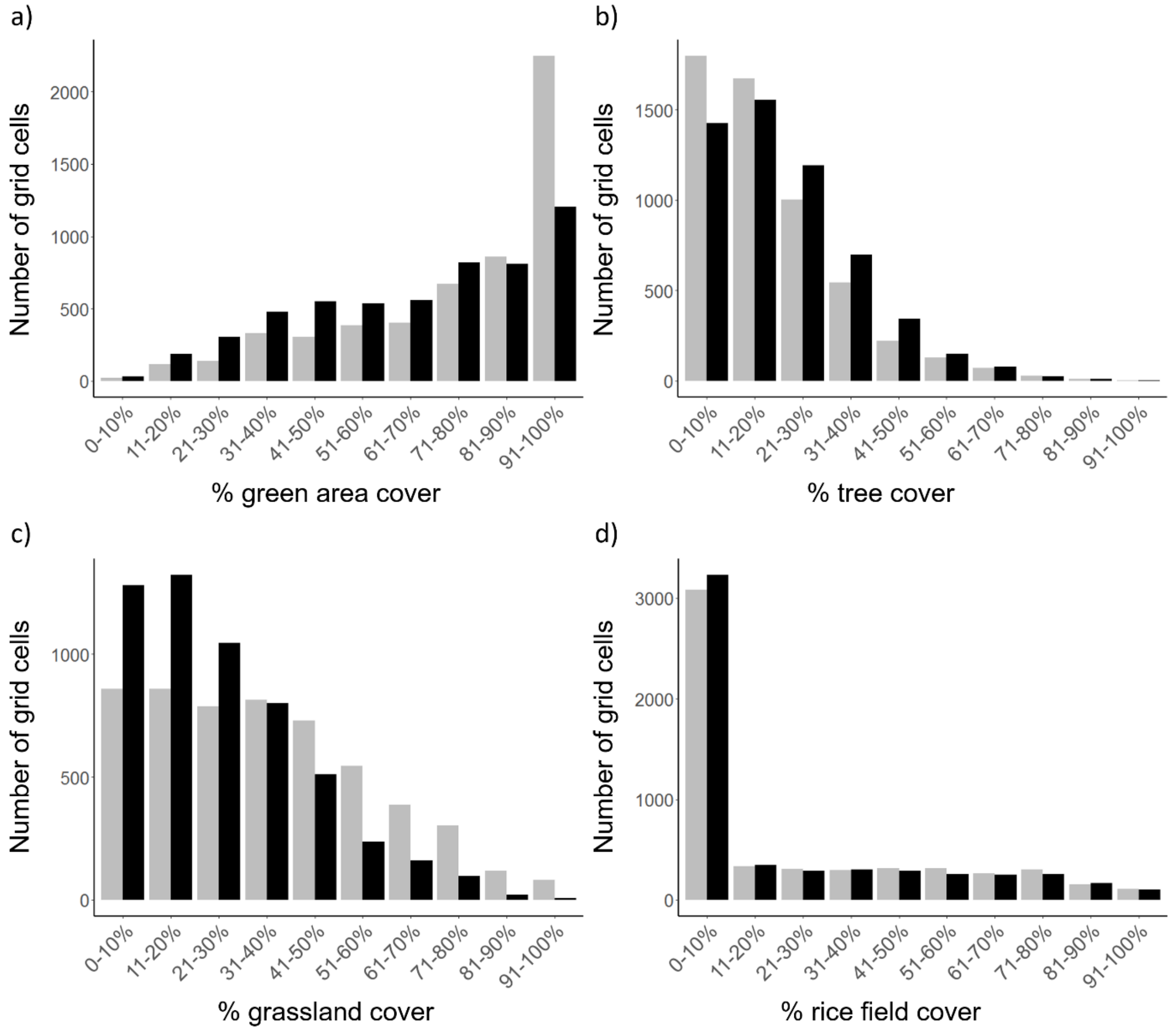

Figure 2.2: Number of grid cells in each vegetated landcover category in ~2004 (grey) and ~2018 (black).

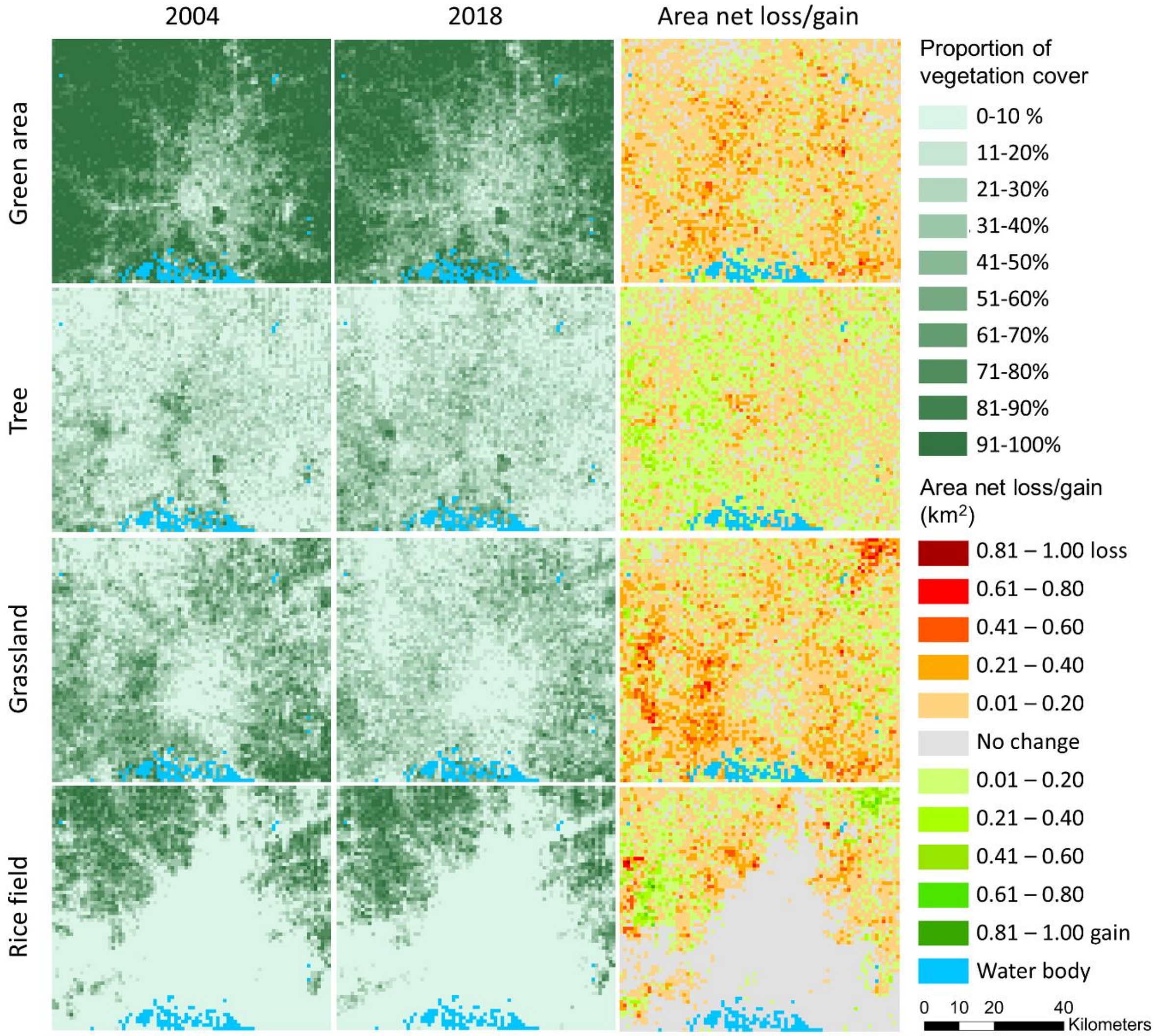

Figure 2.3: Landcover maps show proportion of vegetation cover (total green area and three main vegetation types) of 1 km × 1 km grid cells in both time points and area net loss/gain (km^2) during ~2004 to ~2018.

Impacts of urban expansion and densification on changes in vegetation cover

Despite the increase in impervious surface cover our study region, just, remained primarily rural in our second time period, with 51.0% (n = 2,756) of grid cells being rural (defined as <25% impervious surface cover). 17.4% of grid cells (n = 973) experienced urban expansion between the two surveys period, i.e. switched from being rural to urban. 16.3% of grid cells (n = 910) remained urban during the survey period without experiencing urban densification; 13.6% of grid cells (n = 761) that experienced urban densification during this period, with impervious surface cover in these cells increasing from a mean of 42.5 ± 0.47% (s.e.) to 62.1 ± 0.49% (s.e.) (median values increased from 40.0% to 62.5%).

Total vegetation cover was substantially reduced in formerly rural grid cells that experienced urban expansion, contrasting with the negligible decline in vegetation cover in grid cells that remained rural (Table 2.2; Fig. 2.4a). Similarly, urban cells that experienced urban densification experienced much greater loss of vegetation cover than urban cells that did not experience densification (Fig. 2.4a). Tree cover negligibly increased in formerly rural grid cells that experienced urban expansion and grid cells that remained rural (Table 2.2; Fig. 2.4b). Tree cover slightly declined in urban grid cells that experienced urban densification, whilst there was a negligible increase in tree cover in urban grid cells that did not experience densification (Table 2.2; Fig. 2.4b). Grassland cover declined substantially in rural grid cells that became urban, but only declined very slightly in grid cells that remained rural (Table 2.2; Fig. 2.4c). Similarly, much greater loss of grassland cover was found in urban cells that experienced urban densification than urban cells that did not experience densification (Table 2.2; Fig. 2.4c). Rice field cover declined to a much greater extent in formerly rural grid cells that experienced urban expansion, than those that remained rural (Table 2.2; Fig. 2.4d). Rice field cover declined negligibly and similarly in urban cells that did and did not experience urban densification (Table 2.2; Fig. 2.4d).

Table 2.2: Median, mean (± standard error) percentage cover of each vegetation type in our two time periods ~2004 and ~2018, in 1 km × 1 km grid cells classified as cells that change from rural to urban over this time period (urban expansion; n = 973), remain rural (n = 2,756), experience urban densification (n = 761), and remain urban without experiencing densification (n = 910). *P* values of matched paired t-tests assessing the statistical significance of these changes were corrected using the false discovery rate (FDR) method (p.adjust function in R).

Urbanisation category	~2004		~2018		Matched paired t-test results	
	Median	Mean ± s.e.	Median	Mean ± s.e.	*t*	*P*
Green area cover (all vegetation types)						
Urban expansion	83.33	83.00 ± 0.34	60.87	58.26 ± 0.38	-55.83	$<2.2e^{-16}$
Remain rural	95.45	92.48 ± 0.18	88.00	86.46 ± 0.21	-28.12	$<2.2e^{-16}$
Urban densification	56.00	53.66 ± 0.49	36.00	35.55 ± 0.47	-52.36	$<2.2e^{-16}$
Remain urban	43.48	43.90 ± 0.59	44.00	42.63 ± 0.54	-0.91	0.363
Tree cover						
Urban expansion	18.18	21.24 ± 0.52	20.83	22.54 ± 0.44	2.84	0.005
Remain rural	13.64	17.77 ± 0.30	16.67	21.17 ± 0.33	12.72	$<2.2e^{-16}$
Urban densification	20.00	20.23 ± 0.46	16.00	17.50 ± 0.37	-6.28	$7.6e^{-10}$
Remain urban	16.00	18.04 ± 0.40	21.74	22.92 ± 0.41	12.80	$<2.2e^{-16}$
Grassland cover						
Urban expansion	50.00	48.44 ± 0.68	26.09	28.12 ± 0.46	-32.87	$<2.2e^{-16}$
Remain rural	32.00	36.49 ± 0.48	24.00	28.13 ± 0.40	-22.78	$<2.2e^{-16}$
Urban densification	32.00	31.59 ± 0.60	16.00	17.12 ± 0.41	-30.42	$<2.2e^{-16}$
Remain urban	20.83	23.43 ± 0.56	16.00	18.78 ± 0.47	-11.70	$<2.2e^{-16}$
Rice field cover						
Urban expansion	0.00	13.33 ± 0.63	0.00	7.61 ± 0.41	-13.91	$<2.2e^{-16}$
Remain rural	39.13	38.22 ± 0.59	36.00	37.17 ± 0.59	-3.24	0.001
Urban densification	0.00	1.84 ± 0.21	0.00	0.92 ± 0.12	-6.30	$7.4e^{-10}$
Remain urban	0.00	1.43 ± 0.18	0.00	0.92 ± 0.13	-5.35	$1.4e^{-7}$

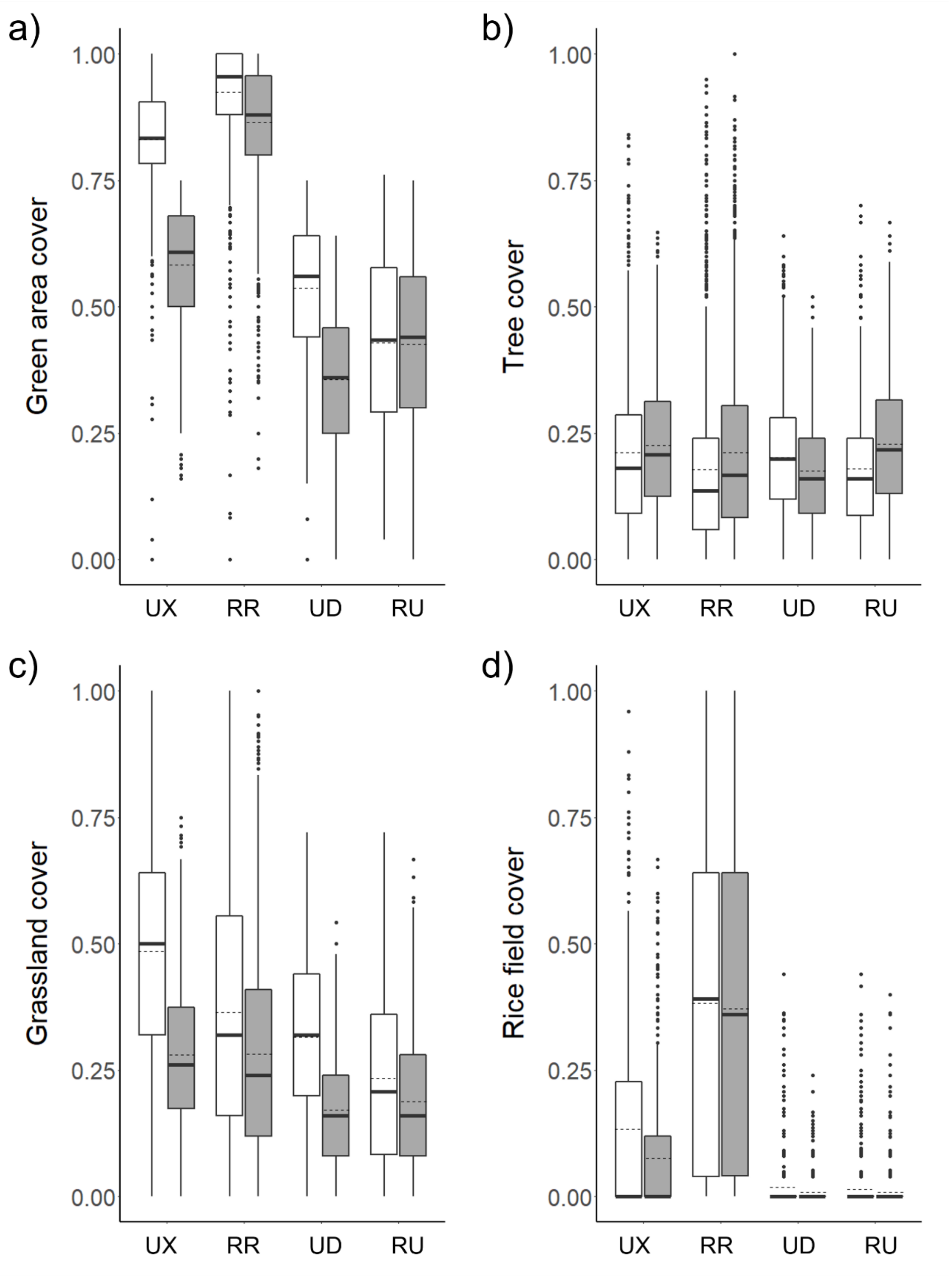

Figure 2.4: Box and whisker plots comparing vegetation cover in ∼2004 (white) and ∼2018 (black) in each urbanisation category of 1 km × 1 km grid cells; urban expansion (UX), remain rural (RR), urban densification (UD), and remain urban (RU). Thick solid horizontal lines represent median, interquartile boxes represent middle 50% (25th to 75th percentile) of the data, and dashed lines represent mean values (on which matched paired t-tests are based; see Table 2.2), whiskers represent 25% ranges for the bottom and top of the data values, and dots represent outliers.

Assessing temporal shifts in vegetation cover-urbanisation intensity relationships

Total vegetation cover declined in a linear manner with increasing urbanisation intensity, and the gradient of these declines was extremely similar in both time periods (Table 2.3; Fig. 2.5a, e). Tree cover declined with increasing impervious surface cover along a cubic curve in the first time period and a quadratic curve in the second time period (Table 2.3). Predicted tree cover values along the urbanisation intensity gradient were, however, very similar during both time periods, with tree cover being maintained at ~25% until impervious surface cover reached approximately ~25%, after which tree cover declined to negligible levels in the most intensely urbanised grid cells (Fig. 2.5b, f). Grassland cover declined along cubic curves in both time periods with declines starting at very low levels of impervious surface cover, approximately 10%, and then declining to negligible levels once impervious surface cover reached 75% (Table 2.3; Fig. 2.5c, g). There is a difference though in the intercepts of these relationships with greater grassland cover at a given urbanisation intensity in the first time period along much of the urbanisation gradient. The area of rice fields declined along a cubic curve in both time periods with sharp reductions as urbanisation increased to approximately 25% impervious surface cover and then remained stable till approximately 80% impervious surface cover, when rice fields rapidly declined to negligible levels (Table 2.3; Fig. 2.5d, h). Consequently, there is limited evidence (for total greenspace, or particular vegetation types) that increasing urbanisation substantially changed the form of the relationship between green-space and urbanisation intensity.

Table 2.3: Parameter coefficients and standard errors of general least squared models (gls function in nlme package) with exponential spatial covariance structure that modelled total green area cover and cover of the three main vegetation types (i.e. trees, grassland, and rice fields) as a function of impervious surface cover in our two time periods (~2004 and ~2018) using linear, quadratic, and cubic models. Predicted values are illustrated in Fig. 2.5 derived from the best fitting model, identified in bold, i.e. that with the lowest AIC value in which 95% confidence intervals of all coefficients do not overlap zero.

Year	Response variable	Model	AIC	Intercept	Impervious surface cover (linear term)		Impervious surface cover (quadratic term)		Impervious surface cover (cubic term)	
				Coeff ± s.e.	Coeff ± s.e	95% CI (lower, upper)	Coeff ± s.e	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)
~2004	Green area cover	**Linear**	-15879.92	0.960 ± 0.006	-0.962 ± 0.006	-0.975, -0.950				
		Quadratic	-15874.99	0.962 ± 0.006	-0.984 ± 0.013	-1.010, -0.958	0.032 ± 0.018	-0.002, 0.067		
		Cubic	-15870.70	0.961 ± 0.006	-0.962 ± 0.022	-1.006, -0.918	-0.052 ± 0.071	-0.191, 0.088	0.074 ± 0.061	-0.045, 0.193
	Tree cover	Linear	-8173.25	0.237 ± 0.021	-0.221 ± 0.013	-0.246, -0.197				
		Quadratic	-8338.09	0.217 ± 0.022	0.093 ± 0.027	0.041, 0.146	-0.470 ± 0.036	-0.540, -0.400		
		Cubic	-8342.25	0.213 ± 0.022	0.201 ± 0.046	0.111, 0.290	-0.879 ± 0.145	-1.163, -0.595	0.321 ± 0.124	0.118, 0.604
	Grassland cover	Linear	-5742.53	0.454 ± 0.027	-0.493 ± 0.016	-0.524, -0.462				
		Quadratic	-5760.65	0.444 ± 0.027	-0.344 ± 0.034	-0.410, -0.278	-0.221 ± 0.045	-0.309, -0.134		
		Cubic	-5829.05	0.432 ± 0.028	0.045 ± 0.057	-0.066, 0.155	-1.708 ± 0.179	-2.059, -1.356	1.310 ± 0.153	1.010, 1.611
	Rice field cover	Linear	-6442.84	0.259 ± 0.043	-0.242 ± 0.015	-0.271, -0.212				
		Quadratic	-6727.25	0.289 ± 0.043	-0.713 ± 0.031	-0.773, -0.652	0.701 ± 0.040	0.621, 0.780		
		Cubic	-6852.43	0.303 ± 0.044	-1.182 ± 0.051	-1.282, -1.082	2.498 ± 0.162	2.180, 2.815	-1.584 ± 0.138	-1.855, -1.313
~2018	Green area cover	**Linear**	-15469.94	0.936 ± 0.009	-0.939 ± 0.006	-0.951, -0.928				
		Quadratic	-15467.48	0.939 ± 0.009	-0.969 ± 0.013	-0.995, -0.943	0.040 ± 0.016	0.008, 0.072		
		Cubic	-15466.49	0.941 ± 0.009	-1.014 ± 0.024	-1.061, -0.966	0.194 ± 0.072	0.053, 0.335	-0.129 ± 0.059	-0.244, -0.014
	Tree cover	Linear	-8511.35	0.288 ± 0.022	-0.278 ± 0.011	-0.299, -0.256				
		Quadratic	-8718.95	0.255 ± 0.023	0.057 ± 0.025	0.008, 0.105	-0.449 ± 0.030	-0.508, -0.390		
		Cubic	-8719.66	0.251 ± 0.023	0.143 ± 0.045	0.055, 0.231	-0.748 ± 0.133	-1.009, -0.488	0.251 ± 0.109	0.038, 0.464
	Grassland cover	Linear	-7257.15	0.366 ± 0.023	-0.386 ± 0.012	-0.410, -0.362				
		Quadratic	-7297.76	0.348 ± 0.023	-0.208 ± 0.028	-0.264, -0.152	-0.238 ± 0.034	-0.305, -0.171		
		Cubic	-7350.98	0.334 ± 0.024	0.115 ± 0.051	0.015, 0.215	-1.355 ± 0.150	-1.650, -1.060	0.935 ± 0.123	0.694, 1.176
	Rice field cover	Linear	-7182.49	0.272 ± 0.045	-0.265 ± 0.012	-0.289, -0.241				
		Quadratic	-7594.96	0.322 ± 0.046	-0.781 ± 0.027	-0.835, -0.728	0.691 ± 0.033	0.626, 0.755		
		Cubic	-7705.16	0.342 ± 0.048	-1.215 ± 0.048	-1.310, -1.120	2.191 ± 0.143	1.911, 2.471	-1.254 ± 0.116	-1.483, -1.026

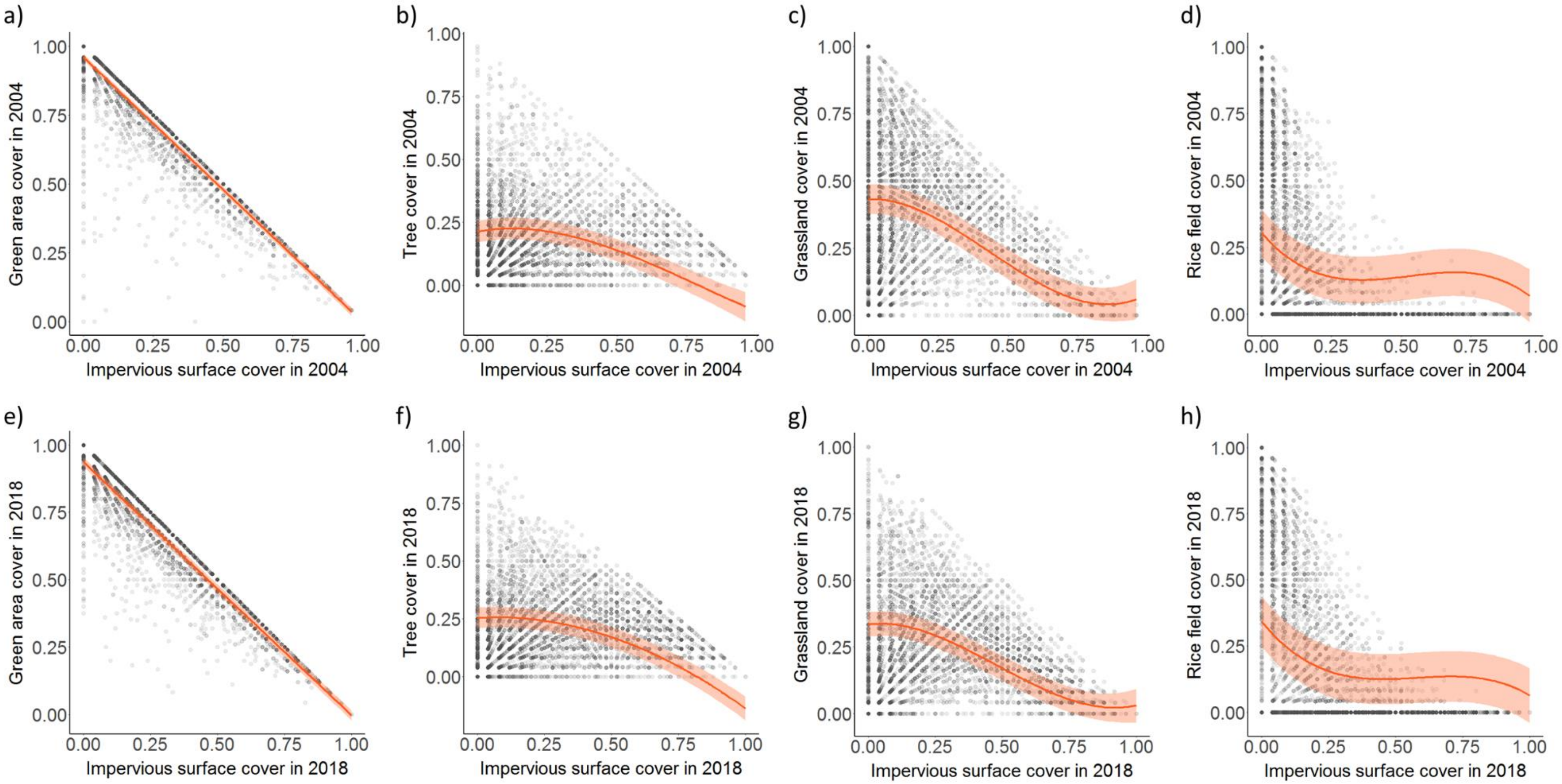

Figure 2.5: Relationships between the proportions of total vegetation cover and each of three main vegetation types (tree, grassland, and rice field) and impervious surface cover in ~2004 (a-d) and ~2018 (e-h). Fitted lines represent predicted values from the best fit spatial models (nlme package in R) reported in Table 2.2.

Vegetation dynamics — net loss/gain along the urbanisation gradient

Change (i.e. net loss/gain) in total vegetation cover between the two time periods varied with urbanisation intensity in the first time period along a positive slightly accelerating curve. The least urbanised cells lost the most vegetation cover, but once impervious surface cover in the first time period exceeded 50% grid cells gained increasing amounts of vegetation cover between the time period (Fig. 2.6a).

Change in tree cover was positively and linearly associated with urbanisation intensity in the first time period, such that the least urbanised areas have negligible gain in tree cover and the most urbanised cells gained the largest amount of tree cover (Table 2.4; Fig 2.6b). Change in grassland cover exhibited a cubic relationship with urbanisation intensity in the first time period (Table 2.4). The least urbanised locations in the first time period exhibited the largest losses in grassland cover, with the amount of grassland lost declining until impervious surface cover in the first time period exceeded 70%, with cells that were originally more urbanised than this gaining grassland areas (Fig. 2.6c). Change in rice field cover exhibited a shallow linear relationship with impervious surface cover in the first time period, with the largest (albeit still very limited) losses occurring in the least urbanised locations. All these models controlled for the slight variation in the number of years between the dates of the images in the first (~2004) and second time periods (~2018), this predictor was significantly negatively associated with change in total vegetation and grassland cover — indicating greater loss of these vegetation types as time progressed. Conversely, the magnitude of gain in tree cover increased as time progressed. These was no significant relationship between rice field net loss/gain and the number of years between the two images.

Table 2.4: Parameter coefficients and standard errors from generalised least squares models (gls function in nlme package) with exponential spatial covariance structure that model area net loss/gain of total vegetation cover and the three main vegetation types (trees, grasslands, and rice fields) as a function of original impervious surface cover (i.e. in ~2004 with linear, quadratic, cubic terms) and number of years between the images. The best fitting models (assessed by AIC values and parameter estimates' 95% confidence intervals not overlapping zero) are shown in bold. Predicted values are illustrated in Fig. 2.5.

Response variable	Model	AIC	Intercept	Impervious surface cover (linear term)		Impervious surface cover (quadratic term)		Impervious surface cover (cubic term)		Numbers of year between image	
			Coeff ± s.e.	Coeff ± s.e.	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)
Green area net loss/gain	Linear	-9153.24	-0.026 ± 0.027	0.267 ± 0.011	0.245, 0.289					-0.008 ± 0.002	-0.011, -0.004
	Quadratic	-9181.39	0.135 ± 0.025	0.196 ± 0.033	0.087, 0.183	0.196 ± 0.033	0.132, 0.261			-0.007 ± 0.002	-0.011, -0.004
	Cubic	-9178.63	-0.017 ± 0.027	0.089 ± 0.043	0.006, 0.173	0.368 ± 0.135	0.103, 0.633	-0.152 ± 0.116	-0.379, 0.075	-0.007 ± 0.002	-0.011, -0.004
Area of tree cover net loss/gain	**Linear**	-8619.20	-0.054 ± 0.024	0.052 ± 0.011	0.030, 0.074					0.005 ± 0.002	0.002, 0.008
	Quadratic	-8620.87	-0.050 ± 0.024	-0.016 ± 0.026	-0.066, 0.035	0.101 ± 0.035	0.034, 0.169			0.005 ± 0.002	0.002, 0.008
	Cubic	-8618.43	-0.052 ± 0.024	0.035 ± 0.045	-0.053, 0.123	-0.091 ± 0.143	-0.371, 0.189	0.170 ± 0.122	-0.070, 0.409	0.005 ± 0.002	0.002, 0.008
Grassland area net loss/gain	Linear	-6173.16	$-6.4e^{-5}$ ± 0.035	0.165 ± 0.015	0.136, 0.194					-0.009 ± 0.002	-0.014, -0.004
	Quadratic	-6183.21	-0.007 ± 0.035	0.047 ± 0.033	-0.017, 0.111	0.177 ± 0.043	0.092, 0.262			-0.009 ± 0.002	-0.014, -0.004
	Cubic	-6185.78	0.011 ± 0.035	-0.069 ± 0.056	-0.178, 0.041	0.616 ± 0.177	0.268, 0.963	-0.387 ± 0.152	-0.685, -0.090	-0.009 ± 0.002	-0.014, -0.004
Rice field area net loss/gain	**Linear**	-9324.70	0.026 ± 0.027	0.041 ± 0.011	0.019, 0.063					-0.004 ± 0.002	-0.007, $2.4e^{-4}$
	Quadratic	-9324.97	0.022 ± 0.027	0.100 ± 0.024	0.052, 0.148	-0.088 ± 0.032	-0.151, -0.024			-0.004 ± 0.002	-0.007, $2.1e^{-4}$
	Cubic	-9321.18	0.021 ± 0.027	0.129 ± 0.042	0.047, 0.210	-0.197 ± 0.132	-0.456, 0.062	0.097 ± 0.113	-0.125, 0.318	-0.004 ± 0.002	-0.007, $2.2e^{-4}$

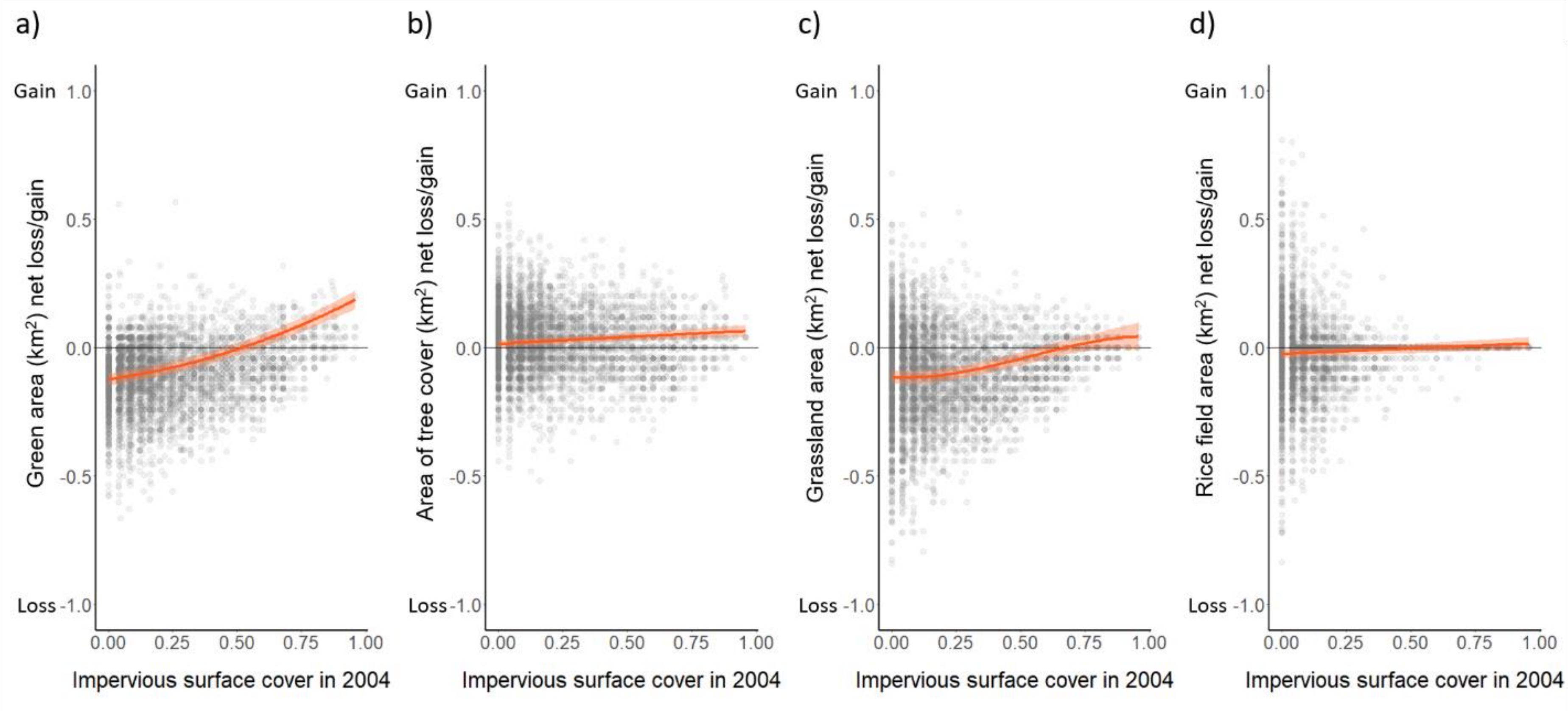

Figure 2.6: Relationships between estimated area (km^2) net loss/gain of total green area (a) and three main vegetation types (b-d) during ~2004 to ~2018 with proportion of impervious surface in ~2004. Fitted lines illustrate predicted values and shading their 95% confidence intervals, derived from the best fitting spatial models (nlme package in R) presented in Table 2.4.

Vegetation dynamics — loss arising from conversion to impervious surface

Total vegetation loss arising from conversion to impervious surface cover declined with impervious surface cover in the first time period along a marginally unimodal curve (Table 2.5), with the greatest loss occurring at low levels of original impervious surface cover of approximately 25% (Fig. 2.7a). Loss of tree cover arising from conversion to impervious surface exhibited a cubic relationship with impervious surface cover in the first time period (Table 2.5), whilst the magnitude of change was limited across the gradient they are lowest at the highest levels of impervious surface cover and declining to negligible levels when impervious surface cover exceeds approximately 70% (Fig. 2.7b). Grassland loss from conversion to impervious surface changed along a cubic curve with the amount of loss peaking at grid cells with approximately 20% impervious surface cover in 2004 then declining to negligible levels at the most urbanised locations (Fig. 2.7c). Rice field area loss due to conversion to impervious surface cover was negligible across the gradient but declined linearly with increasing urbanisation intensity (Fig. 2.7d). The amount of total vegetation, grassland, and rice fields, but not tree cover, loss due to conversion to impervious surface cover increased with time (Table 2.5).

Vegetation dynamics — gain arising from conversion from impervious surface

Gain in total vegetation cover and tree cover arising from conversion of impervious surface cover to green-space increased with impervious surface cover in the first time period along a decelerating quadratic curve, which plateaued at ~50% impervious surface cover for total vegetation (Table 2.6; Fig. 2.7e) and at ~70% impervious surface cover for tree cover (Table 2.6; Fig. 2.7f). Gains in grassland area arising from conversion of impervious surfaces exhibited a unimodal relationship with impervious surface cover in the first time period, with maximum gains when original impervious surface cover was approximately 50% and negligible gains at either extreme of the urbanisation gradient (Table 2.6; Fig. 2.7g). There was no significant relationship between gain in rice fields and original urbanisation intensity (Table 2.6), although conversion of impervious surface to rice field is extremely rare (Fig. 2.7h; Fig. S2.3b).

Table 2.5: Parameter coefficients and standard errors from generalised least squares models (gls function in nlme package) with exponential spatial covariance structure that model loss of total vegetation cover and cover of three main vegetation types (trees, grasslands, and rice fields) arising from conversion of impervious surface in relation to original impervious surface cover (i.e. in ~2004 with linear, quadratic, cubic terms) and number of years between images. The best fitting models (assessed by AIC values and parameter estimates' 95% confidence intervals not overlapping zero) are shown in bold. Predicted values are illustrated in Fig. 2.6.

Response variable	Model	AIC	Intercept	Impervious surface cover (linear term)		Impervious surface cover (quadratic term)		Impervious surface cover (cubic term)		Numbers of year between image	
			Coeff ± s.e.	Coeff ± s.e.	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)
Green area loss to impervious surface	Linear	-12023.50	0.026 ± 0.024	-0.075 ± 0.009	-0.092, -0.058					0.006 ± 0.001	0.003, 0.008
	Quadratic	-12295.73	0.009 ± 0.024	0.211 ± 0.019	0.175, 0.248	-0.422 ± 0.025	-0.471, -0.374			0.005 ± 0.001	0.003, 0.008
	Cubic	-12294.12	0.007 ± 0.024	0.259 ± 0.032	0.197, 0.322	-0.605 ± 0.102	-0.805, -0.406	0.162 ± 0.087	-0.009, 0.332	0.005 ± 0.001	0.003, 0.008
Area of tree cover loss to impervious surface	Linear	-18813.19	0.020 ± 0.015	-0.009 ± 0.004	-0.018, $-4.8e^{-4}$					0.001 ± 0.001	-0.001, 0.001
	Quadratic	-19037.82	0.012 ± 0.017	0.129 ± 0.010	0.110, 0.148	-0.205 ± 0.013	-0.231, -0.180			0.001 ± 0.001	-0.001, 0.002
	Cubic	-19043.53	0.014 ± 0.018	0.080 ± 0.017	0.047, 0.114	-0.021 ± 0.055	-0.129, 0.086	-0.163 ± 0.047	-0.255, -0.071	0.001 ± 0.001	-0.001, 0.002
Grassland area loss to impervious surface	Linear	-15185.08	0.013 ± 0.016	-0.045 ± 0.006	-0.058, -0.032					0.003 ± 0.001	0.001, 0.005
	Quadratic	-15340.59	0.004 ± 0.015	0.120 ± 0.014	0.092, 0.148	-0.243 ± 0.019	-0.280, -0.207			0.003 ± 0.001	0.001, 0.005
	Cubic	-15351.38	0.001 ± 0.015	0.200 ± 0.024	0.153, 0.247	-0.546 ± 0.077	-0.697, -0.395	0.267 ± 0.066	0.138,0.397	0.003 ± 0.001	0.001, 0.005
Rice field area loss to impervious surface	**Linear**	-23055.13	-0.007 ± 0.007	-0.016 ± 0.003	-0.022, -0.010					$0.002 \pm 4.8e^{-4}$	0.001, 0.003
	Quadratic	-23050.00	-0.006 ± 0.007	-0.029 ± 0.007	-0.043, -0.016	0.019 ± 0.009	0.001, 0.038			$0.002 \pm 4.8e^{-4}$	0.001, 0.003
	Cubic	-23044.24	-0.007 ± 0.007	-0.018 ± 0.012	-0.042, 0.005	-0.022 ± 0.038	-0.097, 0.053	0.036 ± 0.033	-0.028, 0.101	$0.002 \pm 4.8e^{-4}$	0.001, 0.003

Table 2.6: Parameter coefficients and standard errors from generalised least squares models (gls function in nlme package) with exponential spatial covariance structure that model gain of total vegetation cover and cover of three main vegetation types (trees, grasslands, and rice fields) arising from conversion of impervious surface in relation to original impervious surface cover (i.e. in ~2004 with linear, quadratic, cubic terms) and number of years between images. The best fitting models (assessed by AIC values and parameter estimates' 95% confidence intervals not overlapping zero) are shown in bold. Predicted values are illustrated in Fig. 2.7.

Response variable	Model	AIC	Intercept	Impervious surface cover (linear term)		Impervious surface cover (quadratic term)		Impervious surface cover (cubic term)		Numbers of year between image	
			Coeff ± s.e.	Coeff ± s.e.	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)	Coeff ± s.e.	95% CI (lower, upper)
Green area converted from impervious surface	Linear	-19393.07	0.003 ± 0.007	0.149 ± 0.004	0.141, 0.156					0.001 ± 0.001	-4.0e^{-4}, 0.002
	Quadratic	-19649.18	-0.003 ± 0.007	0.285 ± 0.009	0.267, 0.303	-0.204 ± 0.012	-0.228, -0.179			3.5e^{-4} ± 4.8e^{-4}	-0.001, 0.001
	Cubic	-19644.19	-0.003 ± 0.007	0.301 ± 0.016	0.269, 0.333	-0.263 ± 0.052	-0.365, -0.162	0.053 ± 0.044	-0.034, 0.140	3.5e^{-4} ± 4.8e^{-4}	-0.001, 0.001
Area of tree cover converted from impervious surface	Linear	-21471.56	0.001 ± 0.006	0.097 ± 0.003	0.091, 0.104					4.0e^{-4} ± 4.4e^{-4}	-4.7e^{-4}, 0.001
	Quadratic	-21538.78	-0.002 ± 0.006	0.157 ± 0.008	0.142, 0.172	-0.092 ± 0.010	-0.112, -0.071			2.9e^{-4} ± 4.4e^{-4}	-0.001, 0.001
	Cubic	-21532.23	-0.002 ± 0.006	0.162 ± 0.014	0.136, 0.189	-0.110 ± 0.043	-0.196, -0.025	0.017 ± 0.037	-0.056, 0.089	2.9e^{-4} ± 4.0e^{-4}	-0.001, 0.001
Grassland area converted from impervious surface	Linear	-24788.49	0.003 ± 0.004	0.047 ± 0.002	0.043, 0.052					1.3e^{-4} ± 3.1e^{-4}	-4.7e^{-4}, 0.001
	Quadratic	-25017.29	-0.001 ± 0.004	0.124 ± 0.005	0.114, 0.135	-0.117 ± 0.007	-0.132, -0.103			8.3e^{-5} ± 2.6e^{-4}	-4.2e^{-4}, 0.001
	Cubic	-25011.44	-0.001 ± 0.004	0.134 ± 0.010	0.115, 0.154	-0.155 ± 0.031	-0.217, -0.094	0.033 ± 0.027	-0.019, 0.086	7.9e^{-4} ± 2.6e^{-4}	-4.3e^{-4}, 5.8e^{-4}
Rice field area converted from impervious surface	Linear	-60847.87	2.7e^{-4} ± 8.3e^{-5}	-3.4e^{-5} ± 5.8e^{-5}	-1.5e^{-4}, 7.9e^{-5}					-1.8e^{-5} ± 6.2e^{-6}	-3.0e^{-5}, -6.0e^{-6}
	Quadratic	-60831.09	2.7e^{-4} ± 8.3e^{-2}	-2.7e^{-5} ± 1.8e^{-4}	-3.7e^{-4}, 3.2e^{-4}	-1.1e^{-5} ± 2.5e^{-4}	-4.9e^{-4}, 4.7e^{-4}			-1.8e^{-5} ± 6.2e^{-6}	-3.0e^{-5}, -6.0e^{-6}
	Cubic	-60817.56	2.6e^{-4} ± 8.3e^{-5}	1.9e^{-4} ± 3.5e^{-4}	-5.0e^{-4}, 8.7e^{-4}	-0.001 ± 0.001	-3.0e^{-3}, 1.4e^{-3}	0.001 ± 0.001	-1.2e^{-3}, 2.6e^{-3}	-1.8e^{-5} ± 6.2e^{-6}	-3.1e^{-5}, -6.1e^{-6}

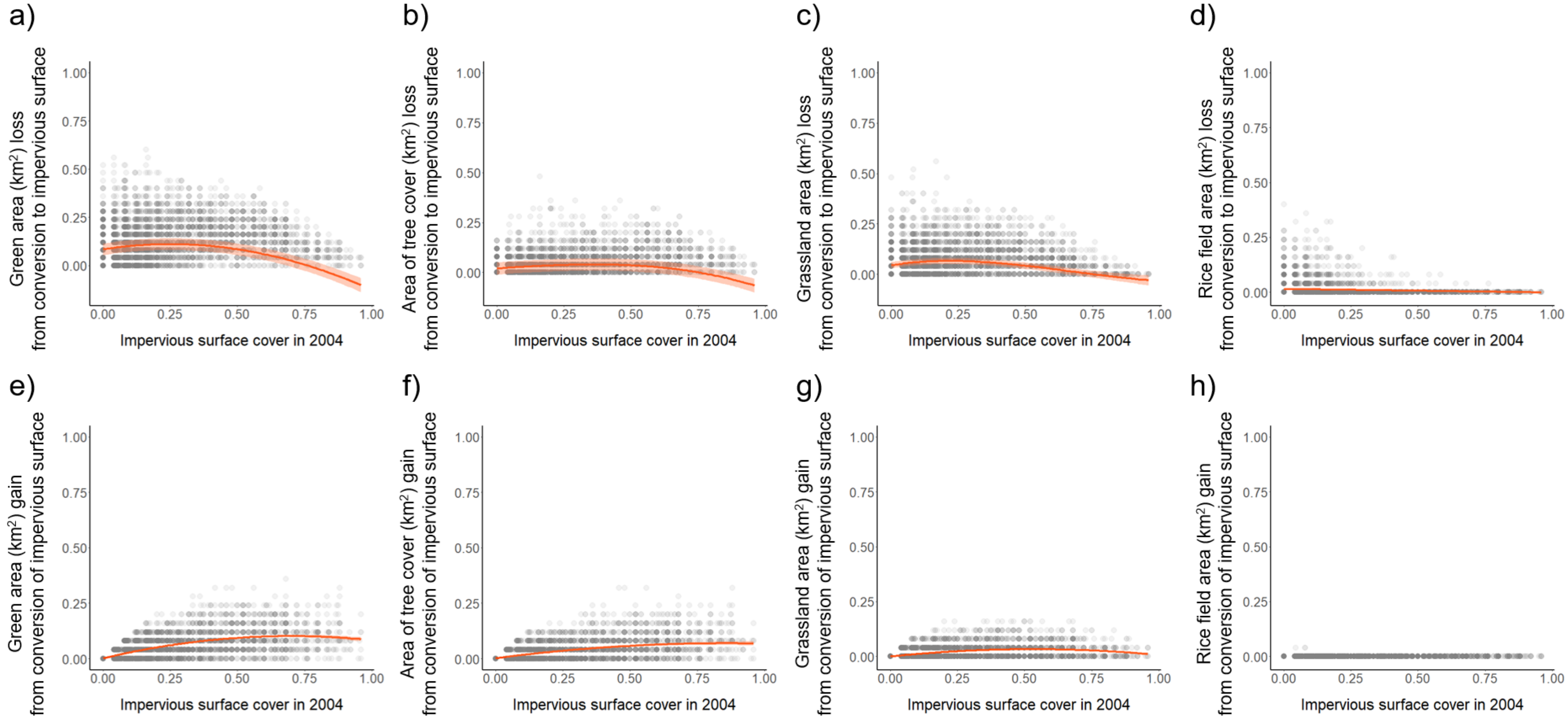

Figure 2.7: Relationships between estimated loss of vegetation cover arising from conversion to impervious surface (a) total vegetation, (b) trees, (c) grasslands, and (d) rice fields, and gain of vegetation cover arising from conversion of impervious surface to vegetation surface (e) total vegetation, (f) trees, (g) grasslands, and (h) rice fields from ~2004 to ~2018 as a function of proportion impervious surface cover in ~2004. Fitted lines illustrate predicted values and shading their 95% confidence intervals, from the best fitting spatial models (nlme package in R) reported in Table 2.5 (panels a-d) and Table 2.6 (panels e-h); no best fir line is illustrated in panel h due to the lack of a significant relationship.

2.4 Discussion

The Bangkok region has undergone intensive urbanisation during the focal study period, with impervious surface cover increasing across our 5,600 km^2 region from 20.5% to 29.2% of sampling points, equating to an additional ~487.2 km^2 of impervious surface cover in our study region. Much of this urbanisation is likely to be driven by the increasing human population in the Bangkok region from 9.6 million inhabitants in 2004 to 10.9 million in 2018 (Bangkok Metropolitan Administration, 2018). Using a similar approach suggests that vegetation cover has been reduced by ~552.1 km^2 (note we don't expect this to match the gain in impervious surface cover as some vegetation loss is due to conversion to bare ground and construction sites), but this hides substantial heterogeneity across vegetation types, with ~595.2 km^2 of grassland and ~96.3 km^2 of rice fields being lost, whilst tree cover increased by ~139.4 km^2.

Impacts of urban expansion and densification on vegetation dynamics

Quantifying the contribution of urban expansion and densification on these regional landcover transitions is dependent on the precise definitions used, but using different thresholds to define urbanised grid cells (i.e. 25% or 40% impervious surface) generates similar estimates of changes in vegetation cover within cells experiencing densification or expansion. Expansion and densification have divergent impacts on vegetation dynamics. Although declines of vegetation cover in grid cells that experienced expansion were approximately equally to those that experienced densification (~20%; Table 2.2), area of vegetation cover loss to urban expansion (~240.7 km^2) was nearly double the loss from densification (~137.8 km^2) due to differences in the spatial extent of these processes. These losses were mainly driven by the conversion of grasslands, and again expansion resulted in almost twice as much grassland being lost than densification (expansion ~197.7 km^2, densification ~110.1 km^2). This is consistent with previous studies of urbanisation in this region indicating urban Bangkok is expanding outward (Estoque and Murayama, 2015; Song *et al.*, 2021; Xu *et al.*, 2019). Greater adverse effects of urban expansion on vegetation cover may be particularly detrimental for conservation as expansion is more likely to impact semi-natural grasslands that occur in such locations rather than the more intensely managed grasslands within urban locations that are often of limited biodiversity value (Norton *et* al., 2019; Round and Gardner, 2008).

Densification is more likely to occur in urban grid cells with relatively large amount of vegetation cover, as this creates space for infill development, yet resulted lower vegetation cover in the second time period (i.e. ~2018) compared to other urbanised areas that did not experience densification. This indicates that a compact city approach to urban development that aims to reduce land consumption could in turn profoundly adversely influence the amount and accessibility of urban greenspaces, leading to negative environmental consequences and implications for the quality of urban life (Haaland and van den Bosch, 2015; Pauleit *et al.*, 2005).

Urban expansion resulted in the loss of approximately half the original cover of rice fields in these cells (equating to a loss of ~55.7 km^2), which is much greater than the loss arising from densification (~7.0 km^2) — primarily because rice fields is extremely rare in urban areas. Adverse impacts on food production are likely to be relatively small, however, given that losses from expansion equate to just 4.7% of the total area of rice fields (~1148.0 km^2) within the study area at the start of our study period. Consequently, within our study region, indirect effects of urbanisation on the conversion of natural forest to replace loss of agricultural land is arguably somewhat limited (Song *et al.*, 2015; van Vliet, 2019), but clearly such indirect impacts are minimised through densification rather than expansion.

In a notable contrast, whilst densification process resulted in a decline of ~20.8 km^2 of tree cover, tree cover increased in all other locations including those that experienced urban expansion (~12.6 km^2 increase). Our results contrast with previous suggestions that urban densification generates no net loss of tree cover as loss is balanced out by newly created tree cover (Kaspar *et al.*, 2017). The increases in tree cover that occur are likely to arise from growth of existing trees’ canopies (Fig. S2.4), woodland succession over vacant lands or degradation of low quality housing (Fig. S2.5), and creation of urban wooded habitat such as woodland blocks in parks, and tree planting in domestic gardens and streets trees (Fig. S2.6). This may at least partially be a consequence of tree planting campaigns in urban areas of Bangkok in the 1990s (Thaiutsa *et al.*, 2008).

Temporal shifts in vegetation dynamics along the urbanisation gradient

Generally, we found no strong evidence for temporal shifts in the form of vegetation cover-urbanisation intensity relationships between our focal time periods. This may suggest that landcover patterns along the spatial urbanisation gradient in Bangkok are broadly constant, indicating the general ability of space-for-time substitution approaches (*sensu* Pickett, 1989) to predict future landcover change arising from urbanisation. A slight shift in the form of grassland cover–urbanisation intensity relationships during our study period, arising from a substantial reduction in grassland cover, especially at the low levels of urbanisation intensity, suggest that the value of space-for-time substitution approaches may, however, vary between vegetation types. The predictive capacity of space-for-time substitution approaches can also be reduced by changes in urban planning or policy. As an example, whilst our data suggest that rice fields have been less impacted by urbanisation in recent decades in the Bangkok region this seems likely to change due to a decision to construct a new airport and associated urban infrastructure in Bang Len district (the rural areas at the northwest corner of our study region; Hongtong, 2019) which is currently dominated by rice fields (Fig. S2.7).

Implications for ecosystem function and tropical biodiversity

Vegetation is crucial for sustaining urban environmental quality and human well-being (Bolund and Hunhammar, 1999; Krekel *et al*., 2016), the substantial loss of vegetation cover that we document could thus contribute to environmental degradation (De Carvalho and Szlafsztein, 2019). It is well documented that increasing impervious surface and declines in vegetation cover contribute to increasing urban heat island intensity (Chapman *et al*., 2018; Morabito *et al*., 2021; Sun and Chen, 2017), with Bangkok's urban heat island intensity increasing from 12.7°C in 2005 to 16.2°C in 2016 (Khamchiangta and Dhakal, 2020). The marked increase in impervious surface cover that we document will severely impact hydrological processes and increase surface water runoff (Ramamurthy and Bou-Zeid, 2014), which combined with the flat lowland geography of the Bangkok regions (Liew *et al*., 2016; Thanvisitthpon *et al*., 2018) and increasing future precipitation (Cooper, 2019) will substantially increase flood risk (Du *et al*., 2015). This in turn increases issues arising from pollutants accumulating in runoff, entering the water system and reducing water quality (Walsh *et al*., 2012). Moreover, recent flooding events, especially the 2011 floods in Bangkok and other regions of Thailand highlight the economic and human well-being impacts of large scale flood events (Poapongsakorn *et al.*, 2013).

Despite these issues arising from urban changes in landcover types it is notable that the Bangkok region has gained considerable tree cover contrasting with the loss of shorter vegetation in grasslands and rice fields. Ecosystem services from these trees can potentially mitigate come of these adverse impacts as ecosystem services such as regulating air temperature (Lin and Lin, 2010; Morabito *et al.*, 2021), reducing air pollution (Vailshery *et al.*, 2013), and reducing surface water runoff (Armson *et al.*, 2013), typically scale with vegetation biomass — which is substantially greater in trees than shorter herbaceous vegetation such as grasses. Whilst it is thus notable that tree cover gain has been highest in locations that were highly urbanised at the start of our study period, urban densification resulted in significant loss of tree cover, and newly created urban tree cover may not always provide equivalent ecosystem services and functions to the original vegetation (Wang *et al.*, 2019). Further research is needed to address spatial and temporal patterns in ecosystem service provision arising from the landcover and vegetation dynamics that we document.

2.5 Conclusions

Using classification of high resolution aerial imagery, our study documents that intensive urbanisation in the Bangkok region during the first part of the 21st century has generated a profound loss of vegetation cover, although there was considerable variation across vegetation types. Despite this, the form of spatial patterns of vegetation cover along the urbanisation gradient appears to largely be invariant in time, indicating the ability of space-in-time substitution approaches to predict future vegetation dynamics. At the scale of individual grid cells, changes in total vegetation and grassland cover arising from urban densification and expansion are similar, but expansion has generated much greater losses then densification as it has occurred across much larger areas. Loss of rice fields is relatively small but has primarily arisen from expansion at the individual grid cell and regional spatial scales. Conversely, densification has generated substantial loss of tree cover contrasting with gains in tree cover throughout the rest of the region. The loss of such trees is likely to be particularly important for provision of ecosystem services as their provision typically scales with vegetation biomass, and demand for such services is often greatest in the most urbanised locations. There is potential to reduce environmental impacts of the continuing demand for additional urban land in the Bangkok region by promoting densification above expansion. Such an approach will, however, require active promotion of tree retention and planting schemes to avoid detrimental impacts on people and biodiversity.

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2.7 Supplementary materials

Table S2.1: Number of sampling points in landcover classification using aerial imagery taken in each year. No image was selected from 2011 due to the great Bangkok flood.

Year	Number of sampling points	%	Year	Number of sampling points	%
First time-period (~2004)			*Second time-period (~2018)*		
2001	3,100	2.21	2017	78,540	56.1
2002	11,920	8.51	2018	61,460	43.9
2003	3,030	2.16			
2004	102,027	72.88			
2005	8,666	6.19			
2006	3,900	2.79			
2007	1,331	0.95			
2008	7	0.01			
2009	124	0.09			
2010	1,486	1.06			
2011	0	0.00			
2012	363	0.26			
2013	4,046	2.89			

Table S2.2: Number of sampling point in ground truthing by habitat types indicating a high degree of accuracy of landcover classification. Based on, approximately, 3 weeks to 8 months interval between the date of aerial imagery and the date of ground truthing, number of mismatched results could arise from the genuine landcover change. Such cases were identified by comparing aerial imagery using in the landcover classification with the aerial imagery taken closely to the date of ground truthing. The percentage of landcover type matches was recalculated by excluding these cases of apparent genuine landcover change.

Landcover type	Number of sampling point in image classification	Number of sampling point in ground truthing	% match across all sampling points	% match excluding cells with genuine landcover change
impervious surface	36,798	644	98.10	99.69 (n = 637)
grassland	30,031	227	90.75	95.15 (n = 207)
rice field	26,311	53	92.45	100.00 (n = 49)
trees	25,838	287	97.91	100.00 (n = 281)
water bodies	16,606	126	96.83	100.00 (n = 122)
bare ground	3,739	8	62.50	100.00 (n = 5)
construction site	646	9	77.78	100.00 (n = 7)
salt pans	30	1	100.00	100.00 (n = 1)
green roof	1	0	-	-

Table S2.3: Median (%), mean (%), standard error of mean, and matched paired t-test results of vegetation cover comparing between ~2004 and ~2018 in 1 km × 1 km grid cells in each of urbanisation categories, i.e. urban expansion (n = 738), urban densification (n = 395), remain urban (n = 650), and remain rural (n = 3,655). In this case, we used 40% impervious surface as threshold to define urbanised grid cells and exclude 44 grid cells that was urban in 2004 but became rural in 2018. *P*-values of matched paired t-test were corrected using the false discovery rate (FDR) method (p.adjust function in R).

Urbanisation category	~2004		~2018		Matched paired t-test results	
	Median	Mean ± s.e.	Median	Mean ± s.e.	t	*P*-value
Green area cover (all vegetation type together)						
Urban expansion	70.00	70.99 ± 0.49	47.83	45.51 ± 0.35	-46.01	$<2.2e^{-16}$
Remain rural	92.00	89.26 ± 0.19	83.33	81.17 ± 0.23	-39.18	$<2.2e^{-16}$
Urban densification	44.00	44.04 ± 0.50	27.78	27.54 ± 0.52	-40.70	$<2.2e^{-16}$
Remain urban	36.00	35.04 ± 0.53	36.00	35.67 ± 0.50	1.94	0.056
Tree cover						
Urban expansion	16.67	20.53 ± 0.55	20.00	19.73 ± 0.42	-1.63	0.103
Remain rural	16.00	18.76 ± 0.27	20.00	22.24 ± 0.28	14.90	$<2.2e^{-16}$
Urban densification	20.00	20.05 ± 0.58	16.00	15.47 ± 0.43	-8.33	$2.0e^{-15}$
Remain urban	16.00	16.80 ± 0.41	20.00	21.04 ± 0.42	10.54	$<2.2e^{-16}$
Grassland cover						
Urban expansion	45.45	44.39 ± 0.69	22.73	23.59 ± 0.41	-31.91	$<2.2e^{-16}$
Remain rural	36.36	38.89 ± 0.40	25.00	28.72 ± 0.32	-29.86	$<2.2e^{-16}$
Urban densification	24.00	23.36 ± 0.70	9.09	11.82 ± 0.45	-20.38	$<2.2e^{-16}$
Remain urban	16.00	17.78 ± 0.53	12.00	14.39 ± 0.45	-8.85	$<2.2e^{-16}$
Rice field cover						
Urban expansion	0.00	6.07 ± 0.48	0.00	2.19 ± 0.20	-10.42	$<2.2e^{-16}$
Remain rural	26.09	31.91 ± 0.51	22.73	30.22 ± 0.50	-6.42	$2.1e^{-10}$
Urban densification	0.00	0.63 ± 0.18	0.00	0.25 ± 0.08	-2.89	0.005
Remain urban	0.00	0.46 ± 0.11	0.00	0.24 ± 0.07	-2.97	0.004

Table S2.4: Moran's I test results of linear regression for total vegetation cover and three main types of vegetation cover (tree, grassland, and rice field cover) with impervious surface cover in both 2004 and 2018 (linear, quadratic, cubic models) revealed spatial autocorrelation in model residuals in all models.

Response variable	Year	Model	Moran's I test result	
			observed	*P*
Green area cover	2004	Linear	0.043	$< 2.2e^{-16}$
		Quadratic	0.041	$< 2.2e^{-16}$
		Cubic	0.041	$< 2.2e^{-16}$
	2018	Linear	0.058	$< 2.2e^{-16}$
		Quadratic	0.055	$< 2.2e^{-16}$
		Cubic	0.055	$< 2.2e^{-16}$
Tree cover	2004	Linear	0.075	$< 2.2e^{-16}$
		Quadratic	0.076	$< 2.2e^{-16}$
		Cubic	0.076	$< 2.2e^{-16}$
	2018	Linear	0.112	$< 2.2e^{-16}$
		Quadratic	0.112	$< 2.2e^{-16}$
		Cubic	0.112	$< 2.2e^{-16}$
Grassland cover	2004	Linear	0.131	$< 2.2e^{-16}$
		Quadratic	0.122	$< 2.2e^{-16}$
		Cubic	0.122	$< 2.2e^{-16}$
	2018	Linear	0.122	$< 2.2e^{-16}$
		Quadratic	0.113	$< 2.2e^{-16}$
		Cubic	0.115	$< 2.2e^{-16}$
Rice field cover	2004	Linear	0.174	$< 2.2e^{-16}$
		Quadratic	0.168	$< 2.2e^{-16}$
		Cubic	0.169	$< 2.2e^{-16}$
	2018	Linear	0.160	$< 2.2e^{-16}$
		Quadratic	0.153	$< 2.2e^{-16}$
		Cubic	0.154	$< 2.2e^{-16}$

Table S2.5: Akaike Information Criterion values of generalised least squares models (gls function in nlme package) for green area cover and three main vegetation types with impervious surface cover (linear, quadratic, and cubic models) in both time points comparing between spatial covariance structure (i.e. Exponential, Spherical, and Gaussian). Best fitted models (lowest AIC value) were shown in bold.

Year	Response variable	AIC (Linear model)			AIC (Quadratic model)			AIC (Cubic model)		
		Exponential	Spherical	Gaussian	Exponential	Spherical	Gaussian	Exponential	Spherical	Gaussian
2004	Green area cover	**-15879.92**	-15781.44	-15693.69	**-15874.99**	-15776.23	-15688.54	**-15870.70**	-15771.76	-15684.66
	Tree cover	**-8173.25**	-8151.86	-7995.28	**-8338.09**	-8314.01	-8158.85	**-8342.25**	-8317.95	-8161.72
	Grassland cover	**-5742.53**	-5708.31	-5452.07	**-5760.65**	-5724.50	-5480.86	**-5829.05**	-5793.47	-5557.28
	Rice field cover	**-6442.84**	-6382.66	-6009.61	**-6727.25**	-6677.10	-6311.99	**-6852.43**	-6827.05	-6446.48
2018	Green area cover	**-15469.94**	-15446.74	-15332.03	**-15467.48**	-15404.74	-15330.75	**-15466.49**	-15443.55	-15329.09
	Tree cover	**-8511.35**	-8461.65	-8295.28	**-8718.95**	-8692.27	-8512.50	**-8719.66**	-8693.42	-8513.46
	Grassland cover	**-7257.15**	-7194.27	-7047.91	**-7297.76**	-7236.73	-7094.75	**-7350.98**	-7289.98	-7149.83
	Rice field cover	**-7182.49**	-7165.92	-6785.25	**-7594.96**	-7577.84	-7208.98	**-7705.16**	-7692.20	-7314.98

Table S2.6: Moran's I test results of linear regression for area of total vegetation cover and three main vegetation cover types (tree, grassland, and rice field cover) net loss/gain with impervious surface cover in 2004 (linear, quadratic, cubic models) and number of years between dates of imagery revealed spatial autocorrelation in model residuals in all models.

Response variable	Model	Moran's I test result	
		observed	*P*
Green area net loss/gain	Linear	0.027	$< 2.2e^{-16}$
	Quadratic	0.023	$< 2.2e^{-16}$
	Cubic	0.023	$< 2.2e^{-16}$
Trees area net loss/gain	Linear	0.021	$< 2.2e^{-16}$
	Quadratic	0.021	$< 2.2e^{-16}$
	Cubic	0.021	$< 2.2e^{-16}$
Grassland area net loss/gain	Linear	0.042	$< 2.2e^{-16}$
	Quadratic	0.042	$< 2.2e^{-16}$
	Cubic	0.042	$< 2.2e^{-16}$
Rice field area net loss/gain	Linear	0.041	$< 2.2e^{-16}$
	Quadratic	0.040	$< 2.2e^{-16}$
	Cubic	0.040	$< 2.2e^{-16}$

Table S2.7: Moran's I test results of linear regression for area of total vegetation cover and three main types of vegetation cover (tree, grassland, and rice field cover) loss and gain due to conversion between impervious surface with impervious surface cover in 2004 (linear, quadratic, cubic models) and number of years between dates of imagery revealed spatial autocorrelation in model residuals in all models except models for rice field area gain from conversion of impervious surface.

Response variable	Model	Moran's I test result	
		observed	*P*
Green area loss to impervious surface	Linear	0.037	$< 2.2e^{-16}$
	Quadratic	0.032	$< 2.2e^{-16}$
	Cubic	0.032	$< 2.2e^{-16}$
Trees area loss to impervious surface	Linear	0.036	$< 2.2e^{-16}$
	Quadratic	0.038	$< 2.2e^{-16}$
	Cubic	0.038	$< 2.2e^{-16}$
Grassland area loss to impervious surface	Linear	0.037	$< 2.2e^{-16}$
	Quadratic	0.025	$< 2.2e^{-16}$
	Cubic	0.025	$< 2.2e^{-16}$
Rice field area loss to impervious surface	Linear	0.033	$< 2.2e^{-16}$
	Quadratic	0.033	$< 2.2e^{-16}$
	Cubic	0.033	$< 2.2e^{-16}$
Green area gain from impervious surface	Linear	0.010	$< 2.2e^{-16}$
	Quadratic	0.011	$< 2.2e^{-16}$
	Cubic	0.011	$< 2.2e^{-16}$
Trees area gain from impervious surface	Linear	0.012	$< 2.2e^{-16}$
	Quadratic	0.014	$< 2.2e^{-16}$
	Cubic	0.013	$< 2.2e^{-16}$
Grassland area gain from impervious surface	Linear	0.007	$< 2.2e^{-16}$
	Quadratic	0.003	$< 2.2e^{-16}$
	Cubic	0.003	$< 2.2e^{-16}$
Rice field area gain from impervious surface	Linear	-0.001	0.202
	Quadratic	-0.001	0.203
	Cubic	-0.001	0.209

Table S2.8: Akaike Information Criterion (AIC) values of generalised least squares models (gls function in nlme package) for area net loss/gain, area converted to impervious surface, and area converted from impervious surface during 2004 to 2018 with impervious surface cover in 2004 comparing between spatial covariance structure (i.e. Exponential, Spherical, and Gaussian). Best fitted models (lowest AIC value) were shown in bold.

Response variable	AIC (Linear model)			AIC (Quadratic model)			AIC (Cubic model)		
	Exponential	Spherical	Gaussian	Exponential	Spherical	Gaussian	Exponential	Spherical	Gaussian
Area net loss/gain									
Green area	**-9153.24**	-9130.18	-9053.15	**-9181.39**	-9154.06	-9085.07	**-9178.63**	-9153.00	-9082.13
Treed area	**-8619.20**	-8583.40	-8572.17	**-8620.87**	-8583.86	-8572.70	**-8618.43**	8581.66	-8570.60
Grassland area	**-6173.16**	-6131.94	-6064.79	**-6183.21**	-6146.84	-6078.32	**-6185.79**	-6141.97	-6081.08
Rice field area	**-9324.70**	-9248.60	-9209.44	**-9324.97**	-9249.23	-9208.68	**-9321.18**	-9245.36	-9204.96
Area loss due to conversion to impervious surface									
Green area	**-12023.50**	-12008.05	-11887.83	**-12295.73**	-12283.07	-12165.79	**-12294.12**	-12281.46	-12164.13
Treed area	**-18813.19**	-18810.47	-18734.39	**-19037.82**	-19042.79	-18970.55	**-19043.53**	-19042.10	-18977.81
Grassland area	**-15185.08**	-15164.85	-15084.53	**-15340.59**	-15319.82	-15251.74	**-15351.38**	-15337.44	-15263.05
Rice field area	**-23055.13**	-22986.70	-22990.71	**-23050.00**	-22981.84	-22985.44	**-23044.24**	-22976.04	-22979.77
Area gain from conversion of impervious surface									
Green area	**-19393.07**	-19257.63	-19360.64	**-19649.18**	-19546.90	-19620.66	**19644.19**	-19540.70	-19615.32
Treed area	**-21471.56**	-21286.72	-21437.96	**-21538.78**	-21338.22	-21504.62	**-21532.23**	-21331.58	-21498.10
Grassland area	**-24788.49**	-24638.43	-24787.25	**-25017.29**	-24961.40	-24962.30	**-25011.44**	-24955.29	-24956.19
Rice field area	-60847.87	-60847.87	-60847.87	-60831.09	-60831.09	-60831.09	-60817.56	-60817.56	-60817.56

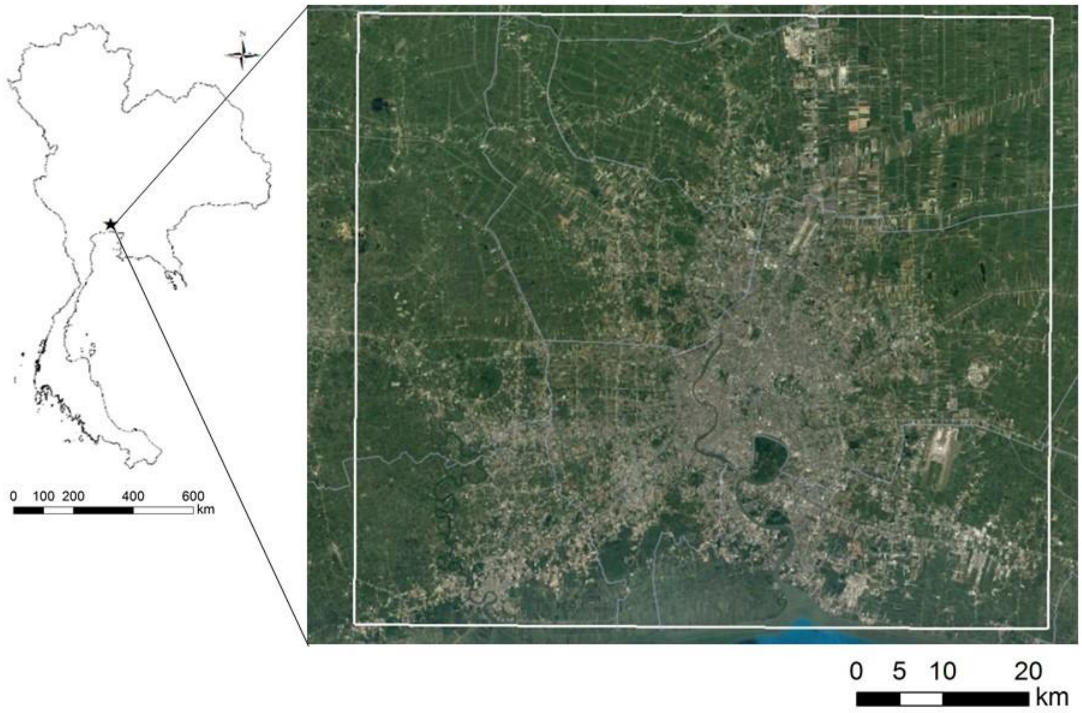


Figure S2.1: Map of Thailand showing the location of Bangkok and an inset map of the Bangkok region (using aerial imagery taken in 2018). The rectangle with grey border represents the 70 km × 80 km rectangle delimiting our study region.

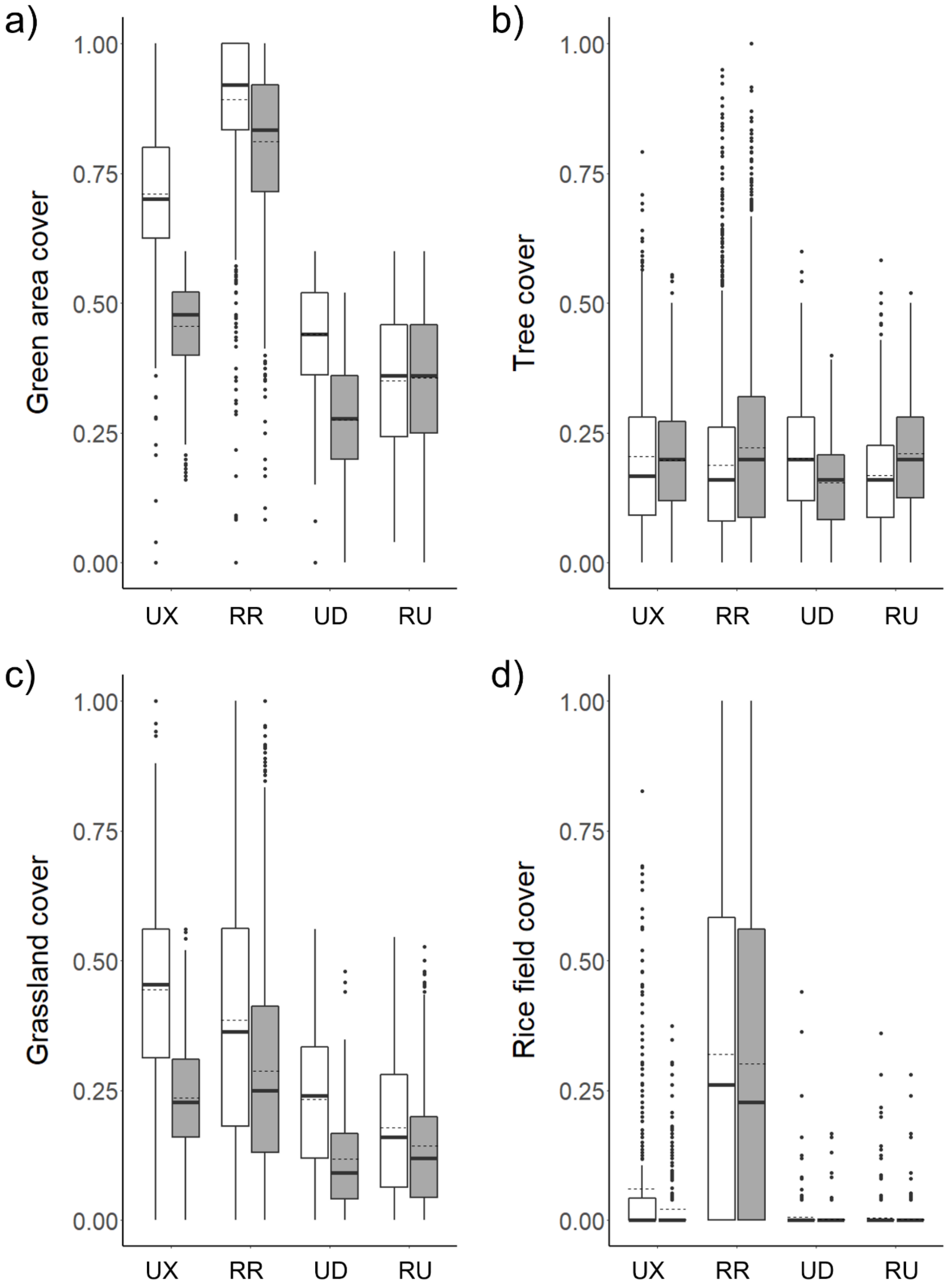


Figure S2.2: Box and whisker plots comparing vegetation cover in 2004 (white) and 2018 (grey) in each urbanisation category of 1 km × 1 km grid cells; urban expansion (UX), remain rural (RR), urban densification (UD), and remain urban (RU). In this case, we used 40% impervious surface as threshold to define urbanised grid cells. Thick solid horizontal lines represent median, interquartile boxes represent middle 50% (25th to 75th percentile) of the data, and dashed lines represent mean values (on which matched paired t-tests are based), whiskers represent 25% ranges for the bottom and top of the data values, and dots represent outliers.

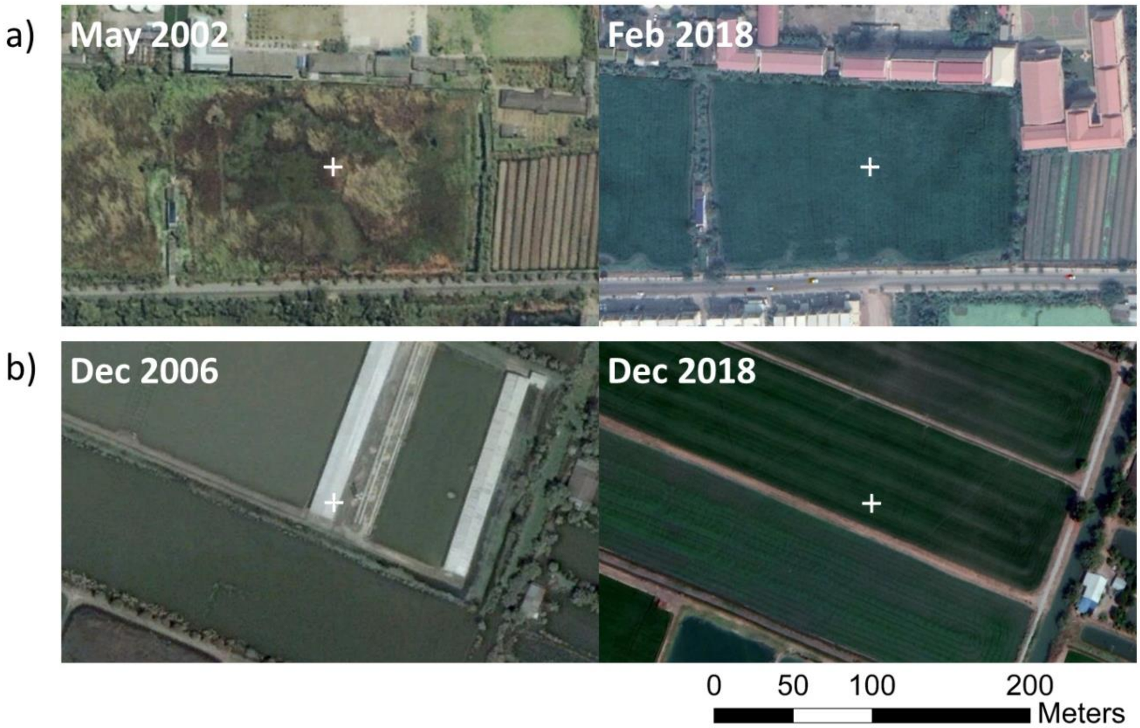


Figure S2.3: Aerial images show examples of increasing rice field cover due to a) conversion of semi-natural grassland and b) conversion of aquaculture farming. White plus signs represent sampling points used in our landcover classification.

Figure S2.4: Aerial images show examples of increasing tree cover arising from growth of existing trees' canopy. White plus signs represent sampling points used in our landcover classification.

Figure S2.5: Aerial images show examples of increasing tree cover arising from woodland succession over (a) degradation of low quality housings and (b) abandoned aquaculture farm. White plus signs represent sampling points used in our landcover classification.

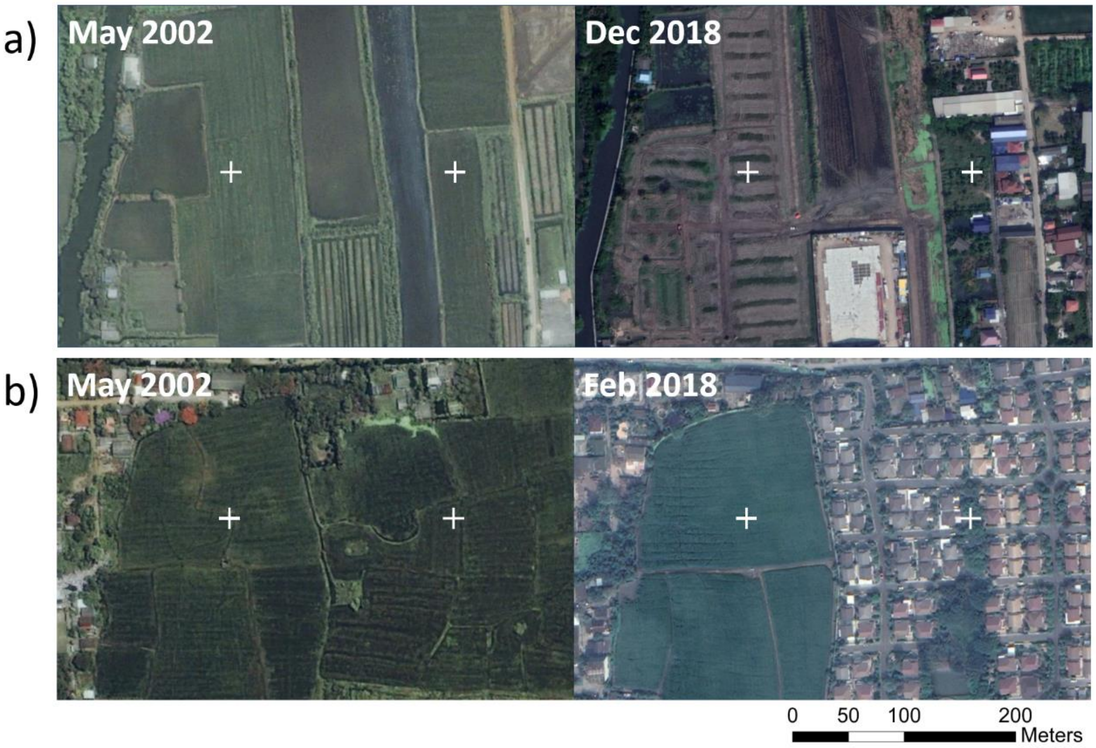


Figure S2.6: Aerial images show examples of increasing tree cover arising from creation of (a) domestic tree planting and (b) public greenspace and streets trees. White plus signs represent sampling points used in our landcover classification.

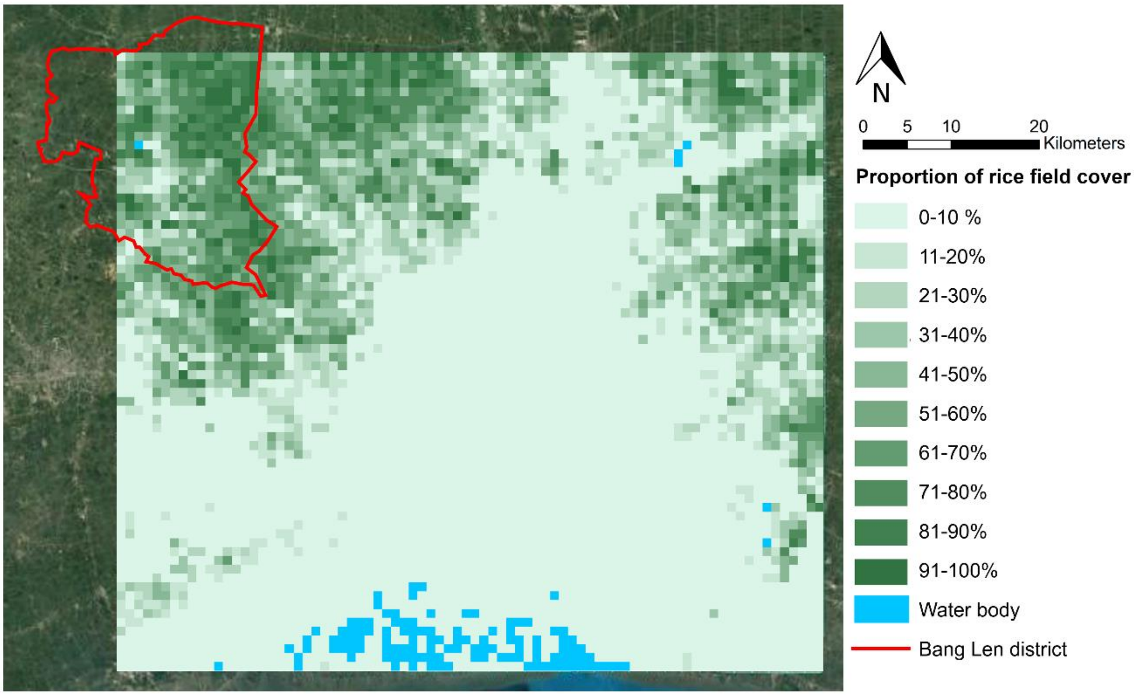


Figure S2.7: Satellite map of the Bangkok region overlaid by 70 km× 80 km landcover map showing proportion of rice field cover of 1 km × 1 km grid cells in ~2018 (shading) and the administrative boundary of Bang Len district (red line), in which it is currently targeted for a construction of a new airport (Hongtong, 2019).

CHAPTER THREE

Squirrel and tree-shrew population responses and hybridisation of *Callosciurus* squirrels along an urbanisation gradient in a tropical mega-city (in review with the journal Animal Conservation)

Urbanisation is increasing at pace and threatening biodiversity, especially in tropical regions. Many squirrel species tolerate urbanisation, but studies are biased towards temperate regions. We quantify the distribution and abundance of squirrels and (ecologically similar) tree-shrews along an urbanisation gradient in a tropical mega-city (Bangkok, Thailand) located within the Indo-Burma biodiversity hotspot. We use repeated point counts in 150 1 km cells, selected using random stratification across the urbanisation gradient. We quantify species responses to i) urbanisation intensity (measured using impervious surface cover), ii) environmental conditions and urban selection pressures (including woodland quantity and quality, human disturbance, and predation pressure from free-ranging cats and dogs), and iii) impacts of urbanisation on hybridisation between congeneric *Callosciurus* squirrels. Three species (*Tupaia belangei*, *Callosciurus finlaysonii*, and *Callosciurus erythraeus*) are relatively widespread, but one species is extremely rare (*Tamiops macclellandii*), and two others from the regional pool are extremely rare or absent (*Callosciurus canieps* and *Menetes berdmorei*). Only *C. finaysonii* has higher abundance in more urban locations. Urbanisation has thus markedly reduced squirrel diversity and abundance, contrasting with the perception that in temperate regions squirrels typically tolerate urbanisation. Important ecological functions provided by this group of species, such as seed dispersal, will be adversely impacted by urban expansion and densification — which is occurring rapidly in the region. Models suggest that improving habitat quality by increasing tree cover at local and landscape scales, and reducing effects of human disturbance and numbers of dogs would enable squirrel populations to increase, thus partially mitigating these adverse impacts. Finally, construction of bridges across the Chao-Praya river has increased the permeability of a geographic barrier that separated *C. finlaysonii* and *C. erythraeus* distributions, increasing hybridisation rates. Our study enhances understanding of the ecological impacts of urbanisation in biodiverse tropical regions and the action required to mitigate these impacts.

Keywords: cities, urban mammals, predation, rodent, Scandentia, synurbic species

3.1 Introduction

The spatial extent of urban land is increasing across much of the globe, especially in tropical regions (Seto *et al*., 2012). The environmental change associated with this rapid urbanisation markedly alters the abiotic and biotic environment creating strong selection pressures in urban environments (Grimm *et al*., 2008; Parris, 2016). These environmental changes include warmer temperatures through urban heat island effects (Diamond *et al*., 2018), habitat fragmentation (Tian *et al*., 2011), altered predation pressure (including increased pressure from human commensals such as dogs *Canis lupus familiaris*; e.g. Doherty *et al*., 2017; Paker *et al*., 2014, and cats *Felis canis*; e.g. Baker *et al*., 2008; Loss and Marra, 2017), increased human disturbance (MacGregor-Fors and Schondube, 2011; Paker *et al*., 2014), and changes in food availability for consumers arising from alterations in species composition and abundance of species at lower trophic levels (Rigacci *et al*., 2021; Schneiberg *et al*., 2020).

The species composition of urban assemblages is thus very different from those occurring in more rural areas (McKinney, 2002; McKinney, 2008), with urban assemblages tending to be relatively homogenous across the globe (Filgueiras *et al*., 2021; McKinney, 2006). Moreover, due to the strong selection pressures the ecological and functional traits of species occurring in urban areas are often rather divergent from those in more natural locations (Oliveira Hagen *et al*., 2017). This has major consequences for the ecological functioning of urban assemblages.

Whilst a diverse range of mammals can occur in urban areas, certain species groups tend to dominate. Rodentia are, for example, amongst the top three mammalian orders that are represented within urban mammalian assemblages (Santini *et al*., 2018). One group of rodents, squirrels are present as native species in almost all urban locations across the globe, including North America (e.g. eastern grey squirrel *Sciurus carolinensis*; Parker and Nilon, 2008), Europe (e.g. red squirrel *Sciurus vulgaris;* Jokimäki *et al*., 2017), Africa (e.g. cape ground squirrel *Xerus inauris*; Chapman *et al*., 2012), South America (e.g. Brazilian squirrel *Sciurus aestuans*; Fernandes *et al*., 2019), and Asia (*Callosciurus* spp.; Lekagul and McKneely, 1977). These species play a number of important ecological functions, especially fruit and seed dispersal (Bobadilla *et al*., 2016) and in some cases pollination (Kobayashi *et al*., 2017), with their contributions in towns and cities likely to be particularly important due to the frequent rarity of other larger-bodied terrestrial frugivores in highly urbanised areas (Tucker *et al*., 2021). In tropical settings tree-shrews (*Tupaia* spp.), whilst phylogenetically distinct overlap with tree squirrels in their ecological functions (Langham, 1982; Lekagul and McNeely, 1977; Shanahan and Compton, 2000). Urban squirrels and tree shrews both create significant urban management problems many of which have important economic impacts, including gnawing electric wires (see Derbridge *et al.*, 2016) and damaging forestry and agricultural operations as well as ornamental plants (Lim, 2016; Lim, 1995). There is also concern that squirrels and tree-shrews can increase the transmission of zoonotic diseases (Deng *et al.*, 2016; Wulandhari *et al.*, In press).

Given the functional importance of squirrels it is important to understand the factors that influence their distribution and abundance in urban settings. Much attention has been given to the ecology of temperate squirrel species in urban environments, such as grey squirrels *S. carolinensis* in urban environments in their native (e.g. Koprowski *et al.*, 2016; Parker and Nilon, 2008) and non-native ranges (e.g. Bonnington *et al.*, 2013; La norgia *et al.*, 2017; Merrick *et al.*, 2016). Far less attention has been paid to the urban ecology of tropical squirrel species, and these regions are currently experiencing the greatest urban expansion rates (Seto *et al.*, 2012).

Our overall objective is to determine how the assemblages of squirrels and tree shrews within the greater Bangkok region respond to urbanisation. We focus on Bangkok as it provides a useful case study of a rapidly urbanising tropical mega-city (Estoque and Murayama 2015; Song *et al.* 2020) and is located within a biodiversity hotspot (Indo-Burma hotspot; Sodhi *et al.*, 2004). We start by assessing which of the species present in the wider region occur within urban locations, and quantify for each of these species how their abundance varies along a gradient of urbanisation intensity. We then assess how the abundance of each species is influenced by environmental conditions including key urban selection pressures namely: human disturbance (i.e. number of people), perceived predation pressure from human commensals (i.e. number of dogs and cats), habitat fragmentation (i.e. size and distance to the nearest suitable habitat — i.e. woodland), habitat quality (i.e. diversity and amount of trees), and availability of food resources (i.e. diversity and amount of fruit-bearing trees). Finally, *Callosciurus* squirrels are known to hybridise when their primarily allopatric geographic ranges come into contact (Balakirev and Rozhnov, 2019; Kuramoto *et al.*, 2012; Oshida *et al.*, 2007; Timmins and Duckworth, 2008). There is increasing evidence that anthropogenic habitat alteration can break down ecological barriers that limit inter-specific gene flow thus promoting hybridisation (Grabenstein and Taylor, 2018; Lamont *et al*., 2003; Nolte *et al*., 2003). Whilst urbanisation could break down ecological barriers (Grabenstein and Taylor, 2018), it is also plausible that urbanisation could reduce hybridisation rates by limiting population densities of one or more parental species. Relatively little research has assessed how urbanisation influences hybridisation although those studies that have been conducted to date have found increased hybridisation rates in a number of vertebrate groups including fish (Heath *et al*., 2010), reptile (Haines *et al*., 2016), and mammals (Frare *et al*., 2017).

3.2 Methods

Study area and survey sites selection

Our focal study region consists of a 70 km × 80 km rectangle (5,600 km^2) and centred on central Bangkok and covering parts of the surrounding provinces (Fig S3.1). Within this study region we constructed a grid of 1,400 2 km × 2 km grid cells, and classified each cell's landcover using high resolution Google Earth's imagery taken during 2017 to 2018 and a finer scale sampling grid comprising 100 uniformly distributed sampling point within each grid cell (based on Evans *et al*. (2009)). Each sampling point was classified as impervious surface cover, trees or other land cover categories (grassland, rice field, salt pan, green roof, bare ground, construction site, and water bodies, although these are not relevant for the purposes of this manuscript). We then delimited our study region as grid cells with over 25% impervious surface (following previous definitions of urbanised locations, e.g. Bonnington *et al*., 2013), resulting in an urban study region of 2,658 km^2 (Fig. 3.1a).

Within the urban study region, we used random stratification to select 15 1 km × 1 km sampling grid cells from each of ten categories of urbanisation intensity (0–10%, 11–20%, …, 91–100% vegetation cover), resulting in a total of 150 sampling grid cells (Fig. 3.1b). Survey points were selected at the centre of the randomly selected cell. When the centre of a grid cell was inaccessible, we used the nearest accessible location.

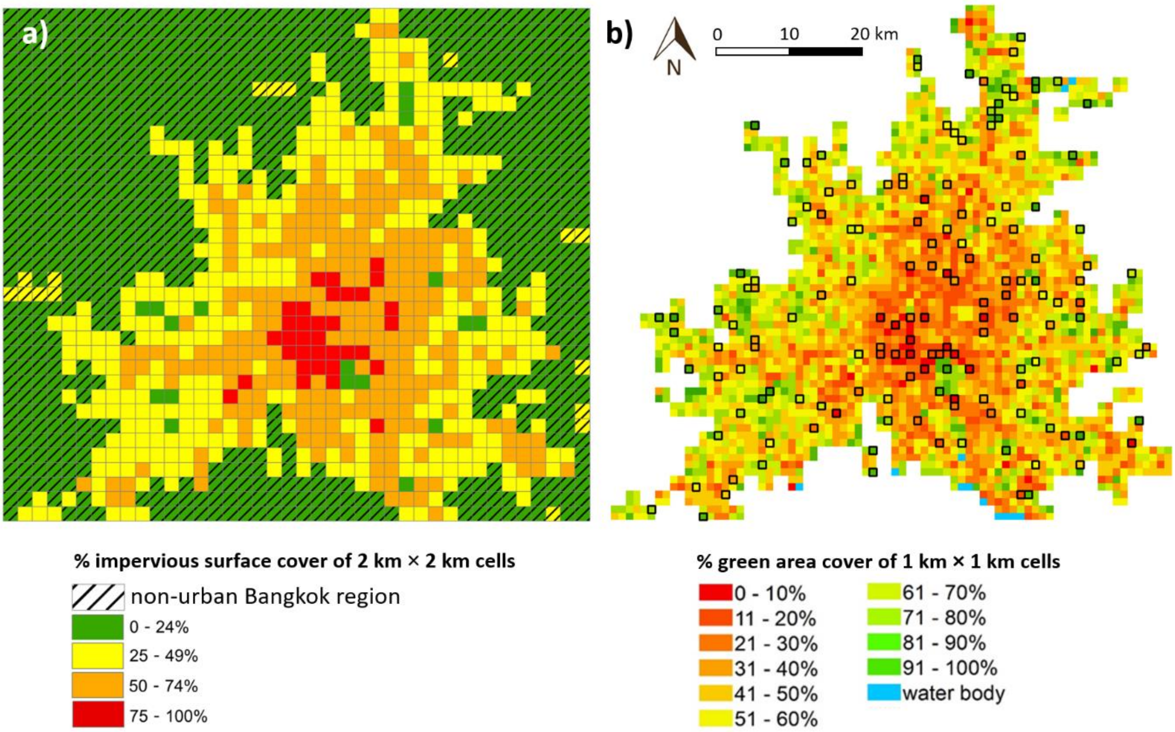


Figure 3.1: a) land cover map of the Bangkok study region showing percentage impervious surface cover of 2 km × 2 km grid cells used to define the study region. Grid cells with ≥25% impervious surface cover that were isolated from the main urban region were considered to be part of other urban settlements. Cells that had <25% impervious surface cover were considered to be non-urban unless they were completely surrounded by urban cells, b) the percentage green-space cover of 1 km × 1 km grid cells across the urban study region with grid cells outlined in black representing the 150 cells selected for sampling using random stratification across each categories of green-space (15 sampling grid cells each).

Squirrel surveys

Our sampling methodology is based on Bonnington *et al*. (2013). Squirrels and tree shrew surveys were conducted using 15-minute point counts with a 50m survey radius. Surveys were conducted on dry calm days from 6.30 am to noon. We used a rangefinder (Viking Compact Laser Rangefinder) combined with Google Earth map to ensure that detections were within the boundary of the survey plot. Each survey point was visited three times during March to July 2018 (first visit 12th March to 28th April; second visit 2nd May to 11th June; third visit 12th June to 25th July). These survey dates avoid the most intense parts of the rainy season whilst overlapping with periods of high squirrel and tree shrew activity. During each survey we recorded the number of adult individuals of each taxon present within the survey area — adults were distinguished from juveniles based on size as per criteria in Francis (2017) and Lekagul and McKneely (1977). When squirrels and tree-shrews were observed eating fruits, nuts, or seeds, we also noted which species they were consuming. Within each sampling period, we visited survey locations in an order that was unbiased with regard to their urbanisation intensity.

All detected squirrels and tree shrews were recorded and identified to species. Identification of northern tree-shrew *Tupaia belangeri* and Himalayan striped squirrel *Tamiops macclellandii* was straightforward and based on Francis (2017) and Lekagul and McKneely (1977). Separation of *Callosciurus* species is more complicated. We followed the criteria advocated by Boonkhaw *et al*. (2017), Francis (2017), Lekagul and McKneely (1977) and identified Finlayson's squirrel *C. finlaysonii*, Pallas's squirrel *C. erthyraeus*, and hybrids between these two species (hereafter called *C*. hybrid) depending on the precise colour patterns of the upperparts, tail, belly, and face (see Table S3.1; Fig. S3.2).

Environmental conditions and urban selection pressures

We recorded the total number of people within each point count radius during each of the three 15 minute surveys. An index of human disturbance was then calculated as the mean of these values. Similarly, we recorded the number of free-ranging cats and free-ranging dogs observed during each point count survey, and calculated mean dog and cat values for each point count to generate indices of predation pressure.

All trees within the point count radius with a diameter-at-breast-height (DBH) >25 cm were identified to species (based on Gardner *et al*. (2000) and Veesommai and Kavduengtian (2004)) and their height recorded (to the nearest 0.5 m, using a clinometer) and DBH (to the nearest 1 cm, measured at 1.3m). We defined tree species that produce food for squirrels as those a) within genera that produce seed, fruits, or nuts recorded as being consumed nby squirrels Kitamura *et al*. (2002) — based on their observation in Khao Yai National Park (a large natural forest located c. 80 km to the north-east of Bangkok), and b) any additional species that squirrels were noted as feeding upon during our surveys (primarily non-native species that are present in our focal survey area but not Khao Yai; Table S3.2). The diet of *Tupaia belangeri* overlaps with those of squirrels but the species only consumes fleshy fruit, and not nuts or seeds (Emmons, 1991; Lim, 1995) — we thus counted only those tree species upon which squirrels feed that have fleshy fruits as providing food for *T. belangeri* (Table S3.2). We then calculated the number of tree species within each point count locality that provide food for squirrels and tree-shrews. A tree's production of fruit is closely related to its size (Chapman *et al*., 1992; Snook *et al*., 2005; Ouedraogo *et al*., 2020) and we thus calculated aboveground tree biomass of each tree within the point count using the allometric equation of Chave et al. (2005). This equation was designed for use in tropical moist forests (annual precipitation 1,500–3,000 mm) which matches the climate in Bangkok (annual precipitation 1,808 mm; Polwiang, 2020). We then summed total biomass of fruit producing trees to provide an estimate of potential food availability for squirrels and tree-shrews within each point count.

We also obtained data on environmental conditions that relate to the area surrounding each point count location. The percentage impervious surface cover and tree cover of each 1 km × 1 km grid cell were obtained from our landcover classifications (see *Study area*). Our focal species primarily use woodland habitats (Bertonilo *et al*., 2004; Lekagul and McNeely, 1977). We thus used measuring tools in Google Earth (Google Earth Pro v7.3.2) to record the distance between our sampling location and the largest patch of woodland within the focal 1 km × 1 km grid cell, and (when the survey location overlapped with woodland) the size of the woodland within which our survey locations were located. These data were calculated using imagery taken within nine months of our field surveys.

The distributions of *C. finlaysonii* and *C. erythraeus* tend to be separated by the Chao-Praya river with *C. finlaysonii* occurring on the east bank and *C. erythraeus* on the western bank (Boonkhaw *et al*., 2017). Bridges that cross this river may enable one or more of these species to cross this geographic barrier, promoting hybridisation. We thus estimated the distance from each survey point to the nearest bridge (considering all bridges for which construction had been completed before our field surveys started, the most recent of which was constructed in 2007) that crosses the Chao-Praya river using the near function in ArcGIS (ArcGIS 10.7.1).

Data analysis

All analyses were performed using R-studio version 3.4.2 (R-studio Team, 2015)**.** There was limited variation in the number of squirrel and tree shrew species recorded at each location, even when pooling data across the three visits (median = 1; range 0–3; mean ± s.e. = 0.8 ± 0.1). Our analyses thus focus on quantifying the relationships between the abundance of each species and our suite of environmental variables. We used maximum abundance of each species recorded during our three surveys as response variables (note that maximum abundance and mean abundance of each species were very strongly correlated with each other; Kendall's Tau correlation test, Tau > 95% for each species; Table S3.3). Abundance of Himalayan striped squirrel is not modelled as it was only recorded at one survey location.

We modelled maximum abundance of each species and *C*. hybrids using generalised linear models (glm function). Poisson models were used for *T. belangeri* and *C*. hybrids (glm function). Negative binomial models (glm.nb function) were used for *C. finlaysonii* and *C. erythraeus* as Poisson models for these species were significantly overdispersed (Table S3.4; assessed using the dispersiontest function in the AER package).

We first quantify how each species responds to urbanisation by modelling maximum abundance of each species as a function of percentage impervious surface cover, including linear and quadratic terms to detect simple non-linear relationships. We select the quadratic model only when the quadratic term is significant (*P*<0.05) and the quadratic models has an Akaike Information Criterion values corrected for small sample size (AICc) that is at least two points lower than the AICc value of the linear model.

We then follow Whittingham et al. (2006) and construct full models that model maximum abundance of each focal species as a function of our indicators of urban conditions and selection pressures, i.e. percentage impervious surface cover (using quadratic terms where indicated by our first set of models), percentage tree cover in the grid cell, size of the woodland in which the sampling point is located (in ha, counted as zero if the point is outside a woodland), and distance to the largest woodland (m), mean number of people (ln-transformed), mean number of cats (ln-transformed), mean number of dogs (ln-transformed), tree species richness (ln-transformed), number of species of fruiting trees (ln-transformed), total aboveground tree biomass (ln-transformed), and aboveground tree biomass of fruit trees (ln-transformed; see Table 3.1 for more details). We modelled the maximum abundance of *C*. hybrids with the same set of predictor variables and with distance to the nearest bridge that crosses the Chao-Praya river as an additional predictor.

Variance inflation factors (VIFs, calculated using 'vif' function in the *car* package) were consistently below the threshold at which model inference is adversely impacted by multi-collinearity (Dorman *et al.*, 2013; Table S3.5). Model and partial r^2 values are calculated as KL-divergence-based r^2 (Cameron and Windmeijer, 1997) using the rsq package.

We used Moran's I tests (ape package) to check for spatial autocorrelation in the residuals from our models. Residuals from the urbanisation models of *C. erythraeus* and *C*. hybrids abundance, and the full model of *C. erythraeus* abundance exhibited significant spatial autocorrelation (P<0.05) although Moran's I values were consistently low (maximum value 0.11; Table S3.6). In these cases, we also constructed alternative models that took spatial autocorrelation into account. These were implemented using generalised linear mixed models approach with exponential spatial correlation structure (nlme package) and the parameter estimates for these models were very similar to those in the original non-spatial models (Table S3.7). We thus only report results from non-spatial models in the main manuscript.

Table 3.1: Description of predictor variables that were used in multiple regression models for maximum abundance of squirrels and tree shrews.

Predictor variables	**Units**	**Mean ± SE**	**Median**	**Range**	**Transformation**
% impervious surface cover of grid cell	%	46.9 ± 2.3	45.9	0 - 96.0	-
% tree cover of grid cell	%	22.6 ± 1.4	20.0	0 - 81.8	ln (x+1)
Woodland size	ha	1.2 ± 0.7	0	0 - 87.7	ln (x+1)
Distance to the largest woodland	m	246.6 ± 10.6	235.0	0 - 540.0	-
Distance to the nearest bridge	km	13.1 ± 0.7	11.9	0.2 - 37.5	-
Mean number of people	people	12.4 ± 1.6	5.0	1.0 - 122.7	ln (x)
Mean number of cats	individual	0.3 ± 0.1	0	0 - 5.3	ln (x + 1)
Mean number of dogs	individual	1.3 ± 0.2	0.7	0 – 10.3	ln (x + 1)
Tree species richness	species	5.9 ± 0.4	6	0 - 22	ln (x + 1)
Species richness of fruit trees for tree-shrews	species	1.2 ± 0.1	1	0 - 6	ln (x + 1)
Species richness of fruit trees for squirrels	species	1.8 ± 0.1	1	0 - 7	ln (x + 1)
Total AGB	t/ha	11.4 ± 1.0	8.0	0 - 89.9	ln (x + 1)
AGB of fruit trees for tree-shrews	t/ha	3.4 ± 0.7	0.7	0 - 86.1	ln (x + 1)
AGB of fruit trees for squirrels	t/ha	4.8 ± 0.8	2.1	0 - 86.6	ln (x + 1)

3.3 Results

We detected three species in the family Sciuridae. *Tamiops macclelandii* was extremely rare, being detected in just one location. *C. finlaysonii* was the most widespread species, occurring in approximately one third of grid cells, whilst *C. erythraeus* occurred in approximately one quarter of grid cells. The distribution of *C. finlaysonii* and *C. erythraeus* in Bangkok were largely separated by the Chao-Praya river (Fig. 3.3), with *C. finlaysonii* predominantly occurring on the eastern bank of the river and *C. erythraeus* primarily on the western bank. Hybrids between these two species occurred in 6% of grid cells, and were detected on both the eastern and western banks (Fig. S3.3). The one tree-shrew species (*Tupaia belangeri*) occurred in approximately one quarter of grid cells (Table S3.8).

Response to urbanisation intensity

T. belangeri abundance declined linearly with increasing urbanisation intensity, and was not detected at any survey locations in grid cells with over 80% impervious surface cover (Table 3.2; Fig. 3.2). *C. erythraeus* occurred across the entire urbanisation gradient and its abundance declined linearly with increasing urbanisation intensity (Table 3.2; Fig. 3.2). *C. finlaysonii* also occurred across the entire urbanisation gradient, and its abundance increased linearly with increasing urbanisation. Hybrids between *C. finlaysonii* and *C. erythraeus* did not occur in highly urbanised grid cells (>80% impervious surface cover), and their abundance was not significantly associated with urbanisation intensity (Table 3.2; Fig. 3.2).

Responses to urbanisation conditions and selection pressures

The full model of *T. belangeri* abundance had a model KL-divergence-based r^2 of 55% (Table 3.3). Abundance increased significantly with increasing grid cell tree cover (natural log-transformed) and tree species richness at the point count location (natural log-transformed), and marginally significantly with the biomass of tree species that provided fruit consumed by tree shrews (natural log-transformed). There were marginally significant negative relationships between *T. belangeri* abundance and mean number of dogs (natural log-transformed), distance to the largest woodland and woodland size (natural log-transformed). No other predictor variables, including the percentage of impervious surface cover, were significantly or marginally significantly associated with *T. belangeri* abundance.

The full model of *C. finlaysonii* abundance had a model KL-divergence-based r^2 of 41% (Table 3.3). Abundance was significantly positively associated with tree biomass within the point count (natural log-transformed). There were marginally significant positive associations with percentage impervious surface cover and marginally significant negative associations with distance to the largest woodland. Other predictor variables did not exhibit any significant or marginally significant relationship with *C. finlaysonii* abundance.

The full model of *C. erythraeus* abundance had a model KL-divergence-based r^2 of 46% (Table 3.3). Abundance of *C. erythraeus* increased significantly with percentage tree cover and impervious surface cover (note the switch from a negative relationship in the simpler urbanisation models). There was a significant negative relationship between *C. erythraeus* abundance and ln-transformed mean number of people, and a marginally significant negative relationship with log-transformed mean number of dogs. No other predictor variables were significantly or marginally significantly associated with *C. erythraeus* abundance.

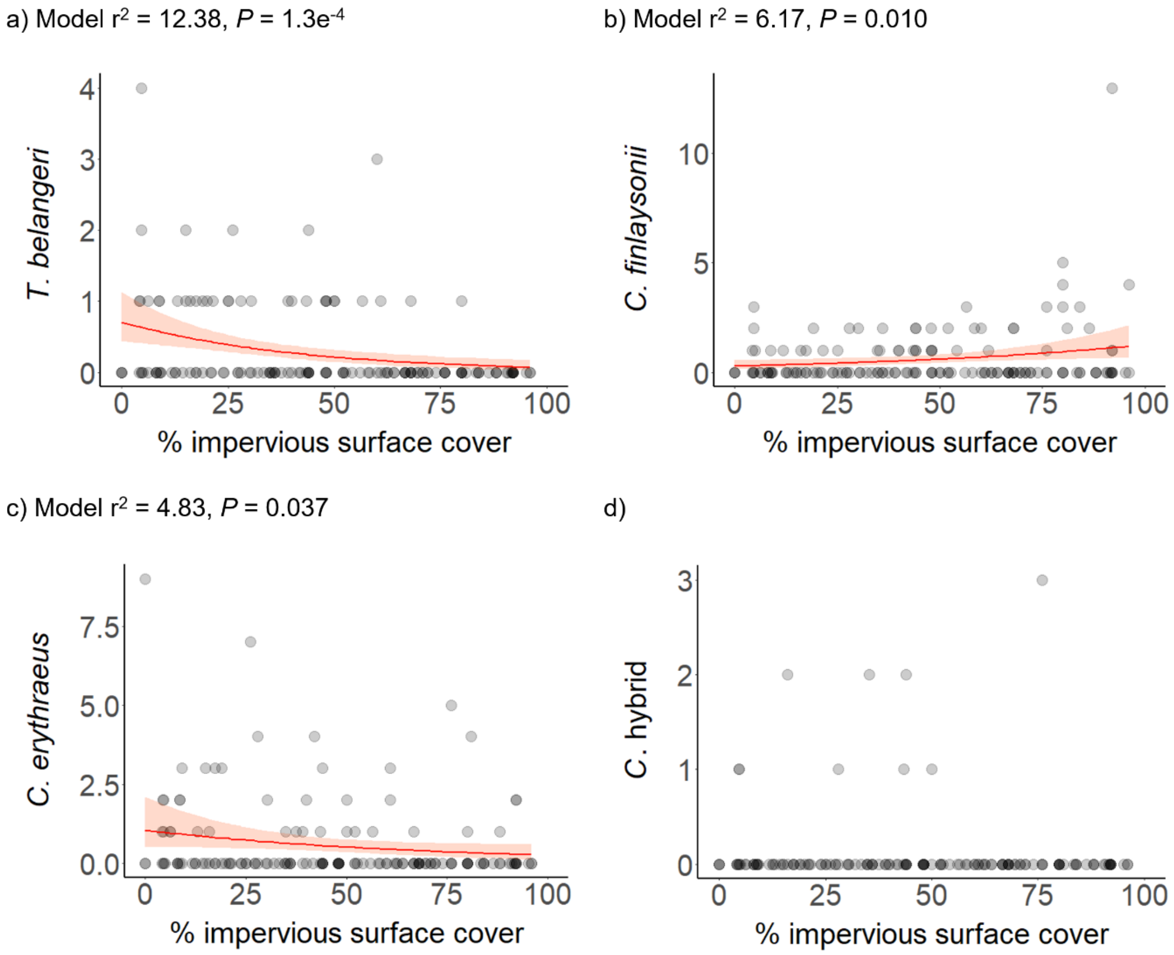
The full model of *C.* hybrids abundance had a model KL-divergence-based r^2 of 66% (Table 3.3). *C.* hybrids abundance increased significantly with tree biomass in the point count area (natural log-transformed), and marginally significantly with percentage tree cover in the grid cell (natural log-transformed). There were significant negative relationships between *C.* hybrids abundance with woodland size (ln-transformed), and distance to the nearest bridge, and marginally significant negative relationships with mean number of people (ln-transformed). No other predictors had significant or marginally significant associations with the abundance of *C.* hybrids.

Table 3.2: Model of the maximum abundance of each taxon in response to urbanisation intensity using generalised linear models (*T. belangeri* and *C*. hybrids abundance modelled with Poisson error structure; *C. finlaysonii* and *C. erythraeus* abundance modelled with a negative binomial error structure).

Response variable	Model	Model r^2	AICc	Intercept	%impervious surface (Linear term)		%impervious surface (Quadratic term)	
					Coeff ± SE	*P*	Coeff ± SE	*P*
T. belangeri	Linear	12.38	196.15	-0.349 ± 0.239	-0.024 ± 0.006	$1.3e^{-4}$		
	Quadratic	14.63	195.17	-0.773 ± 0.365	0.013 ± 0.023	0.562	$-4.8e^{-4} \pm 3.0e^{-4}$	0.103
C. finlaysonii	Linear	6.17	315.31	-1.260 ± 0.341	0.015 ± 0.006	0.010		
	Quadratic	6.61	316.91	-0.997 ± 0.492	-0.001 ± 0.023	0.971	$1.6e^{-4} \pm 2.2e^{-4}$	0.481
C. erythraeus	Linear	4.83	291.72	0.043 ± 0.354	-0.014 ± 0.007	0.037		
	Quadratic	5.21	293.47	0.247 ± 0.500	-0.029 ± 0.026	0.259	$1.6e^{-4} \pm 2.7e^{-4}$	0.550
C. hybrids	Linear	1.27	105.20	-1.953 ± 0.466	-0.010 ± 0.010	0.317		
	Quadratic	2.71	106.11	-2.514 ± 0.760	0.030 ± 0.039	0.448	$-4.5e^{-4} \pm 4.4e^{-4}$	0.303

Table 3.3: Multiple regression models of maximum abundance of *T. belangeri, C. finlaysonii, C. erythraeus*, and *C*. hybrid. Models are generalised linear models fitted with a Poisson error structure for *T. belangeri* and *C*. hybrid, and a negative binomial structure for *C. finlaysonii* and *C. erythraeus*. Parameter estimates and standard errors are in bold for significant predictors ($P<0.05$) and in italics for marginally significant predictors ($0.05 \le P < 0.10$). Model r^2 and partial r^2 were estimated as KL-divergence-based r^2 using rsq package which uses the methodology from Cameron and Windmeijer (1997). Asterisks indicate natural log-transformed predictor variables.

	T. belangeri (model r^2 = 55.07)			*C. finlaysonii* (model r^2 = 41.38)			*C. erythraeus* (model r^2 = 45.86)			*C.* hybrid (model r^2 = 65.56)		
	Coeff ± SE	Partial r^2	P	Coeff ± SE	Partial r^2	P	Coeff ± SE	Partial r^2	P	Coeff ± SE	Partial r^2	P
% impervious surface	-0.007 ± 0.010	0.86	0.469	*0.014 ± 0.008*	*2.82*	*0.075*	**0.023 ± 0.010**	**5.46**	**0.019**	0.010 ± 0.024	0.62	0.675
% tree cover*	**0.668 ± 0.305**	**9.21**	**0.029**	0.177 ± 0.219	0.56	0.420	**1.379 ± 0.367**	**15.89**	**1.7e^{-4}**	*1.585 ± 0.938*	*16.73*	*0.091*
Woodland size*	*-0.403 ± 0.220*	*5.66*	*0.067*	-0.202 ± 0.257	0.69	0.433	-0.146 ± 0.234	0.23	0.532	**-0.860 ± 0.414**	**16.34**	**0.038**
Distance to largest woodland	*-0.003 ± 0.002*	*5.57*	*0.063*	*-0.002 ± 0.001*	*3.21*	*0.081*	-0.002 ± 0.001	2.45	0.126	-0.005 ± 0.004	7.52	0.167
Mean no. of people*	-0.220 ± 0.225	1.59	0.328	0.207 ± 0.171	1.26	0.226	**-0.601 ± 0.218**	**7.28**	**0.006**	*-0.868 ± 0.498*	*11.50*	*0.081*
Mean no. of cats*	-0.540 ± 0.679	1.11	0.427	-0.348 ± 0.387	0.80	0.368	0.134 ± 0.539	0.06	0.803	0.738 ± 1.085	1.51	0.496
Mean no. of dogs*	*-0.512 ± 0.282*	*5.23*	*0.069*	0.024 ± 0.237	0.01	0.918	*-0.528 ± 0.276*	*4.07*	*0.055*	-1.042 ± 0.714	7.59	0.144
Tree species richness*	**1.112 ± 0.493**	**8.08**	**0.024**	0.264 ± 0.490	0.21	0.590	0.349 ± 0.565	0.45	0.537	0.927 ± 1.135	2.36	0.414
Fruit tree species richness*	-0.106 ± 0.557	0.06	0.849	0.567 ± 0.544	0.32	0.298	0.757 ± 0.608	1.84	0.213	-0.084 ± 0.890	0.03	0.925
Tree biomass*	0.501 ± 0.312	3.91	0.109	**0.945 ± 0.309**	**7.16**	**0.002**	0.427 ± 0.368	1.57	0.246	**3.234 ± 1.001**	**36.21**	**0.001**
Fruit tree biomass*	0.478 ± 0.289	*4.21*	*0.099*	-0.043 ± 0.271	0.02	0.874	-0.137 ± 0.321	0.20	0.671	*-1.108 ± 0.590*	*12.69*	*0.061*
Distance to the nearest bridge*										**-0.278 ± 0.106**	**37.01**	**0.009**



a) Model $r^2 = 12.38$, $P = 1.3e^{-4}$

b) Model $r^2 = 6.17$, $P = 0.010$

c) Model $r^2 = 4.83$, $P = 0.037$

d)

Figure 3.2: Relationships between the maximum abundance of *T. belangeri, C. finlaysonii, C. erythraeus*, and *C.* hybrids and percentage impervious surface cover. Fitted lines indicate predicted values, with shading indicating 95% confidence intervals, from generalised linear models reported in Table 3.2. *C.* hybrids abundance was not significantly associated with urbanisation intensity so no fitted line is provided.

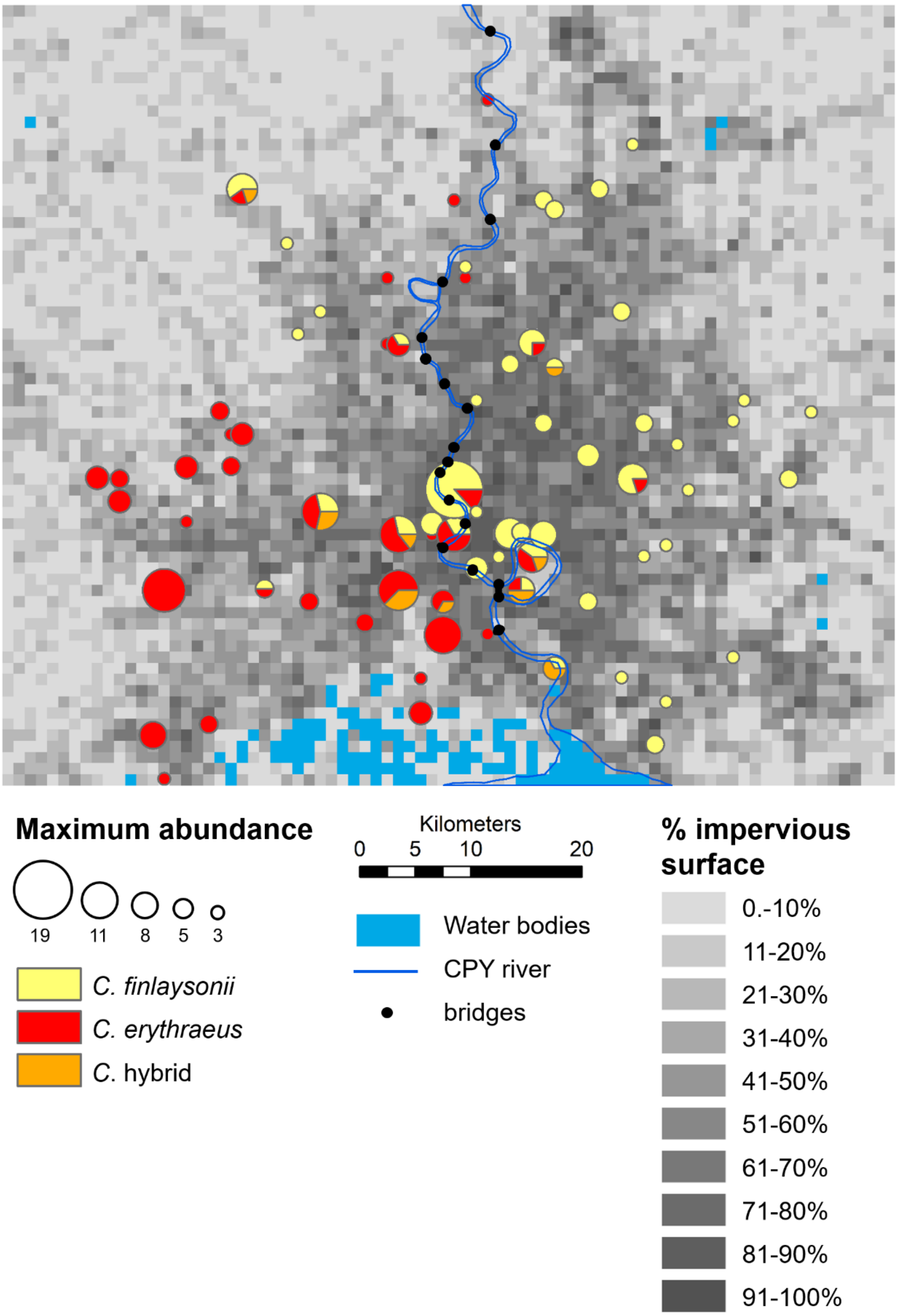


Figure 3.3: Maximum abundance and distribution of *C. finlaysonii* (yellow), *C. erythraeus* (red), and *C.* hybrids (orange) in 1 km × 1 km grid cells located along the urbanisation gradient. The size of the circles represents the maximum abundance of each species. Grey shading of the 1 km × 1 km grid cells represents percentage impervious surface cover, blue shading represents grid cells with >80% water bodies. Chao-Praya (CPY) river is shown a blue, with black circles indicating bridges crossing the river.

3.4 Discussion

Urban filtering of the regional species pool

Northern tree-shrew *Tupaia belangeri*, Finlayson's squirrel *C. finlaysonii*, and Pallas's squirrel *C. erythraeus* were widespread throughout much of our study region. In contrast, Himalayan striped squirrel *Tamiops macclellandii* was only detected at one sampling location. Two other diurnal squirrel species that occur in the Chao-Praya lowlands were not detected in our surveys, i.e. grey-bellied squirrel *Callosciurus caniceps* (Duckworth, 2016a) and Indochinese ground squirrel *Menetes berdmorei* (Duckworth, 2016b). Given our considerable sampling effort these species are either very rare or genuinely absent from the greater urban Bangkok area. One additional species, common giant flying squirrel *Petaurista philippensis*, also occurs in the Chao-Praya lowlands (Walston *et al*., 2016) and was not detected in our surveys, but is primarily nocturnal and our surveys are not well designed to detect this species. It is clear that urbanisation has driven a marked reduction in the number of squirrel species that occur regularly within the greater Bangkok region. This is perhaps surprising given that rodents and squirrels are amongst the mammalian groups that do relatively well in urban areas, although most such studies are based in temperate regions (Santini *et al*., 2018). Urbanisation induced declines in the number of squirrel species are thus likely to occur in other large tropical urban areas.

The absence of these squirrel species combined with the absence or extreme rarity of larger-bodied frugivorous arboreal mammals during our surveys that occur in more natural areas within the region, such as white-handed gibbon *Hylobates lar* (not detected; Brockelman and Geissmann, 2020), Indochinese silvered langur *Trachypithecus germaini* (not detected; Duc *et al*., 2021), and long-tailed macaque *Macaca fascicularis* (detected at just one sampling site; Eudey *et al*., 2020), suggests that habitat loss and alteration due to urbanisation in the Bangkok region will radically alter the contribution of mammalian frugivores to seed dispersal and other key ecological functions that such species provide (Corlett, 2017; Phiphatsuwannachai *et al*., 2018; Savini and Kanwatanakid-Savini, 2011)

Species responses to urbanisation

Despite being widespread within our study area the abundance of Northern tree-shrew *T. belangeri* and Pallas's squirrel *C. erythraeus* declined as urbanisation intensity increased.

Whilst such declines in abundance with increasing urbanisation are exhibited by urban avoiders (sensu Blair, 1996) both species occur in highly urbanised locations (up to 80% and 92% impervious surface cover respectively for *T. belangeri* and *C. erythraeus*), and this term thus seems inappropriate for these species. More importantly, our study region has experienced marked urban expansion into rural areas in recent decades (Estoque and Murayama 2015; Song *et al*. 2020), alongside increased impervious surface cover in areas that are already urbanised (see chapter 2) suggesting that increasing urbanisation will have reduced the regional population size of *T. belangeri* and *C. erythraeus*.

In contrast to *C. erythraeus*, the abundance of the congeneric Finlayson's squirrel *C. finlaysonii* increased with urbanisation intensity, indicating that this species is an urban exploiter (sensu Blair, 1996). Notably, the abundance of hybrids between *C. finlaysonii* and *C. erythraeus* was not significantly associated with urbanisation intensity. This pattern is intermediate between the contrasting patterns exhibited by the parental species and would thus be expected to occur if species' urban tolerance was partially genetically determined. This seems plausible given that studies find strong phylogenetic signals in inter-specific variation in urbanisation tolerance of some groups (e.g. reptiles; Winchell *et al*., 2020, birds; Callaghan *et al*., 2019; mammals, Johnson and Munshi-South, 2017), and evidence that urbanisation influences polymorphisms of candidate genes for behavioural traits influenced by urban selection pressures (Müller *et al*., 2013).

Impacts of environmental factors — woodland characteristics and human disturbance

When taking the amount of impervious surface cover into account, the availability of urban tree cover, at local or landscape scales, was positively associated with the abundance of each of our focal taxa. *T. belangeri* and *C. erythraeus* responded positively to percentage tree cover at the grid cell level, and *C. finlaysonii* and *C.* hybrids responded positively to tree biomass within the point count. In all cases a measure of tree abundance was the predictor variable with the greatest explanatory capacity, as expected again given the arboreal nature of these species (Bertonilo *et al*., 2004; Lekagul and McNeely, 1977). Our results thus strongly suggest that increasing urban tree cover can mitigate some of the adverse impacts of urbanisation intensity on our focal species. We found no evidence that measure of the abundance or diversity of food resources (in the form of fruit, nuts etc.) influenced the abundance of any if our focal taxa, suggesting that food availability is not regulating squirrel population sizes in our study system. This contrasts with research on factors determining urban squirrel population sizes in temperate areas (e.g. Bonnington *et al*., 2013; Jokimäki *et al*., 2017). The diversity of tree species was, however, positively correlated with *T. belangeri* abundance, suggesting that diverse woodlands provide either greater resources or a more temporally stable resources supply throughout the year (with different species providing resources at different time points). This provides further evidence to calls to diversity urban tree planting schemes (e.g. Alvey, 2006; Sjöman *et al*., 2012).

C. erythraeus and *C*. hybrids abundance declines with the numbers of people, suggesting that human disturbance negatively impacts these species. Notably when taking into account human disturbance and tree availability in our full models the abundance of *C. erythraeus* no longer exhibits a negative relationship with urbanisation intensity. This suggests that these two factors are contributing to the species' negative response to urbanisation and pointing towards potential mitigation. Previous research has shown that large mammals (George and Crooks, 2006) and some bird species (Kang *et al*., 2015) respond negatively to human activity in urban systems, but we are less aware of such evidence for smaller mammal species (although see Sauvajot *et al*., 1998). These are multiple benefits for increasing urban residents' interactions with nature for well-being and developing an interest in conservation (Coldwell and Evans, 2017). This needs to be balanced, however, against the conservation value of reducing disturbance in urban systems, which could potentially be achieved through a zoning system that limits human disturbance at some locations.

Impacts of environmental factors — predators (dogs and cats)

There is much concern regarding the adverse impacts of domestic cats *Felis catus* on wildlife populations, especially in temperate cities (Baker *et al*., 2008; Blancher, 2013; Loss and Marra, 2017), but we find no evidence for negative associations between free-ranging cat abundance and numbers of squirrels and tree-shrews. In contrast, when taking into account other measures of environmental quality, we find marginally significant negative associations between abundance of free-ranging dogs and the densities of *T. belangeri* and *C. erythraeus*. The ecological impacts of dogs *Canis lupus familiaris* have received less attention than those of *Felis catus* but evidence is increasing that negative impacts can arise either through disturbance or predation induced mortality (Young *et al*., 2011; Doherty *et al*., 2017). Our results are suggestive of the potential of such adverse impacts to be occurring in urban

Bangkok, as reported in some other studies of the impacts of free-ranging dogs on urban mammal assemblages (e.g. Mella-Méndez *et al*., 2019; Soultan *et al*., In press). Experimental manipulations of dog populations would be required to confirm a causal link between dog and squirrel abundances, and quantify the extent to which populations need to be reduced to minimise adverse ecological impacts. Such research is urgently required as the feral dog population is continuing to increase in urban Bangkok with an estimated population size of 140,000 individuals in 2016 (DLD, 2016), relative to just 40,000 individuals in 1992 (Kasempimolporn *et al*., 2011). Such increases are primarily driven by ineffective control measures (Hemachudha, 2005; Toukhsati *et al*., 2015), which is a common situation across the globe (Smith *et al*., 2019).

Urbanisation influences on inter-specific hybridisation

Our results confirmed the previous suggestion Boonkhaw *et al*. (2017) that the Chao-Praya river acts as a geographic barrier that, in our study region partially, separates the distributions of *C. finlaysonii* and *C. erythraeus.* These hybridising congeneric species exhibit divergent responses to urbanisation (see section *Species responses to urbanisation*), thus creating the potential for urbanisation to reduce hybridisation rates. This potential is not, however, realised as we find that hybrids are relatively frequent within our study area – including in highly urbanised locations. Notably, we find that hybrids are more abundant in grid cells that are closer to bridges crossing the Chao-Praya river – suggesting that urban infrastructure is breaking down the effectiveness of geographic barriers and increasing hybridisation rates. Studies using genetic markers or genome sequencing to document more completely the impacts of urbanisation on inter-specific gene flow between *C. finlaysonii* and *C. erythraeus* are now required. Bridges that crossed the Chao-Praya river at the time of our study were largely devoid of vegetation and bridge assisted dispersal across the river barrier is thus likely to have been a relatively rare event given that parental species distribution are still primarily confined to either side of the river. This situation is, however, likely to be changing following the construction in 2020 the first garden, i.e. vegetated, bridge across the Chao-Praya river. Our data provide a suitable base-line for assessing the impacts of this potential corridor on species distributions and hybridisation rates.

3.5 Conclusions and recommendations

Rapid and ongoing urbanisation in the Bangkok region has reduced the diversity and abundance of squirrels and tree-shrews, with likely negative impacts on the ecosystem services these species provide — especially seed dispersal. These is inter-specific variation in responses to urbanisation, however, with one species *C. finlaysonii* becoming more abundant in urbanised locations. As expected for arboreal species tree abundance is a key determinant of squirrel and tree-shrew abundance, and increasing tree cover (and diversity) can help mitigate the generally adverse impacts of urbanisation on our focal mammal assemblage. Our focal suite of species is also likely to benefit from policy interventions that reduce disturbance from people and more effective control of the free-ranging dog population. Urbanisation also appears to be increasing hybridisation between *C. finlaysonii* and *C. erythraeus* although rates of inter-specific gene flow need to be confirmed with genetic markers or sequencing.

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3.7 Supplementary materials

Table S3.1: Identification of *Callosciurus* squirrels present in this study based on morphological characteristics described by Francis (2017) and Lekagul and McKneely (1977) – see Fig. S3.2 for example photos. Descriptions of *C. finlaysonii* were based on two subspecies (*C. finlaysonii bocourti* and *C. finlaysonii floweri*) that can be commonly found in the Chao-Praya lowland (Boonkhaw *et al*., 2017; Lekagul and McKneely, 1977).

	Taxa		
	C. finlaysonii	*C. erythraeus*	*C.* hybrid
Upperparts	Varies from completely creamy white to creamy white with dark colour (i.e. grey, black, or olive-brown), may have white hairs scattered through the dark upperparts	Agouti brown, sometimes with black dorsal stripe	Agouti brown
Tail	Varies from completely creamy white to creamy white with dark colour (i.e. grey, black, or olive-brown), or completely fulvous in which sometimes form faint blackish stripes	Agouti brown, usually form blackish stripes	Agouti brown, usually form blackish stripes
Belly	Creamy white	Red with grey or agouti midventral band	Red with grey or black midventral band
Face	Varies from completely creamy white to creamy white with dark colour (i.e. grey, black, or olive-brown) extend from the back with a complete or partial white ring around the eyes	Agouti brown, without a partial white ring around the eyes	Agouti brown, with a partial white ring around the eyes

Table S3.2: Lists of tree species in this study whose seeds, fruits, or nuts are consumed by squirrels and tree-shrews based on a) data from a study in Khao Yai National Park (squirrel only; Kitamura et al., 2002) or b) observations of squirrels and tree-shrews during fieldwork for this study. We assume, following Emmons (1991), that tree-shrews consume all fleshy fruits but not other type of fruits, that are consumed by squirrels.

Scientific name	Fruit consumed by squirrels	Fruit consumed by tree-shrews	Occurrence
Mangifera indica	a, b	yes	64 (42.7%)
Cocos nucifera	b	no	24 (16.0%)
Artocarpus heterophyllus	b*	no	22 (14.7%)
Terminalia catappa	a, b	no	22 (14.7%)
Ficus religiosa	a	yes	21 (14.0%)
Ficus benjamina	a, b	yes	20 (13.3%)
Delonix regia	b	no	16 (10.7%)
Terminalia ivorensis	a, b	no	14 (9.3%)
Syzygium cumini	a, b	yes	13 (8.7%)
Sandoricum koetjape	a	yes	11 (7.3%)
Ficus benghalensis	a	yes	7 (4.7%)
Elaeocarpus hygrophilus	a	yes	6 (4.0%)
Monoon longifolium var. pendula	a	yes	6 (4.0%)
Syzygium malaccense	a	yes	6 (4.0%)
Michelia champaca	a	yes	5 (3.3%)
Syzygium samarangense	a	yes	5 (3.3%)
Ficus microcarpa	a	yes	4 (2.7%)
Ficus racemosa	a	yes	3 (2.0%)
Monoon longifolium var. longifolium	a	yes	3 (2.0%)
Michelia alba	a	yes	2 (1.3%)
Borassus flabellifer	b	no	1 (0.7%)
Diospyros decandra	a	Yes	1 (0.7%)
Ficus altissima	a	Yes	1 (0.7%)

Table S3.3: Correlations between mean abundance and maximum abundance of the focal taxa. Kendall's Tau correlation is used due to the non-parametric distributions of the data.

Species	Kendall's Tau correlation test results Between mean abundance × maximum abundance		
	z	Tau	*P*
T. belangeri	12.325	0.986	$6.6e^{-35}$
C. finlaysonii	12.571	0.957	$3.1e^{-36}$
C. erythraeus	12.816	0.970	$1.3e^{-37}$
C. hybrids	12.200	0.991	$3.1e^{-34}$

Table S3.4: Overdispersion test (AER package) results (dispersion parameter and *P*-values) for each response variable when modelled in a Poisson model as a linear function of percentage impervious surface cover, a quadratic function of percentage impervious surface cover, and a full model including our suite of predictor variables describing urban environmental conditions and selection pressures. Response variables with significant overdispersion (in bold) are modelled using a negative binomial model.

Response variable	Overdispersion test results					
	Linear urbanisation model		Quadratic urbanisation model		Full model	
	Dispersion	*P*	Dispersion	*P*	Dispersion	*P*
Maximum number of *T. belangeri*	1.214	0.170	1.223	0.161	0.878	0.980
Maximum number of *C. finlaysonii*	**2.245**	**0.047**	**2.118**	**0.038**	**1.911**	**0.028**
Maximum number of *C. erythraeus*	**2.780**	**0.001**	**2.713**	**0.001**	**2.317**	**0.010**
Maximum number of *C.* hybrids	1.529	0.063	1.927	0.084	0.983	0.726

Table S3.5: Variance Inflation Factors (VIFs) values of multiple regression models of maximum abundance of each focal taxa when using our complete suite of predictor variables in full models. Note that distance to the nearest bridge is only used as a predictor when modelling the abundance of *C.* hybrids. There is no evidence that multi-collinearity is sufficiently large to distort model inference (VIF < 10; Dormann *et al.*, 2013).

Predictor	VIFs		
	T. belangeri	*C.* spp	*C.* hybrid
% impervious surface	2.38	2.18	4.32
% tree cover	1.82	1.97	3.57
Size of woodland	3.38	2.00	6.33
Distance to largest woodland	1.82	1.39	2.70
Mean numbers of people	2.40	2.17	3.41
Mean number of cats	1.61	1.51	2.36
Mean number of dogs	1.41	1.19	3.82
Tree species richness	2.27	3.51	2.63
Fruit tree species richness	3.41	4.22	2.84
Tree biomass	1.55	2.97	4.37
Fruit tree biomass	3.10	3.68	3.70
Distance to the nearest bridge	-	-	4.04

Table S3.6: Moran's I test (ape package) results of models for each response variable as a linear function of percentage impervious surface cover, a quadratic function of percentage impervious surface cover, and a full model including our suite of predictor variables describing urban environmental conditions and selection pressures. Models with significant spatial autocorrelation were shown in bold.

Response variable	Moran's I test results					
	Linear urbanisation model		Quadratic urbanisation model		Full model	
	Observed	*P*	Observed	*P*	Observed	*P*
Maximum number of *T. belangeri*	0.009	0.291	0.001	0.600	-0.008	0.951
Maximum number of *C. finlaysonii*	0.018	0.123	0.019	0.096	0.013	0.188
Maximum number of *C. erythraeus*	**0.104**	**$2.5e^{-13}$**	**0.104**	**$1.9e^{-13}$**	**0.054**	**$3.1e^{-5}$**
Maximum number of *C.* hybrid	**0.019**	**0.049**	**0.016**	**0.039**	-0.009	0.654

Table S3.7: omparison of coefficients and standard errors in non-spatial and spatial models of response variables where there is evidence of significant spatial autocorrelation (Table S3.6): a) maximum abundance of *C. erythraeus* and *C.* hybrids as function of impervious surface percentage (linear and quadratic urbanisation models), b) maximum abundance of *C. erythraeus* as a function of the full suite of predictor variables. Spatial models were constructed using generalised linear mixed models (nlme package) with an exponential covariance structure.

a)

Model	Model type	Intercept	%impervious surface (Linear term)		%impervious surface (Quadratic term)	
			Coeff ± SE	*P*	Coeff ± SE	*P*
C. erythraeus (Linear model)	Non Spatial	0.043 ± 0.354	-0.014 ± 0.007	0.037		
	Spatial	0.026 ± 0.386	-0.014 ± 0.008	0.057		
C. erythraeus (Quadratic model)	Non Spatial	0.247 ± 0.500	-0.029± 0.026	0.259	$1.6e^{-4} \pm 2.7e^{-4}$	0.550
	Spatial	0.287 ± 0.518	-0.034 ± 0.026	0.189	$2.2e^{-4} \pm 2.7e^{-4}$	0.409
C. hybrids (Linear model)	Non Spatial	-1.953 ± 0.466	-0.010 ± 0.010	0.317		
	Spatial	-1.241 ± 0.737	-0.024 ± 0.017	0.163		
C. hybrids (Quadratic model)	Non Spatial	-2.514 ± 0.760	0.030 ± 0.039	0.448	$-4.5e^{-4} \pm 4.4e^{-4}$	0.303
	Spatial	-2.090 ± 1.147	0.034 ± 0.058	0.558	-0.001 ± 0.001	0.379

b)

Predictor	Maximum abundance of *C. erythraeus*			
	Non-spatial		Spatial	
	Coeff ± SE	*P*	Coeff ± SE	*P*
% impervious surface	0.023 ± 0.010	0.019	0.023 ± 0.010	0.021
% tree cover*	1.379 ± 0.367	$1.7e^{-4}$	1.379 ± 0.368	$3.0e^{-4}$
Woodland size*	-0.146 ± 0.234	0.532	-0.146 ± 0.235	0.534
Distance to largest woodland	-0.002 ± 0.001	0.126	-0.002 ± 0.001	0.129
Mean no. of people*	-0.601 ± 0.218	0.006	-0.601 ± 0.219	0.007
Mean no. of cats*	0.134 ± 0.539	0.803	0.134 ± 0.541	0.804
Mean no. of dogs*	-0.528 ± 0.276	0.055	-0.528 ± 0.277	0.058
Tree species richness*	0.349 ± 0.565	0.537	0.348 ± 0.567	0.540
Fruit tree species richness*	0.757 ± 0.608	0.213	0.757 ± 0.610	0.216
Tree biomass*	0.427 ± 0.368	0.246	0.427 ± 0.369	0.249
Fruit tree biomass*	-0.137 ± 0.321	0.671	-0.137 ± 0.322	0.673

Table S3.8: Data on occupancy (defined as present in at least one of three surveys) and maximum abundance of each taxa at randomised survey points at the centre of 150 1 km × 1 km grid cells selected using random stratification across the urbanisation gradient.

Species	Occurrence		Maximum abundance		
	Number of grid cell	%	Range	Mean ± SE	Median
Family: SCANDENTIA					
Tupaia belangeri	34	23.0	0 - 4	0.29 ± 0.05	0
Family: SCIURIDAE					
Callosciurus finlaysonii	47	31.3	0 - 13	0.63 ± 0.11	0
Callosciurus erythraeus	38	25.3	0 - 9	0.58 ± 0.11	0
Callosciurus hybrid	9	6.0	0 - 3	0.09 ± 0.03	0
Tamiops macclelandii	1	0.7	0 - 2	0.01 ± NA	0

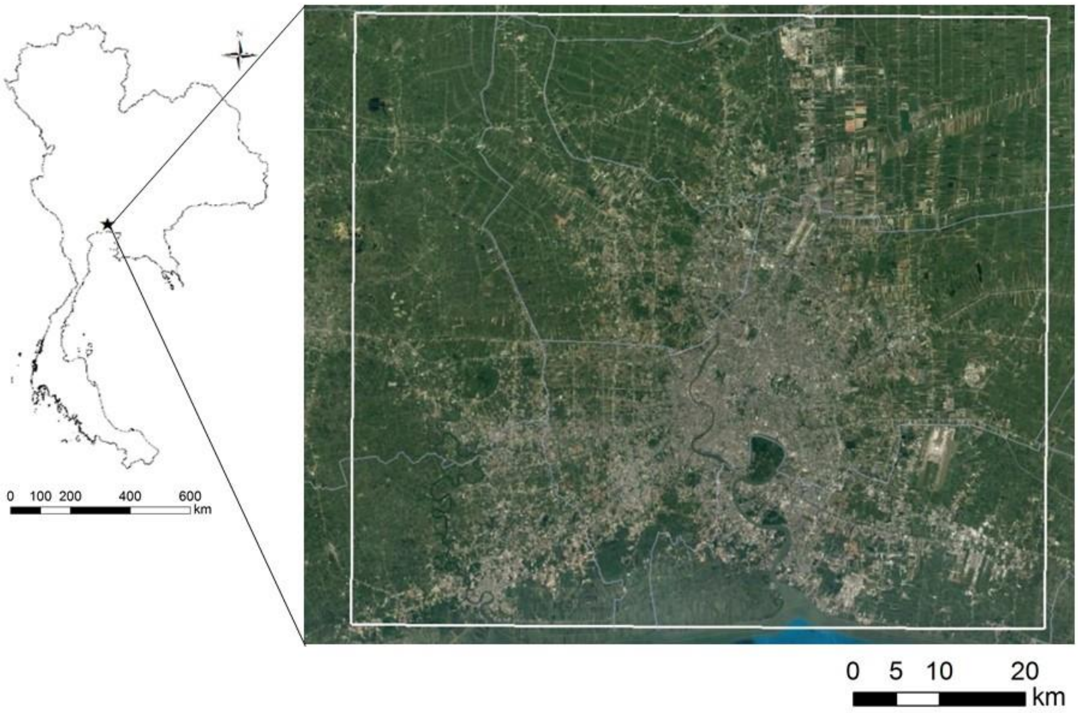

Figure S3.1: Map of Thailand showing the location of Bangkok and an inset map of the Bangkok region (using aerial imagery taken in 2018). The rectangle with grey border represents the 70 km × 80 km rectangle delimiting our study region.

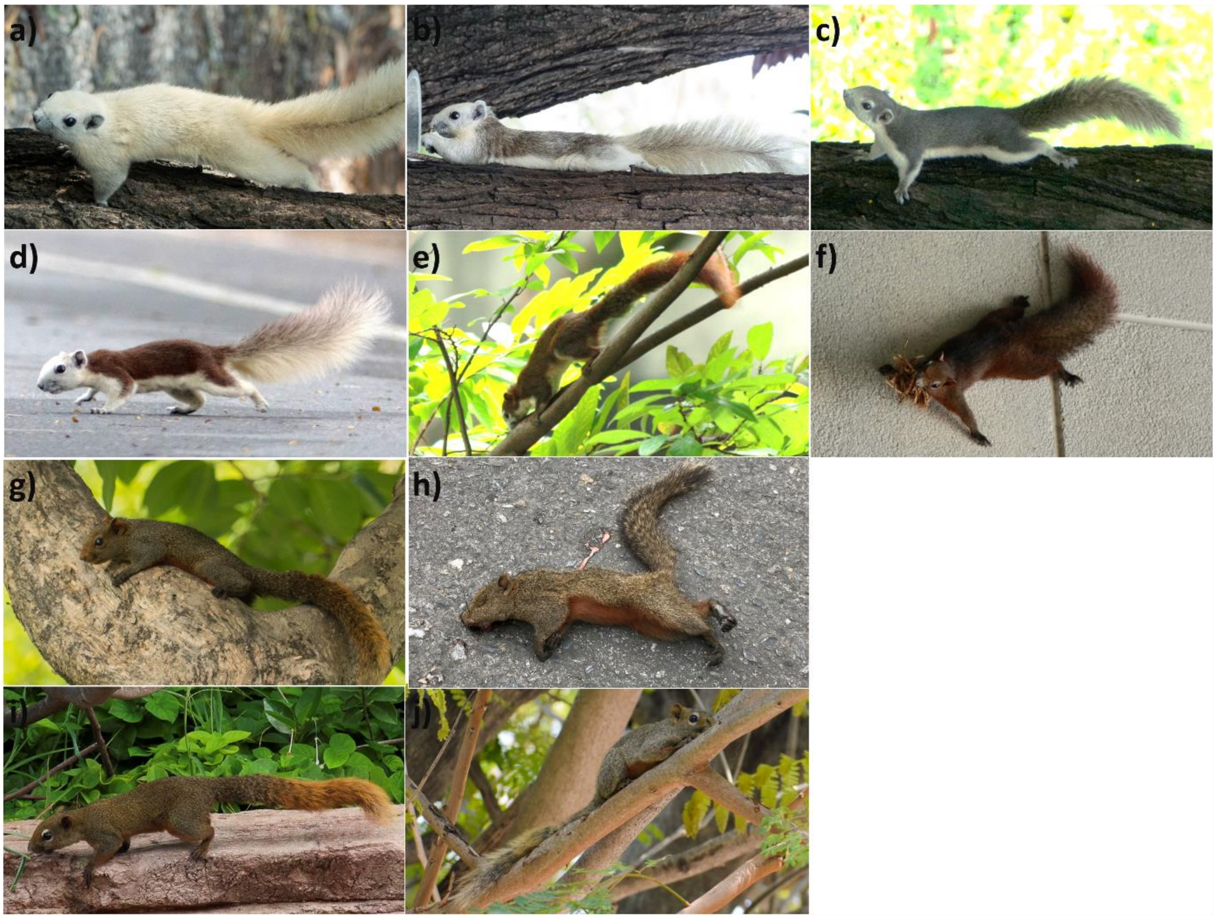

Figure S3.2: *Callosciurus* squirrels in Bangkok: *C. finlaysonii* (a-f), *C. erythraeus* (g, h), and *C.* hybrids (i, j). Photos taken by Budda Chotimanvijit (a-d, g), Phakhawat Thaweepworadej (e, f, h), Thanawat Jinjarak (i), and Nidchakan Chidcheaw (j).

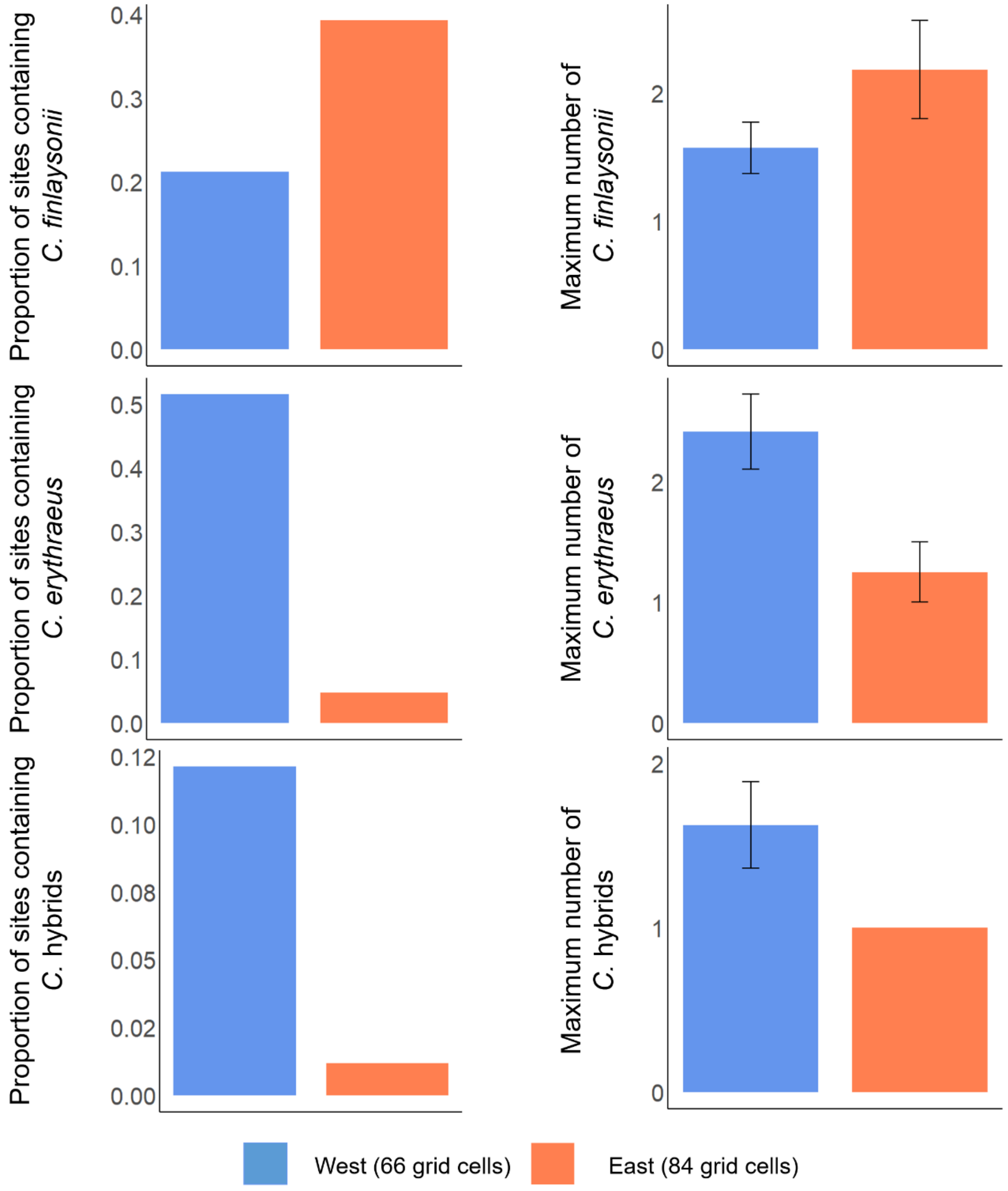

Figure S3.3: Proportion of grid cells containing squirrels and mean maximum abundance of *Callosciurus* squirrels, with error bars representing standard error, comparing between western (blue) and eastern (orange) side of the Chao-Praya river.

CHAPTER FOUR

Species richness and ecosystem services of tree assemblages along an urbanisation gradient in a tropical mega-city: consequences for urban design (in preparation for the journal Urban Forestry & Urban Greening)

Abstract

Understanding how urban tree species richness and ecosystem service contributions vary along tropical urbanisation gradients is incomplete. We explore these questions use a rapidly expanding mega-city (Bangkok, Thailand) as a case-study and quantify contributions of native and non-native species to ecosystem services. We conduct tree surveys in 150 1 km grid cells selected by random stratification across a gradient of urbanisation intensity. In each cell, surveys were conducted at the centre (representing typical conditions) and in the largest patch of trees (assessing woodland retention impacts). We estimated trees' contributions to i) carbon storage, ii) food production for people, iii) biodiversity support (using production of food for frugivorous birds as an indicator), and iv) economic value (assessed by regulations regarding use of trees as collateral for financial loans). Urbanisation has substantially reduced tree species richness relative to nearby natural forests, yet species richness (including of natives) and ecosystem service provision is relatively stable across the urbanisation gradient. These patterns contrast with those typically found in temperate regions. Moreover, they suggest that in tropical regions, with large amounts of natural tree cover, providing additional urban land through high intensity developments that require less space may benefit regional biodiversity without compromising ecosystem services. Results from woodland points highlight the potential of woodland retention to enhance biodiversity and ecosystem service provision – even in highly urbanised locations. Ecosystem services and species richness were not strongly positively correlated with each other. Urban planners must therefore pay attention to both attributes as biodiversity and ecosystem services will not automatically accrue from each other. Policies promoting use of trees as collateral for economic loans may reduce tree removal and encourage tree planting, but the list of eligible tree species warrants expansion to promote biodiversity support and ecosystem service provision, and increase resilience against future environmental instability.

Keywords: exotic trees, food security, fruit trees, land sparing and land sharing, payment for ecosystem services, urban forest

4.1 Introduction

Trees are a key component of urban biodiversity that deliver numerous ecosystem services that enhance urban residents' quality of life. Trees provide aesthetic and cultural services which contribute to human well-being and mental health (Nesbitt *et al*., 2017). They also play a major role in regulatory services (e.g. cooling urban heat islands (Ziter *et al*., 2019), reduction of air pollution (Nowak *et al*., 2018), and flood mitigation (Berland *et al*., 2017)). Urban trees can also provide food for people (Bunge *et al*., 2019), thus contributing to initiatives that aim to increase food security via urban horticulture (Edmondson *et al*., 2020). Urban trees further contribute to provisioning services via timber production, which in some countries, e.g. Thailand, is monetarised by allowing tree owners to use trees as collateral for financial loans (BAAC, 2020; Thailand. Ministerial Regulation, 2018). In addition to these ecosystem service contributions, urban trees play a key functional role in sustaining urban biodiversity by providing habitat and resources for a wide range of invertebrates and vertebrates (Somme *et al*., 2016; Wood and Esaian, 2020).

Despite these benefits urban trees are threatened from increasing urban expansion and densification (Nowak and Greenfield, 2020). Urbanisation is a major driver of changes in plant communities, especially in tropical regions where urban development often profoundly degrades areas of high biodiversity value (Hughes, 2017). During the early stages of urban development, original tree cover is frequently lost to impervious surface (i.e. building, road, pave ground etc.) as human population density increases (Nowak and Greenfield, 2012). In some locations, this loss of original tree cover is subsequently partially compensated for by tree planting along streets and in newly created urban green spaces, such as gardens and parks, but typically only many decades after the initial phases of urban establishment and expansion (Díaz-Porras *et al*., 2014; Thaiutsa *et al*., 2008). Moreover, urban tree planting schemes typically use fewer species and have a greater proportion of non-native species than originally present (Morgenroth *et al*., 2016; Schlaepfer *et al*., 2020)

Changes in tree abundance, size, and community composition along the urban-rural gradient alters their capacity to provide ecosystem services and support other forms of biodiversity (Radford and James, 2013; Tratalos *et al*., 2007). Studies typically find that plant species richness, at least of native species, peaks at intermediate levels of urbanisation intensity (McKinney, 2008), although some studies report linear declines with increasing urbanisation intensity (Burton and Samuelson, 2008; Zhang *et al.*, 2017). There is, however, a geographical bias in these studies towards temperate regions, concurring with a general bias in ecological studies away from the tropics (Martin *et al.*, 2012). It is thus unclear if changes in species richness along urbanisation gradients in tropical locations will match those documented in temperate regions. Contrasting patterns may well arise in tropical locations as semi-natural and agricultural habitats in such landscapes are often less intensively managed than in temperate locations — thus increasing species richness at the rural end of the gradient. In addition, human planting decisions are a key driver of plant diversity in the urban landscape (Whitney and Adams, 1980), and the cultural and economic factors influencing these are likely to differ between temperate and tropical locations.

Due to the multi-functional nature of urban green-space, there is much interest in assessing if spaces that maximise provision of one function, such as carbon storage, also maximise the provision of alternative functions, such as supporting biodiversity (Nelson *et al.*, 2009). Such questions relate to the debate regarding the relationship between biodiversity and provision of ecosystem services. One view is that high quality relatively intact ecosystems are likely to be diverse whilst also maximising ecosystem function and provision of services (Gamfeldt *et al.*, 2013). Species richness alone may not, however, be a strong indicator of ecosystem function and ecosystem service provision, as it ignores the functional traits of the component species that ultimately determine ecosystem service provision (Schuler *et al.*, 2017). Annual fluctuations in environmental conditions can generate a situation where species' relative contributions to ecosystem services change from year to year. Consequently, increasing species richness enhances the probability that, in all years, conditions will be optimal for at least one species. Therefore, provision of ecosystem services that are determined by accumulation of plant biomass over multiple years, such as carbon storage, are predicted to be greatest in more diverse assemblages (Slade *et al.*, 2019).

Conservationists have traditionally prioritised planting of native species, including in urban ecosystems, due to a perceived enhanced ability of natives to support biodiversity, but this idea has been challenged as non-natives can contribute to ecosystem services (Almas and Conway, 2016; Castro-Díez *et al.*, 2019) and may support native biodiversity (Davis, 2011; Schlaepfer *et al.*, 2020). There is thus a need for empirical assessment of the relative contributions of native and non-native species to provision of ecosystem services and capacity to support biodiversity to inform the sustainable planning and management of urban environments. Ideally, such assessments should consider how these relative contributions change along the urbanisation gradient. It is plausible, for example, that urban heat islands increase the risk that native species will face unfavourable climatic conditions in highly urbanised locations (Burley *et al.*, 2019). Consequently, at least in temperate regions, where non-native species typically originate from warmer climates, non-natives may be more capable of providing ecosystem services (Walther *et al.*, 2009).

In this study, our core research questions are to quantify how i) tree species richness, ii) exemplar key ecosystem services — carbon storage, human food provisioning potential, economic value, and the capacity to support biodiversity (using food provision for frugivorous birds as an indicator) vary along a tropical urbanisation gradient. When addressing these questions, we assess if native and non-native species exhibit similar or divergent patterns along the urbanisation gradient. We then assess if patterns vary when sampling trees in randomly selected locations across the urbanisation gradient or in the largest patch of trees within each sampling grid cell. This sampling design provides useful data for assessing the potential for retention and creation of urban woodlands to alter species richness and ecosystem services provision along the urbanisation gradient. Finally, we quantify associations between tree species richness and ecosystem service provision to assess the extent to which hotspots of biodiversity and ecosystem service provision overlap. We use Bangkok (Thailand) as a case study as it is located within the Indo-Burma biodiversity hotspot and is one of the most rapidly urbanising mega-cites in southeast Asia (Xu *et al.*, 2019).

4.2 Methods

Study area and selecting survey points

We delimited a 5,600 km^2 area (1,400 2 km × 2 km grid cells) centred on central Bangkok and covering the wider region (Fig. S4.1). We defined the urban study regions as cells with at least 25% impervious surface cover, using landcover classifications from high-resolution Google Earth's imagery (images from 2017 or 2018) at 100 uniformly distributed sampling points within each cell (Fig. 4.1a). We classified each 1 km × 1 km grid cell as one of ten urbanisation intensity bands based on percentage vegetation cover (i.e., 0–10%, 11–20%, …, 91–100%) and used random stratification to select 15 1 km × 1 km grid cells within each green area category, resulting in a total of 150 sampling grid cells (Fig. 4.1b; this approach and use of different spatial scales to define an urban region and select grid cells follows Bonnington *et al*., 2014).

Tree surveys

Tree surveys were conducted at two locations within each randomly selected cell. The first was at the cell centre, using the nearest accessible location if this was inaccessible (Fig. 4.1b). These points represent tree assemblages typical of urbanisation intensity, hereafter called 'randomised points'. A second survey was conducted within the largest patch of trees within each cell, hereafter termed 'woodland points'. These points purposefully target locations that represent how woodland retention or creation can influence biodiversity and ecosystem service provision given surrounding levels of urbanisation. Woodland survey points were selected in all but three cells in which the randomised point was located within the largest patch of trees.

Surveys were conducted in a 50 m fixed radius plot centred on the sampling point. All trees located within this plot (i.e. their trunk's centre was within the plot) and with a diameter-at-breast-height (DBH) >25 cm were identified to species and their DBH recorded (to the nearest 1 cm) and height (to the nearest 0.1 m) recorded using a clinometer. Species were classified as native or non-native to Thailand using Thai Plant Names (Smitinand, 2014), distribution maps from Plants of the World (POWO, 2019) and Agroforestree Database (Orwa *et al*., 2009; Table S4.1).

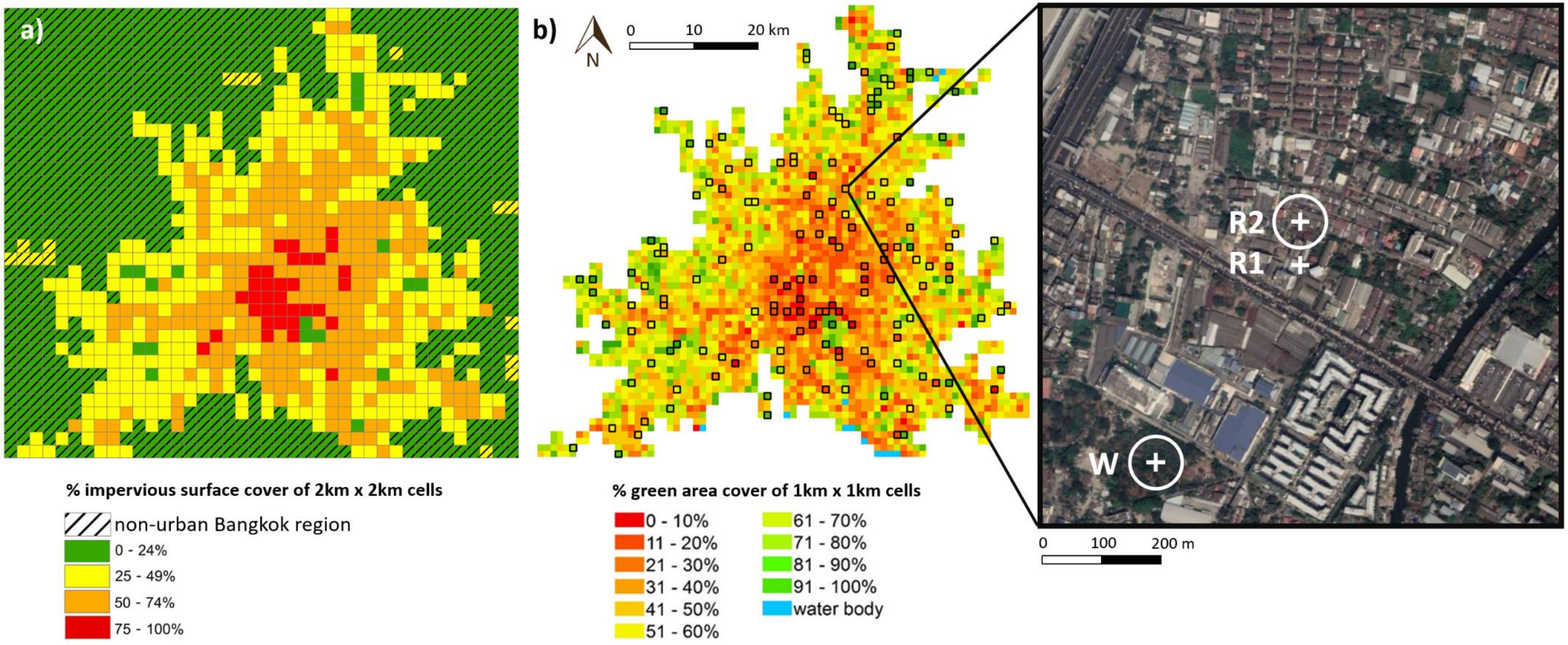

Figure 4.1: a) land cover map of the Bangkok study region showing percentage impervious surface cover of 2 km × 2 km grid cells used to define the study region. Grid cells with ≥25% impervious surface cover that were isolated from the main urban region were considered to be part of other urban settlements. Cells that had <25% impervious surface cover were considered to be non-urban unless they were completely surrounded by urban cells, b) the percentage green-space cover of 1 km × 1 km grid cells across the urban study region with grid cells outlined in black representing the 150 cells selected for sampling using random stratification across each category of green-space (15 sampling grid cells each). The inset map shows an example 1 km × 1 km grid cell with locations of the randomised point (R2), which is located at the nearest accessible point to the north of the grid cell's centre (R1) which is inaccessible, and the woodland sampling point (W) which is located in the largest area of woodland within the focal grid cell. White circles show point counts' 50 m sampling radii.

Tree biomass and carbon storage estimation

Tree biomass was calculated by combining aboveground (AGB) and belowground biomass (BGB). Urban trees can exhibit divergent growth patterns from those in more natural settings, reducing the accuracy of allometric questions applied to urban areas (Ngo and Lum, 2018). Generalised allometric equations parameterised for tropical urban areas are, however, still very limited (Ngo and Lum, 2018). AGB was thus estimated using the allometric equation (equation 1 below) developed for tropical moist forests by Chave et al. (2005); this follows methods used in other tropical cities (e.g. Khadanga and Jayakumar, 2018; Ngo *et al*., 2013):

$$AGB = 0.0509\ \rho\ DBH^2\ H \qquad \text{Equation 1}$$

ρ is wood specific density (g/cm^3), DBH is diameter-at-breast-height (cm), and H is tree height (m). Species' wood densities were obtained from Zanne *et al*. (2009), with genus-mean or family-mean values used if species specific values were unavailable (Table S4.1). Below ground biomass was estimated using a universal allometric equation, which captures the relationship between above and below ground biomass, that has previously been applied to tropical forests from Saatchi *et al*. (2011), equation 2.

$$BGB = 0.489\ AGB^{0.089} \qquad \text{Equation 2}$$

Carbon storage (CS) was estimated by multiplying total tree biomass by the carbon fraction parameter, i.e. 0.5, following Marklund and Schoene (2006) and then scaled to tonnes/ha.

Human food production potential

Tree species that provide food for people were identified using the Thai Plant Production Database provided by Thailand Department of Agricultural Extension (DOAE, 2020). This identifies species whose products are collected and stored by the Department of Agricultural Extension, Ministry of Agriculture and Cooperatives for use in human consumption (see Table S4.1). People consume fruits (e.g. mango *Mangifera indica*, tamarind *Tamarindus indica*) or nuts (i.e. coconut *Cocos nucifera* and tal palm *Borassus flabellifer*) from most of these species. The yield of such products is strongly correlated with tree size (Chapman *et al*., 1992) and we summed the aboveground biomass of focal species as an index of potential human food production (HFP).

Biodiversity support function — frugivorous birds

Tree species that provide food resources for frugivorous birds were identified as those in genera listed by Snow (1981) as contributing to southeast Asian frugivorous birds' diets, or species recorded by Kitamura *et al*. (2002) as consumed by frugivorous birds in Khao Yai National Park (the largest block of natural forest close to Bangkok). These two sources did not contain any conflicting classifications. We summed the AGB of these trees to provide an index of their potential to provide food for frugivorous birds as a biodiversity support index (BDS).

Economic value

The economic value (ECV) of trees used as collateral for financial loans is calculated following Thai government procedures for the 211 species included in the regulations (BAAC, 2020; Thailand. Ministerial Regulation, 2018). ECV is primarily based on timber value (Royal Forest Department, 2005). Each species is classified into one of four price per volume categories. ECV of each individual tree is calculated as the product of price and tree volume (V), where $V = 0.0002\ DBH^{2.3162}$ (BAAC, 2020). This is a simplistic equation which does not consider inter-specific variation in relationships between DBH and tree volume, but we consider it crucial to calculate financial value following the actual regulations used in our study system. We converted values from local currency (Thai Baht) to GBP (i.e. sterling) following the UK government guidance for foreign exchange rate calculations at the time of our tree surveys, i.e. 1 GBP = 43.17 THB (HMRC, 2018).

Data analysis

All analyses were performed using R-studio version 3.4.2 (R-studio Team, 2015)**.**

We quantified how tree species richness changes along the urban-rural gradient using generalised linear models to model species richness as a function of impervious surface cover, and comparing between linear and quadratic models. Models were constructed separately for randomised and woodland points, and for total, native, and non-native species richness. We tested if Poisson or Gaussian error structures provided a better fit based on models' Akaike Information Criterion values corrected for small sample size (AICc), calculated using AICcmodavg package. In all cases we selected a Gaussian model (Table S4.2). We selected quadratic models when their AICc values were at least 2 points lower than that of linear models and the quadratic term was significant ($P < 0.05$).

We used Moran's I tests (ape package) to quantify spatial autocorrelation in the models' residuals. Moran's I values were low (≤0.04) but significant ($P < 0.05$) in models of total and native species richness at the randomised points (Table S4.3). Parameter estimates in models that take spatial correlation structure into account (implemented using generalised linear model approach (nlme packages) with exponential covariance structure) were similar to those that did not take spatial autocorrelation into account (Table S4.4). We thus only report results from non-spatial models in the main manuscript.

We use matched paired t-tests or Wilcoxon signed rank tests (the non-parametric equivalent) to assess if native or non-native species contributed more to ecosystem service provision at the randomised and woodland points. We then assessed spatial patterns of urban trees' ecosystem service provision along the urbanisation gradient by constructing generalised linear models (glm function) of carbon storage (CS), human food production (HFP), economic value (ECV), and biodiversity support (BDS) as a function of percentage impervious surface (including linear and quadratic terms to detect simple non-linear relationships). Models were constructed separately for randomised and woodland locations, and for total, native, and non-native trees. Moran's I tests only detected significant positive spatial autocorrelation in models for HFP from both randomised and woodland points (Table S4.5). However, Moran's I values were low (<0.04) and parameter estimates in models that did and did not take spatial correlation structure into account were very similar (Table S4.6) and we thus only report results from non-spatial models in the main manuscript.

Finally, we use generalised linear models to model each of our ecosystem service metrics as a function of species richness, whilst taking percentage impervious surface into account. We first do so by modelling ecosystem service provision from all tree species as a function of total species richness. This enables us to test the theory that a greater number of species will maximise service provision (Slade *et al.*, 2019). We then model ecosystem service provision from all tree species as a function of native species richness to assess if areas with greater provision of ecosystem services are also hotspots for conservation (which almost invariably focuses exclusively on native species). In these models total and native species richness are natural log transformed to reduced skewness in their distributions. We only use the linear term of impervious surface as previous models did not detect quadratic relationships between urbanisation intensity and ecosystem service provision (see results), but did consider linear and quadratic effects of species richness metrics. We use AICc and *P*-values to assess the relative fit of linear and quadratic models. Moran's I tests detected significant spatial autocorrelation in models for HFP with total and native species richness (Table S4.7). Parameter estimates from models of HFP as a function of total species richness were similar in models that did and did not take spatial correlation into account (Table S4.8), so only the non-spatial model is presented in the main manuscript. However, when modelling HFP as a function of native species richness results differed depending on if spatial correlation was or was not taken into account — so results from both models are reported in the main manuscript. In all models, we used rsq package in R to calculate model (or partial) r^2 as variance-function-based r^2 based on the methodology described by Zhang (2017), with partial r^2 being calculated for percentage impervious surface and species richness.

4.3 Results

Tree assemblage structure

Our surveys documented 7,633 trees, from 162 species (99 natives) and 48 families (Table S4.1, S9). Most species were very rare with 113 represented by <20 individuals (Table S4.9). 15 and 43 species respectively only occurred at randomised and woodland points, and all these were very rare. Legumes (Fabaceae) were the most common family in terms of individuals (37.7%) and species (34 species, 21.0%). Most trees (62.0%) were non-native and these represented a large minority of species (63; 38.9% of the total). The commonest species at the randomised points was mango *Mangifera indica*, whilst white leadtree *Leucaena leucocephala* was the commonest species at the woodland points, both are non-natives (Table S4.1).

Shape of species richness-urbanisation intensity relationships

At the randomised locations, there were no significant relationships between total, native, or non-native species richness and urbanisation intensity (Table 4.1; Fig. 4.2). At the woodland locations, total, native, and non-native species richness increased slightly, and linearly, with increasing urbanisation intensity although explanatory capacity was consistently limited (variance-function-based r^2 range between 4.0% and 5.4%; Table 4.1; Fig. 4.2).

Table 4.1: Total species richness, species richness of native trees, and species richness of non-native trees as a function of percentage impervious surface cover (linear and quadratic models) with Gaussian error structure. Model r^2 values are calculated using the rsq package to implement the variance-function-based r^2 methodology described by Zhang (2017). Bold text indicates if, when significant, the linear or quadratic model provides a better fit to the data (based on models' AICc values and *P* values of the quadratic term).

Response variable	Location type	Model	Model r^2	AICc	%impervious surface (Linear term)		%impervious surface (Quadratic term)	
					Coeff ± SE	*P*	Coeff ± SE	*P*
Total species richness	Randomised	Linear	0.60	871.38	-0.012 ± 0.013	0.346		
		Quadratic	0.67	873.39	-0.027 ± 0.049	0.577	$1.6e^{-4} \pm 4.9e^{-4}$	0.743
	Woodland	**Linear**	5.70	897.36	0.043 ± 0.015	0.004		
		Quadratic	6.66	897.97	-0.024 ± 0.058	0.675	0.001 ± 0.001	0.226
Native species richness	Randomised	Linear	0.50	700.19	-0.006 ± 0.007	0.391		
		Quadratic	0.51	702.29	-0.010 ± 0.028	0.726	$3.8e^{-5} \pm 2.8e^{-4}$	0.893
	Woodland	**Linear**	4.73	810.38	0.029 ± 0.011	0.008		
		Quadratic	5.97	810.57	-0.028 ± 0.043	0.517	$0.001 \pm 4.3e^{-4}$	0.170
Non-native species richness	Randomised	Linear	0.47	717.62	-0.006 ± 0.008	0.406		
		Quadratic	0.64	719.47	-0.021 ± 0.029	0.483	$1.5e^{-4} \pm 3.0e^{-4}$	0.612
	Woodland	**Linear**	4.67	708.78	0.021 ± 0.008	0.009		
		Quadratic	4.81	710.68	0.007 ± 0.030	0.813	$1.4e^{-4} \pm 3.1e^{-4}$	0.651

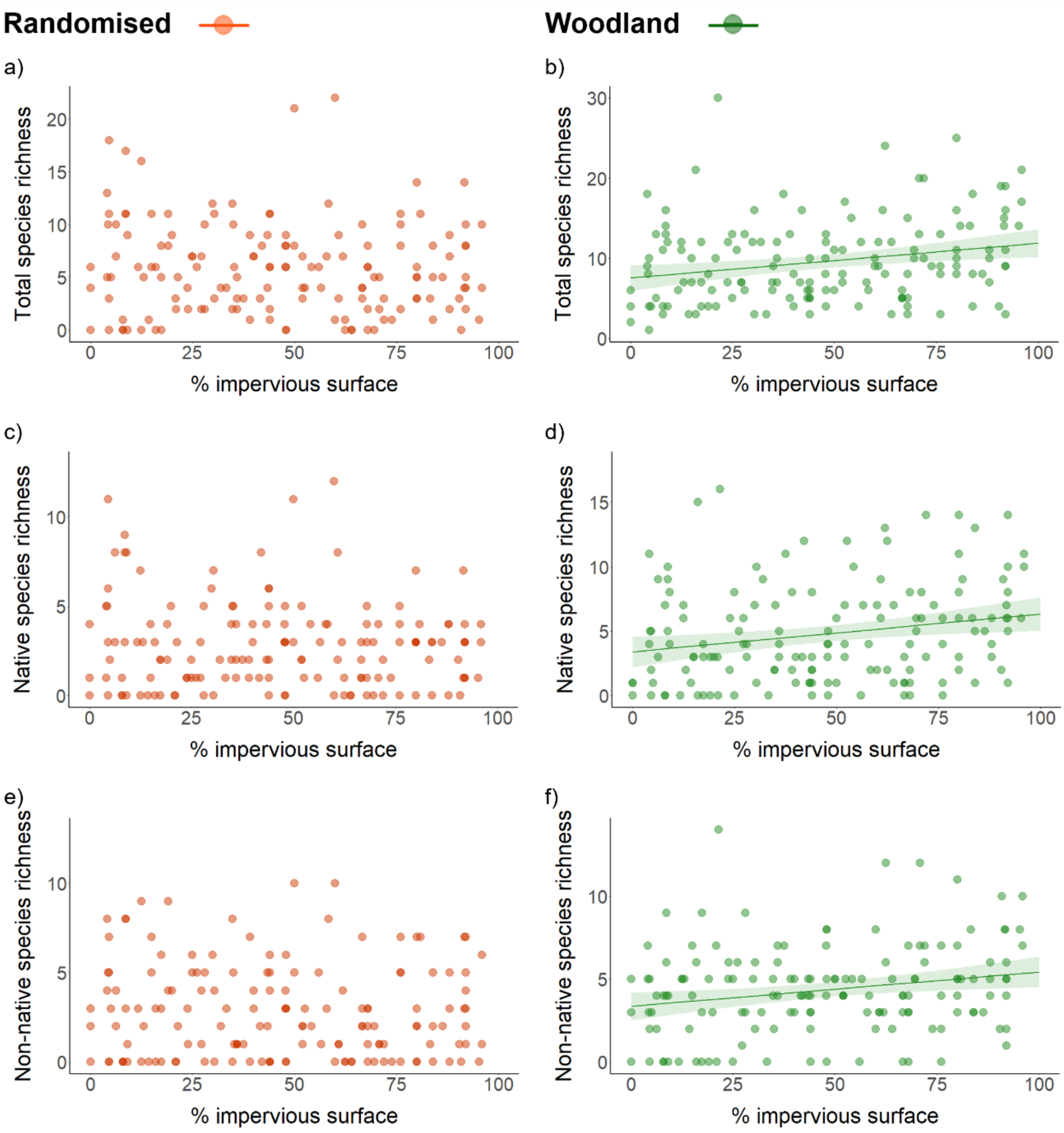

Figure 4.2: Relationships between (a and b) total, (c and d) native, and (e and f) non-native species richness (respectively at the randomised and woodland points) and percentage impervious surface cover. Fitted lines indicate predicted values, with shading indicating 95% confidence intervals, from generalised linear models reported in Table 4.1. All measures of species richness at the randomised points were not significantly associated with percentage impervious surface cover so no fitted lines are provided.

Ecosystem services–urbanisation intensity relationships

Carbon storage (CS, t/ha) was significantly higher in non-native than native trees at the randomised (non-native trees contributing 54.9% of total CS) and woodland points (non-native trees contributing 60.8%; Table S4.10). Total CS was not significantly associated with urbanisation intensity at randomised (Table 4.2) and woodland points (Table 4.3). CS in native species was positively, and linearly, associated with urbanisation intensity in the woodland points (Table 4.3; Fig. 4.3d), but not the randomised ones (Table 4.2). CS in non-native trees in the randomised points declined linearly with increasing urbanisation intensity (Table 4.2; Fig. 4.3a). Explanatory power of these models was consistently low (variance-function-based r^2 between 3.7% and 3.8%).

Non-native trees contributed significantly more than native trees to potential human food production (HFP, measured as biomass of trees producing fruits for people; t/ha) in the randomised (non-native trees contributing 90.6% of total HFP) and woodland points (non-native trees contributing 92.2%; Table S4.10). Total HFP and that from non-native trees declined linearly with urbanisation intensity in the randomised points (Table 4.2; Fig. 4.3b, c), but was not significantly associated with urbanisation intensity at the woodland points (Table 4.3). HFP of native trees was not significantly associated with urbanisation intensity at either the randomised (Table 4.2) or woodland points (Table 4.3). Explanatory power of models with significant relationships was consistently low (variance-function-based r^2 between 3.3% and 3.9%).

Native trees contributed significantly more to biodiversity support (BDS, measured as biomass of trees producing fruits for birds; t/ha) than non-native trees at the randomised (native trees contributing 81.4% of total BDS) and woodland points (native trees contributing 74.5%; Table S4.10). Total BDS was not significantly associated with urbanisation intensity at the randomised points (Table 4.2), but it increased linearly with urbanisation intensity at the woodland points (Table 4.3; Fig. 4.3e). BDS of native trees increased linearly with urbanisation intensity at the woodland points (Fig. 4.3f) but was not significantly associated with urbanisation intensity at the randomised points (Table 4.2). BDS of non-native trees was not significantly associated with urbanisation intensity in either the randomised (Table 4.2) or woodland points (Table 4.3). Explanatory power of models with significant relationships was consistently limited (variance-function-based r^2 between 5.8% and 6.3%).

Native trees contributed slightly, but significantly, more to economic value (ECV, £) than non-native trees at the randomised points (native trees contributing 53.4%; Table S4.10), whilst at the woodland points there was no significant difference in the contributions of native and non-native trees (Table S4.10). Total ECV was not significantly associated with urbanisation intensity at the randomised points (Table 4.2), but increased linearly with urbanisation intensity at the woodland points (Table 4.3; Fig. 4.3g). Similarly, ECV of native trees increased linearly with urbanisation intensity at the woodland points (Table 4.3; Fig. 4.3h) but was significantly associated with urbanisation intensity at the randomised ones (Table 4.2). There was no significant relationship between ECV of non-native trees and urbanisation intensity in either randomised (Table 4.2) or woodland points (Table 4.3). In all relationships, explanatory power was consistently low (variance-function-based r^2 between 2.8% and 4.9%).

Table 4.2: Ecosystem services metrics, i.e. carbon storage (CS; t/ha), human food production (HFP; t/ha), biodiversity support (BDS; t/ha), and economics value (ECV; £) of urban trees at the randomised points as a function of impervious surface percentage (linear and quadratic models). Model r^2 values are calculated using the rsq package to implement the variance-function-based r^2 methodology described by Zhang (2017). Bold text indicates if, when significant, the linear or quadratic model provides a better fit to the data (based on models' AICc values and *P* values of the quadratic term).

Response variable	Model	Model r^2	AICc	%impervious surface (Linear term)		%impervious surface (Quadratic term)	
				Coeff ± SE	*P*	Coeff ± SE	*P*
Total CS	Linear	1.71	1108.83	-0.045 ± 0.028	0.110		
	Quadratic	1.74	1110.90	-0.023 ± 0.108	0.832	$-2.3e^{-4}$ ± 0.001	0.838
CS of native trees	Linear	0.16	903.81	0.007 ± 0.014	0.625		
	Quadratic	0.22	905.84	0.022 ± 0.055	0.689	$-1.6e^{-4}$ ± 0.001	0.776
CS of non-native trees	**Linear**	3.83	1027.99	-0.005 ± 0.021	0.016		
	Quadratic	3.83	1030.09	-0.045 ± 0.053	0.588	$-6.7e^{-5}$ ± 0.001	0.937
Total HFP	**Linear**	3.91	861.01	-0.030 ± 0.012	0.015		
	Quadratic	3.94	863.07	-0.040 ± 0.047	0.401	$1.1e^{-4}$ ± $4.8e^{-4}$	0.825
HFP of native trees	Linear	2.04	329.03	-0.004 ± 0.002	0.082		
	Quadratic	3.29	329.22	0.007 ± 0.008	0.379	$1.1e^{-4}$ ± $8.1e^{-5}$	0.170
HFP of non-native trees	**Linear**	3.31	848.29	-0.026 ± 0.012	0.026		
	Quadratic	3.46	850.17	-0.047 ± 0.045	0.303	$2.2e^{-4}$ ± $4.6e^{-4}$	0.636
Total BDS	Linear	1.16	1074.39	0.033 ± 0.025	0.190		
	Quadratic	1.41	1076.11	-0.025 ± 0.097	0.793	0.001 ± 0.001	0.536
BDS of native trees	Linear	1.14	1073.12	0.032 ± 0.025	0.193		
	Quadratic	1.33	1074.95	-0.017 ± 0.096	0.863	0.001 ± 0.001	0.600
BDS of non-native trees	Linear	$5.6e^{-4}$	481.30	$3.1e^{-4}$ ± 0.003	0.928		
	Quadratic	0.34	482.91	-0.009 ± 0.013	0.515	$9.5e^{-5}$ ± $1.4e^{-4}$	0.486
Total ECV	Linear	1.63	2485.55	-4.269 ± 2.729	0.120		
	Quadratic	2.30	2486.64	6.067 ± 10.638	0.569	-0.109 ± 0.108	0.316
ECV of native trees	Linear	0.08	2343.70	-0.569 ± 1.701	0.738		
	Quadratic	0.68	2344.90	5.493 ± 6.633	0.409	-0.064 ± 0.067	0.346
ECV of non-native trees	Linear	2.22	2392.74	-3.668 ± 2.002	0.069		
	Quadratic	2.36	2394.63	-0.133 ± 7.828	0.987	-0.037 ± 0.080	0.641

Table 4.3: Ecosystem services metrics, i.e. carbon storage (CS; t/ha), human food production (HFP; t/ha), biodiversity support (BDS; t/ha), and economics value (ECV; £) of urban trees at the woodland points as a function of impervious surface percentage (linear and quadratic models). Model r^2 values are calculated using the rsq package to implement the variance-function-based r^2 methodology described by Zhang (2017). Bold text indicates if, when significant, the linear or quadratic model provides a better fit to the data (based on models' AICc values and *P* values of the quadratic term).

Response variable	Model	Model r^2	AICc	%impervious surface (Linear term)		%impervious surface (Quadratic term)	
				Coeff ± SE	*P*	Coeff ± SE	*P*
Total CS	Linear	0.04	1253.31	0.012 ± 0.049	0.807		
	Quadratic	0.25	1255.01	-0.092 ± 0.194	0.636	0.001 ± 0.002	0.580
CS of native trees	**Linear**	4.51	978.34	0.051 ± 0.019	0.010		
	Quadratic	5.66	978.68	-0.046 ± 0.076	0.542	0.001 ± 0.001	0.188
CS of non-native trees	Linear	0.57	1209.53	-0.039 ± 0.042	0.365		
	Quadratic	0.57	1211.64	-0.046 ± 0.168	0.785	$7.5e^{-5}$ ± 0.002	0.965
Total HFP	Linear	1.77	1166.84	-0.059 ± 0.037	0.108		
	Quadratic	1.79	1168.92	-0.032 ± 0.145	0.827	$-2.9e^{-4}$ ± 0.001	0.844
HFP of native trees	Linear	0.24	406.14	0.002 ± 0.003	0.558		
	Quadratic	0.27	408.20	-0.001 ± 0.011	0.941	$2.5e^{-5} \pm 1.1e^{-4}$	0.818
HFP of non-native trees	Linear	1.87	1166.23	-0.061 ± 0.037	0.098		
	Quadratic	1.90	1168.29	-0.031 ± 0.145	0.831	$-3.1e^{-4}$ ± 0.001	0.830
Total BDS	**Linear**	7.42	1009.95	0.073 ± 0.022	0.001		
	Quadratic	7.86	1011.37	0.006 ± 0.085	0.947	0.001 ± 0.001	0.410
BDS of native trees	**Linear**	8.26	999.39	0.075 ± 0.021	$4.2e^{-4}$		
	Quadratic	9.06	1000.23	-0.013 ± 0.082	0.870	0.001 ± 0.001	0.265
BDS of non-native trees	Linear	0.04	664.88	-0.002 ± 0.007	0.803		
	Quadratic	0.50	666.31	0.019 ± 0.026	0.469	$-2.2e^{-4} \pm 2.7e^{-4}$	0.416
Total ECV	**Linear**	2.70	2764.37	16.860 ± 8.407	0.047		
	Quadratic	2.74	2766.42	8.900 ± 33.182	0.789	0.083 ± 0.336	0.805
ECV of native trees	**Linear**	5.00	2654.39	15.979 ± 5.783	0.006		
	Quadratic	5.56	2655.63	-4.379 ± 22.764	0.848	0.213 ± 0.231	0.357
ECV of non-native trees	Linear	0.28	2610.61	3.187 ± 4.983	0.523		
	Quadratic	0.29	2612.72	4.72 ± 19.673	0.811	-0.016 ± 0.199	0.936

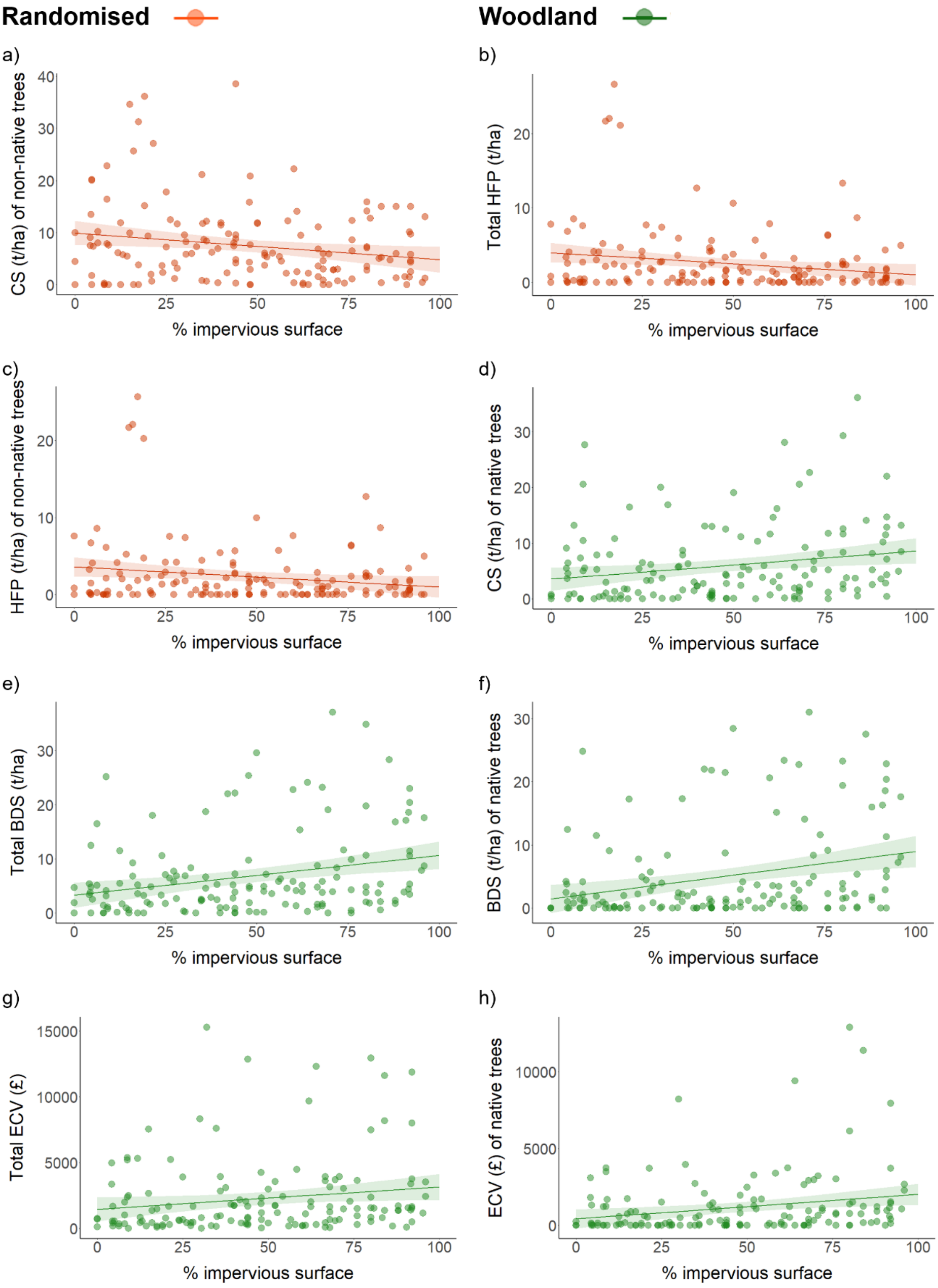

Figure 4.3: Plots of significant relationships between ecosystem service provision (CS, cabon storage; HFP; human food production potential; BDS, biodiversity support; ECV, economic value) and percentage impervious surface cover at the randomised (orange, a-c) and woodland points (green, d-h). Fitted lines indicate predicted values and shading indicates 95% confidence interval derived from the generalised linear models in Table 4.2 (randomised points) and Table 4.3 (woodland points).

Relationships between ecosystem service provision and tree species richness

When taking percentage impervious surface cover into account, total CS increased with ln-transformed total species richness along an accelerating quadratic curve at the randomised points (Fig. 4.4a; variance-function-based partial r^2 40.7%) and linearly at the woodland points (Table 4.4, Fig. 4.4b), although explanatory power of species richness was limited at woodland points (variance-function-based partial r^2 5.3%). Total CS increased linearly with ln-transformed native species richness at randomised points (Fig. 4.5a) and along an accelerating quadratic curve at woodland points (Table 4.5, Fig. 4.5b), although explanatory power of species richness was limited at woodland points (variance-function-based partial r^2 7.6%).

HFP (measured as biomass of trees providing food for people) increased linearly with ln-transformed total species richness (Fig. 4.4c), explaining c.16.5% of the variation, whilst no significant relationship was detected at the woodland points (Table 4.4, Fig. 4.4d). HFP increased linearly with ln-transformed native species richness at the randomised points (Fig. 4.5c); whilst it declined slightly and linearly with ln-transformed native species richness at the woodland points in a non-spatial model; there was no significant relationship in the spatial model (Table 4.5, Fig. 4.5d). Explanatory capacity of the native species richness predictor in statistically significant models was consistently limited (variance-function-based partial r^2 between 3.1% and 5.8%; Table 4.5).

BDS (measured as the biomass of trees providing food for frugivorous birds) increased linearly with ln-transformed total species richness in both randomised (Fig. 4.4a; variance-function-based partial r^2 4.7%) and woodland points (Table 4.4; Fig. 4.4f; variance-function-based partial r^2 12.1%). Similarly, BDS increased linearly with ln-transformed native species richness in both randomised (Fig. 4.5e) and woodland points (Table 4.5; Fig. 4.5f). Explanatory power of the species richness predictor was again more limited from the randomised point model (variance-function-based partial r^2 7.3%) than at the woodland points (variance-function-based partial r^2 15.2%).

ECV increased linearly with ln-transformed total species richness at randomised (Fig. 4.4g; variance-function-based partial r^2 20.6%) and woodland points (Table 4.4; Fig. 4.4h; variance-function-based partial r^2 7.2%). ECV increased linearly with ln-transformed native species richness at randomised points (variance-function-based partial r^2 18.9%) and along an accelerating quadratic curve at woodland points (Table 4.5; Fig. 4.5h; variance-function-based partial r^2 9.9%).

Table 4.4: Ecosystem services metrics, i.e. total carbon storage (CS; t/ha), total human food production (HFP; t/ha), total biodiversity support (BDS; t/ha), and total economic value (ECV; £) of urban trees modelled as a function of percentage impervious surface and ln-transformed total species richness (fitting linear and quadratic relationships with species richness). Model and partial r^2 values are calculated using the rsq package to implement the variance-function-based r^2 methodology described by Zhang (2017). Bold text indicates if, when significant, linear or quadratic models provide a better fit to the data (based on models' AICc values and *P* values of the quadratic term).

Response variable	Location type	Model	AICc	Model r^2	% impervious surface			Total species richness Linear term		Quadratic term		
					Coeff ± SE	*P*	Partial r^2	Coeff ± SE	*P*	Coeff ± SE	*P*	Partial r^2
CS	Randomised	Linear	1022.82	45.38	-0.041 ± 0.021	0.048	2.64	8.080 ± 0.745	$<2.2e^{-16}$			44.43
		Quadratic	1016.37	48.42	-0.030 ± 0.021	0.141	1.48	1.386 ± 2.394	0.563	2.422 ± 0.832	0.004	47.52
	Woodland	**Linear**	1247.42	5.28	-0.025 ± 0.050	0.616	0.18	6.902 ± 2.447	0.005			5.24
		Quadratic	1245.79	7.68	-0.022 ± 0.049	0.655	0.14	-15.085 ± 11.658	0.198	5.564 ± 2.886	0.056	7.64
HFP	Randomised	**Linear**	836.04	19.78	-0.029 ± 0.011	0.010	4.40	2.157 ± 0.400	$2.7e^{-7}$			16.52
		Quadratic	836.31	20.78	-0.026 ± 0.011	0.022	3.56	0.464 ± 1.314	0.724	0.618 ± 0.457	0.178	17.55
	Woodland	Linear	1166.34	3.50	-0.043 ± 0.038	0.255	0.90	-2.985 ± 1.857	0.110			1.76
		Quadratic	1167.13	4.38	-0.042 ± 0.038	0.269	0.85	-13.014 ± 8.921	0.147	2.538 ± 2.208	0.252	2.66
BDS	Randomised	**Linear**	1069.27	5.81	0.033 ± 0.024	0.169	1.28	2.345 ± 0.870	0.008			4.71
		Quadratic	1069.42	7.05	0.040 ± 0.025	0.108	1.76	-1.454 ± 2.857	0.612	1.386 ± 0.993	0.165	5.96
	Woodland	**Linear**	994.45	17.88	0.050 ± 0.021	0.020	2.54	4.431 ± 1.035	$3.4e^{-5}$			11.30
		Quadratic	996.34	18.02	0.050 ± 0.021	0.020	3.69	2.013 ± 4.990	0.687	0.612 ± 1.235	0.621	11.45
ECV	Randomised	**Linear**	2452.98	21.93	-4.058 ± 2.439	0.098	1.85	542.02 ± 87.651	$5.9e^{-9}$			20.64
		Quadratic	2451.94	23.57	-3.268 ± 2.462	0.187	1.19	58.738 ± 286.650	0.838	176.336 ± 99.654	0.079	22.31
	Woodland	**Linear**	2754.86	10.09	9.231 ± 8.407	0.274	0.83	1419.38 ± 412.437	0.001			7.60
		Quadratic	2755.02	11.30	9.584 ± 8.383	0.255	0.90	-1278.826 ± 1977.066	0.519	682.831 ± 489.398	0.165	8.84

Table 4.5: Ecosystem services metrics, i.e. total carbon storage (CS; t/ha), total human food production (HFP; t/ha), total biodiversity support (BDS; t/ha), and total economics value (ECV; £) of urban trees modelled as a function of percentage impervious surface and ln-transformed native species richness (fitting linear and quadratic relationships with species richness). Model and partial r^2 values are calculated using the rsq package to implement the variance-function-based r^2 methodology described by Zhang (2017). Bold text indicates if, when significant, linear or quadratic models provide a better fit to the data (based on models' AICc values and *P* values of the quadratic term).

Response variable	Location type	Model	AICc	Model r^2	% impervious surface			Native species richness Linear term		Quadratic term		
					Coeff ± SE	*P*	Partial r^2	Coeff ± SE	*P*	Coeff ± SE	*P*	Partial r^2
CS	Randomised	**Linear**	1032.63	41.69	-0.043 ± 0.021	0.046	2.67	8.857 ± 0.882	$<2.2e^{-16}$			40.67
		Quadratic	1034.33	41.86	-0.041 ± 0.022	0.064	2.33	7.207 ± 2.677	0.008	0.805 ± 1.232	0.515	40.85
	Woodland	Linear	1247.48	5.24	-0.022 ± 0.05	0.662	0.13	5.080 ± 1.808	0.006			5.20
		Quadratic	1241.72	10.20	-0.019 ± 0.048	0.702	0.10	-10.359 ± 5.770	0.075	5.893 ± 2.097	0.006	10.16
HFP	Randomised	**Linear**	854.18	9.47	-0.030 ± 0.012	0.014	4.08	1.463 ± 0.487	0.003			5.79
		Quadratic	854.69	10.45	-0.032 ± 0.012	0.008	4.69	3.216 ± 1.471	0.030	-0.855 ± 0.677	0.209	6.81
	Woodland	**Linear**	1164.58	4.65	-0.040 ± 0.037	0.282	0.80	-2.845 ± 1.364	0.039			2.93
		Quadratic	1166.03	5.10	-0.040 ± 0.037	0.292	0.78	-6.348 ± 4.461	0.157	1.337 ± 1.621	0.411	3.39
	Woodland (spatial model)	Linear	1152.17	2.23	-0.035 ± 0.039	0.371	0.93	-1.829 ± 1.169	0.118			1.51
		Quadratic	1152.91	2.69	-0.028 ± 0.040	0.477	0.57	-6.157 ± 3.788	0.104	1.639 ± 1.363	0.229	1.97
BDS	Randomised	**Linear**	1065.20	8.33	0.033 ± 0.024	0.168	1.29	3.336 ± 0.984	0.001			7.26
		Quadratic	1066.81	8.66	0.036 ± 0.024	0.140	1.48	1.310 ± 2.983	0.661	0.987 ± 1.372	0.473	7.59
	Woodland	**Linear**	989.53	20.58	0.049 ± 0.021	0.019	3.76	3.673 ± 0.752	$2.7e^{-6}$			14.21
		Quadratic	991.39	20.74	0.049 ± 0.021	0.019	3.81	2.439 ± 2.463	0.324	0.471 ± 0.895	0.600	14.38
ECV	Randomised	**Linear**	2456.19	20.25	-4.171 ± 2.465	0.093	1.91	594.581 ± 101.50	$3.0e^{-8}$			18.93
		Quadratic	2458.32	20.25	-4.122 ± 2.509	0.103	1.82	560.731 ± 308.38	0.071	16.498 ± 141.868	0.908	18.93
	Woodland	Linear	2756.20	9.27	10.280 ± 8.397	0.223	1.03	988.608 ± 306.074	0.002			6.75
		Quadratic	2750.97	13.71	10.804 ± 8.220	0.191	1.19	-1538.799 ± 978.704	0.118	964.733 ± 355.654	0.007	11.32

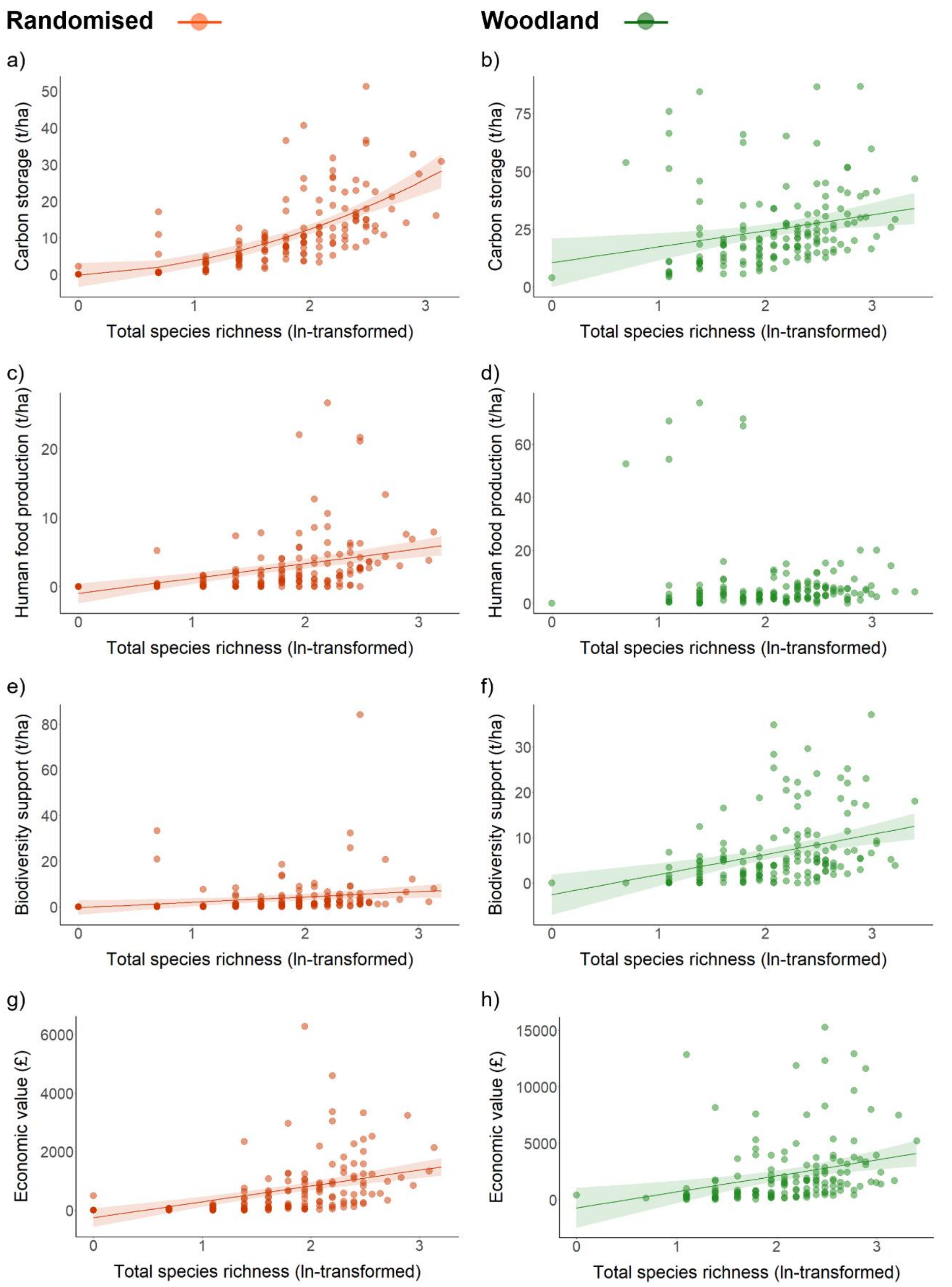

Figure 4.4: Relationships between ecosystem service provision and total species richness (ln-transformed) at the randomised (orange) and woodland points (green). Fitted lines indicate predicted values and shading indicates 95% confidence intervals derived from the best fitting multiple regression models presented in Table 4.4. Human food production at the woodland points was not significantly associated with total species richness so no fitted line is exhibited.

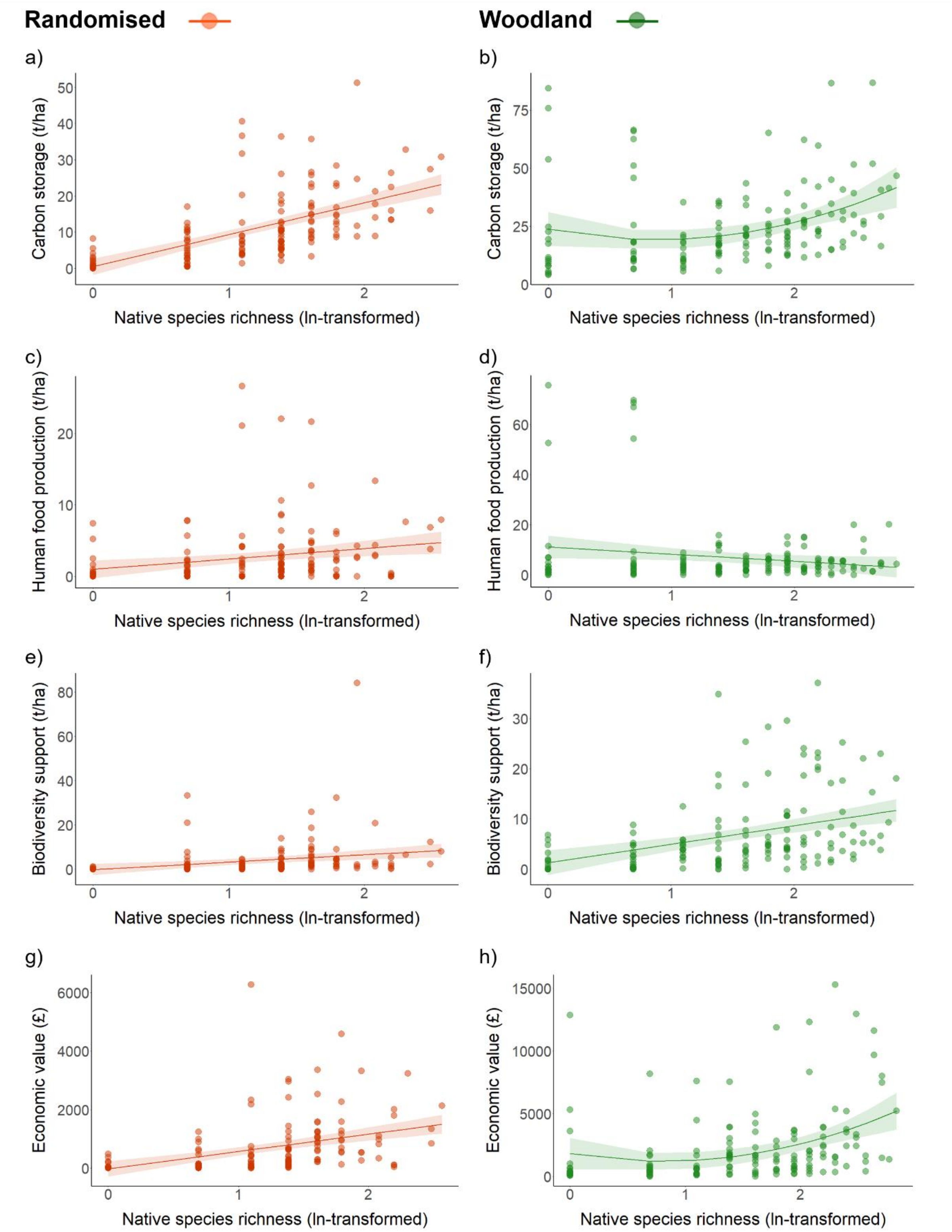

Figure 4.5: Relationships between ecosystem service provision and native species richness (ln-transformed) at the randomised (orange) and woodland points (green). Fitted lines indicate predicted values and shading indicates 95% confidence intervals derived from the best fitting multiple regression models presented in Table 4.5; note that the predicted values in panel d are derived from the non-spatial model, but that the spatial model indicates no significant relationship.

4.4 Discussion

Impoverished and non-native dominated urban tree communities

Our surveys recorded 162 tree species and 99 native tree species in a cumulative survey area of 230 ha. Native, and even total, tree species richness thus appears to be lower than that estimated to occur in natural forests in southeast Asia (e.g. a much smaller 30 ha study plot in Khao Yai National Park (the nearest large block of natural forest) contained 204 species (Brockelman *et al*., 2011). Such comparisons contrast with conclusions reached from studies outside the tropics that tree species richness in urban forests typically exceeds that of more natural forests outside urban areas (e.g. Gillespie *et al*., 2017). The extreme rarity of most species further emphasises that the number of species that contribute significantly to ecological functions and ecosystem service provision, will be substantially lower than our headline figures regarding total species richness.

The numerical dominance of non-native trees confirms the conclusions from other studies that tropical urban tree assemblages are dominated by non-native species (e.g. de Souza *et al*., 2020). It is thus unsurprising that non-native species contributed significantly more to carbon storage and provisioning of human food than native species. Indeed, tree species composition in tropical cities is often driven by exotic fruit trees (e.g. Jaganmohan *et al*., 2012). Approximately a quarter of the species in our study provide food for people, with the commonest species being non-native, such as mango *Mangifera indica* (Table S4.1), which is consistent with other tropical studies (e.g. Panyadee *et al*., 2016) and underlines this species dominant role in supporting urban food security.

In contrast, despite their reduced abundance relative to non-native species, native trees provide the vast majority of food for frugivorous birds — highlighting the key role of native species in supporting urban biodiversity (Threlfall *et al*., 2016). It is thus notable that native trees already make substantial contributions to economic valuations that can be used as collateral in securing financial loans, and this could be increased further as 93.4% of eligible species under current regulations are native (BACC, 2020). This scheme thus provides a potentially powerful incentive for landowners to retain trees on their land and to increase tree planting. This can be viewed as a form of indirect payment for ecosystem service scheme although there is no clear link between the magnitude of payment (via increased access to loans) and the magnitude of service provision, for example all tree species detected in our survey will contribute to carbon storage but only 43 of these can be used as collateral, similarly only seven and ten species respectively provide food for people and for frugivorous birds and can be used as collateral (Fig. S4.2a). There is thus a clear need to assess the effectiveness of the financial collateral scheme in determining land owners' tree retention and planting decision, and how impacts on biodiversity and ecosystem service provision can be enhanced through altering the eligible species or their relative economic value.

Tree species richness and the urbanisation gradient

At randomised points, we find no evidence for significant changes in tree species richness (total, native, or non-native) along the urbanisation gradient. This contrasts with evidence from temperate locations that tree species richness peaks at intermediate levels of urbanisation intensity (e.g. Porter *et al.*, 2001; Zhang *et al.*, 2016). Studies from tropical regions are more limited although Ortega- Álvarez et al. (2011) report that species richness of native and non-native trees peaks in land-uses relating to intermediate levels of urbanisation intensity in Mexico City. The lack of significant relationships in our study highlights the need for more studies from tropical regions describing biodiversity responses to urbanisation. We consider that the 'flat-lining' of tree species richness across the urbanisation gradient is likely to be partly driven by our focal spatial scale (1 km × 1 km cells) as use of smaller spatial grains is more likely to generate a negative relationship between urbanisation intensity and species richness (Pautasso, 2007). Our choice of grain size does, however, match that of numerous other studies reporting variation in biodiversity along urbanisation gradients (e.g. Smith *et al.*, 2006). High levels of heterogeneity in landscape types across the urbanisation gradient is also likely to contribute to the lack of a biodiversity-urbanisation intensity relationship in our study. Areas of low urbanisation intensity in the Bangkok region for example comprise locations with limited tree cover (such as rice fields), those with high levels of tree cover but with few species (e.g. patches of mangrove forests; or coconut *Cocos nucifera* plantations) and patches of semi-natural forest with high tree diversity. Similar variation occurs in areas with intermediate and high levels of urbanisation intensity (e.g. areas of semi-natural grassland and impervious surface typically have limited tree cover with low species richness, whilst domestic gardens, public parks, and remnants of semi-natural forests have much higher tree species richness). Our study thus highlights that even highly urbanised locations within a rapidly expanding tropical mega-city can support relatively high tree species richness (mean of 5.71 ± 0.70 (s.e.) species in total and 2.68 ± 0.34 (s.e.) natives), which is similar to values in the least urbanised locations (mean of 6.47 ± 0.87 (s.e.) species in total and 3.17 ± 0.50 (s.e.) natives; see Fig. 4.2).

At the woodland points, we found slight increases in total, native, and non-native tree species richness as urbanisation intensity increased. Whilst explanatory capacity was limited, such patterns are again somewhat surprising but clearly indicate that retaining woodland patches, even in highly urbanised locations, can benefit biodiversity. This pattern probably arises because the largest woodland patches in the less urbanised locations consist primarily of commercial plantations, especially coconut, that contain very few species, whilst in urban locations the largest patches of trees comprise a wider range of forest types.

Ecosystem services along the urbanisation gradient

Provision of our ecosystem services remains largely stable across the urbanisation gradient, contrasting with the general pattern of provision decreasing at highly urbanised locations (e.g. Li *et al.*, 2016). Carbon storage was substantially lower in the Bangkok region (mean randomised points: 10.4 t/ha; woodland points: 25.1 t/ha) compared to nearby natural forests (60–320 t/ha in Khao Yai; Piyaphongkul *et al.*, 2011), yet was consistently maintained along the urbanisation gradient. Urbanisation has thus significantly reduced carbon storage relative to the original forested landscape, but accommodating future urban growth at high urbanisation intensities could limit the spatial extent of new urban areas without adversely impacting carbon storage in urban trees. The pattern that we document contrasts with observations from European temperate regions where carbon storage peaks at intermediate urbanisation intensities (e.g. Larondelle and Haase, 2013) and temperate and subtropical Chinese cities where carbon storage peaked in highly urbanised locations due to urban reforestation programs (Ren *et al.* 2011; Zhang *et al.* 2015). There is thus a clear need to recognise considerable regional heterogeneity in urbanisation's impacts on carbon storage in trees.

HFP (measured as biomass of trees that produce food for people) is largely maintained across the urbanisation gradient. At randomised points there is a declining pattern, but the gradient and explanatory capacity are very limited, and this is probably largely generated by a few randomised locations in the least urbanised areas comprising commercial fruit farms. Most species contributing to HFP produce fleshy fruits, which play a key role in nutritional security (Kongkachuichai *et al*., 2010). Notably, urbanisation is associated with reduced fruit (and vegetable) consumption in Asian diets due to behavioural changes and inflation of fruit prices induced by urbanisation (Cheung *et al*., 2021). Planting of fruit trees, such as mango *M. indica*, in domestic gardens can thus plat a vital role in nutritional security by providing easy-to-access low cost fruits with potential additional economic benefits from selling them (Arsenault *et al*., 2015). It is thus encouraging that there is no evidence for a substantial decline in HFP even in the most urbanised locations.

The biomass of trees providing food for frugivorous birds was maintained across the urbanisation gradient at randomised points and increased with urbanisation intensity at the woodland points. Our study only assessed one aspect of biodiversity support, but the biomass of fruiting trees that benefit frugivorous birds is also likely to benefit other taxa — such as insect pollinators of fruit trees. It is thus notable that our results contrast with the pattern observed in temperate cities that biodiversity support functions are often greatest in suburban and peri-urban regions (Radford and James, 2013). Further work is required that assesses the temporal stability of food production for frugivorous birds along the urbanisation gradient as far fewer species provided this service in our urban region (42 species) than documented in nearby natural forests (148 species in Khao Yai; Kitamura *et al*., 2002), and in most locations only a few species (2.71 ± 0.12 (s.e.) species) contributed to this services. This is important as most tree species have distinct fruiting phenologies (Pancharoen *et al*., 2021) and a much greater number of fruiting species may be required to generate a functional food supply across the annual wet/dry season cycle than are currently present.

The economic value of urban trees (defined as collateral values for securing financial loans) was not associated with urbanisation intensity at the randomised points, and increased along the urbanisation gradient in the woodland points. These findings further draw attention to the potential value of this scheme in promoting retention and creation of woodland areas.

Associations between tree species richness and ecosystem service provision

Associations between native species richness and ecosystem service provision, with the exception of carbon storage at the woodland points, were not strongly positively correlated with each other. Consequently, hotspots for biodiversity protection and ecosystem service provisioning are typically in different locations and managing for one of these attributes will not automatically benefit the other (Knapp *et al.*, 2018). This complicates urban planning decisions given the growing debate regarding on the relative priority of biodiversity conservation and ecosystem service provisioning (e.g. Conway *et al.*, 2019). Despite a positive relationship between total species richness and carbon storage at the randomised points we generally find little evidence to support the theory that species diversity enhances ecosystem service provision (Burley *et al.*, 2019; Slade *et al.*, 2019), perhaps because of the very low abundance of most species. The data on species richness-ecosystem service provision highlights that in some locations high levels of ecosystem service provision is generated from a small number of tree species. This increases the vulnerability of trees and their ecosystem services to future environmental stresses in Bangkok, such as disease and insect pests (Bumrungsri *et al.*, 2008), rising urban heat island intensity (Khamchiangta and Dhakal, 2020), and flooding (Leksungnoen *et al.*, 2017).

4.5 Conclusions and recommendations

Our study highlights a number of aspects in which the tree assemblage of a tropical mega-city differs from those in temperate urban areas including reduced species richness, especially for native species, relative to nearby natural forests, and the lack of decline in species richness (including of natives) and ecosystem service provision along the urbanisation gradient. These patterns combine to highlight that meeting the need for additional urban land through developments at a high urbanisation intensity is likely to benefit regional biodiversity in tropical regions with large amounts of natural tree cover — without necessarily compromising provision of ecosystem services. They also highlight the value of trees for ecosystem service provision. Urban planners in Bangkok need, however, to focus on protection and promotion of biodiversity alongside ecosystem services as focusing on just one of these attributes will not automatically lead to gains in the other. Results from woodland points suggest there is considerable potential for woodland retention as a nature-based solution to enhance biodiversity and ecosystem service provision, even in highly urbanised locations. The use of trees' economic value as collateral for securing financial loans may facilitate urban tree protection. There is, however, a need to revise the suite of eligible species in order to enhance the value of this approach in delivering biodiversity and ecosystem service goals, and enhance the resilience of these benefits to future environmental instability.

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4.7 Supplementary materials

Table S4.1: Lists of tree species recorded in this study arranged by family. Classification asnative or non-native to Thailand is based on Thai Plant Names (Smitinand, 2014) and considering distribution maps from Plants of the World (POWO, 2019) and Agroforestree Database (Orwa et al., 2009). Wood specific density data was obtained from Global Wood Density Database (Zanne et al, 2009), with superscripts indicating species for which genus (G) and family (F) mean values were used. Species that provide food resources for people were based on Thai Plant Production Database (DOAE, 2020). Species that provide food resources for birds were classified according to Snow (1981) and Kitamura et al. (2002). Economic value is calculated following BACC (2020) which groups 213 species into one of five groups which vary in price per volume and the rate at which price increases with size (i.e. DBH).

Family	Scientific name	Native status	Wood specific density (g/m^3)	Food for people	Food for birds	Economic value
Acanthaceae	*Avicennia alba*	native	0.587	no	no	not valuated
	Avicennia marina	native	0.648	no	no	not valuated
	Avicennia officinalis	native	0.605	no	no	not valuated
Achariaceae	*Hydnocarpus anthelminthicus*	native	0.634^G	no	no	not valuated
Anacardiaceae	*Mangifera indica*	non-native	0.553	yes	no	not valuated
	Spondias pinnata	native	0.294	yes	no	not valuated
Annonaceae	*Cananga odorata*	native	0.327	no	yes	not valuated
	Monoon longifolium var. *longifolium*	non-native	0.564	no	yes	not valuated
	Monoon longifolium var. *pendula*	non-native	0.564	no	yes	not valuated
Apocynaceae	*Alstonia scholaris*	native	0.382	no	no	group 1
	Cerbera manghas	native	0.380	no	yes	not valuated
	Cerbera odollam	native	0.300	no	yes	not valuated
	Kopsia arborea	native	0.567^F	no	no	not valuated
	Plumeria alba	non-native	0.800	no	no	not valuated
	Plumeria rubra	non-native	0.500	no	no	not valuated
Araliaceae	*Schefflera actinophylla*	non-native	0.413	no	yes	not valuated
Araucariaceae	*Araucaria cookii*	non-native	0.473^G	no	no	not valuated
Arecaceae	*Borassus flabellifer*	native	0.870	yes	no	group 4
	Cocos nucifera	non-native	0.557^F	yes	no	not valuated
	Elaeis guineensis	non-native	0.557^F	no	no	not valuated
	Phoenix roebelenii	native	0.557^F	no	no	not valuated

	Roystonea regia	non-native	0.557^F^	no	yes	not valuated
	Wodyetia bifurcata	non-native	0.557^F^	no	no	not valuated
Bignoniaceae	*Crescentia cujete*	non-native	0.634	no	no	not valuated
	Dolichandrone serrulata	native	0.441	no	no	not valuated
	Jacaranda filicifolia	non-native	0.500	no	no	not valuated
	Millingtonia hortensis	native	0.577	no	no	group 2
	Oroxylum indicum	native	0.411	yes	no	not valuated
	Radermachera sinica	non-native	0.626	no	no	not valuated
	Spathodea campanulata	native	0.351	no	no	not valuated
	Tabebuia argentea	non-native	0.756^G^	no	no	not valuated
	Tabebuia pallida	non-native	0.580	no	no	not valuated
	Tabebuia rosea	non-native	0.531	no	no	not valuated
Bixaceae	*Cochlospermum religiosum*	non-native	0.234	no	no	not valuated
Boraginaceae	*Cordia sebestena*	non-native	0.700	no	no	not valuated
Calophyllaceae	*Calophyllum inophyllum*	native	0.585	no	no	not valuated
Capparaceae	*Crateva religiosa*	native	0.467	no	no	not valuated
Casuarinaceae	*Casuarina equisetifolia*	native	0.809	no	no	group 2
	Casuarina junghuhniana	non-native	0.900	no	no	group 1
Clusiaceae	*Garcinia schomburgkiana*	native	0.735^G^	yes	no	not valuated
Combretaceae	*Combretum quadrangulare*	native	0.791	no	no	not valuated
	Terminalia catappa	native	0.478	no	yes	not valuated
	Terminalia chebula	native	0.880	no	yes	group 2
	Terminalia ivorensis	non-native	0.444	no	yes	not valuated
Dilleniaceae	*Dillenia indica*	native	0.700	yes	no	not valuated
Dipterocarpaceae	*Dipterocarpus alatus*	native	0.599	no	no	group 2
	Hopea odorata	native	0.635	no	no	group 4
	Shorea roxburghii	native	0.700	no	no	group 4
	Vatica diospyroides	native	0.696	no	no	not valuated
Ebenaceae	*Diospyros decandra*	native	0.697	no	yes	not valuated
	Diospyros mollis	native	0.697	no	yes	group 1
Elaeocarpaceae	*Elaeocarpus hygrophilus*	native	0.593	yes	yes	not valuated

Euphorbiaceae	*Excoecaria indica*	native	0.485[G]	no	no	not valuated
	Hura crepitans	non-native	0.367	no	no	not valuated
Fabaceae	*Abrus precatorius*	native	0.678[F]	no	no	not valuated
	Acacia auriculiformis	non-native	0.680	no	no	group 1
	Acacia mangium	non-native	0.507	no	no	group 1
	Adenanthera pavonina	native	0.687	no	no	not valuated
	Afzelia xylocarpa	native	0.692[G]	no	yes	group 4
	Albizia lebbeck	native	0.597	no	no	group 2
	Albizia lebbekoides	native	0.568	no	no	not valuated
	Albizia odoratissima	native	0.639	no	no	not valuated
	Albizia procera	native	0.573	no	no	group 2
	Bauhinia purpurea	non-native	0.720	no	no	not valuated
	Brownea ariza	non-native	1.210[G]	no	no	not valuated
	Butea monosperma	native	0.433	no	no	group 1
	Caesalpinia coriaria	non-native	1.138	no	no	not valuated
	Cassia bakeriana	native	0.739[G]	no	no	not valuated
	Cassia fistula	native	0.798	no	no	not valuated
	Cassia grandis	non-native	0.739[G]	no	no	not valuated
	Dalbergia cochinchinensis	native	0.880	no	no	group 4
	Delonix regia	non-native	0.579	no	no	not valuated
	Erythrina fusca	native	0.298	no	no	not valuated
	Erythrina variegata	native	0.280	no	no	not valuated
	Gliricidia sepium	non-native	0.617	no	no	not valuated
	Leucaena leucocephala	non-native	0.683	no	no	group 1
	Millettia brandisiana	native	0.592	no	no	not valuated
	Millettia leucantha	native	0.884	no	no	group 4
	Peltophorum dasyrrhachis	native	0.595	no	no	not valuated
	Peltophorum pterocarpum	native	0.565	no	no	group 1
	Phyllocarpus septentrionalis	non-native	0.678[F]	no	no	not valuated
	Pithecellobium dulce	non-native	0.684	yes	yes	not valuated
	Pterocarpus indicus	native	0.636	no	no	group 2

	Pterocarpus macrocarpus	native	0.700	no	no	group 4
	Samanea saman	non-native	0.495	no	no	group 1
	Senna siamea	native	0.660	no	no	not valuated
	Tamarindus indica	non-native	0.978	yes	no	not valuated
	Xylia xylocarpa	native	0.680	no	no	group 4
Lamiaceae	*Tectona grandis*	native	0.601	no	no	group 3
Lecythidaceae	*Barringtonia acutangula*	native	0.525	no	no	not valuated
	Barringtonia racemosa	native	0.454	no	no	not valuated
	Couroupita guianensis	non-native	0.434	no	no	not valuated
	Gustavia gracillima	non-native	0.641[G]	no	no	not valuated
Lythraceae	*Lagerstroemia floribunda*	native	0.610	no	no	not valuated
	Lagerstroemia loudonii	native	0.597[G]	no	no	group 4
	Lagerstroemia macrocarpa	native	0.647	no	no	not valuated
	Lagerstroemia speciosa	native	0.595	no	no	group 2
	Sonneratia caseolaris	native	0.389	no	no	not valuated
Magnoliaceae	*Michelia × alba*	non-native	0.504[G]	no	yes	group 2
	Michelia champaca	native	0.528	no	yes	group 2
Malvaceae	*Bombax ceiba*	native	0.314	no	no	not valuated
	Ceiba pentandra	non-native	0.305	no	no	not valuated
	Durio zibethinus	non-native	0.516	yes	no	group 1
	Hibiscus tiliaceus	native	0.450	no	yes	not valuated
	Pterospermum littorale	native	0.521	no	no	not valuated
	Sterculia foetida	native	0.448	no	yes	not valuated
	Thespesia populnea	native	0.627	no	no	not valuated
Melastomataceae	*Memecylon edule*	native	0.675	no	no	not valuated
Meliaceae	*Aglaia edulis*	native	0.710	no	yes	not valuated
	Azadirachta indica	non-native	0.640	no	no	group 4
	Chukrasia tabularis	native	0.548	no	no	group 4
	Sandoricum koetjape	native	0.473	yes	no	group 2
	Swietenia macrophylla	non-native	0.520	no	no	group 1
	Swietenia mahagoni	non-native	0.541	no	no	not valuated

	Xylocarpus granatum	native	0.567	no	no	not valuated
Moraceae	*Artocarpus altilis*	non-native	0.433	yes	yes	not valuated
	Artocarpus heterophyllus	non-native	0.492	yes	yes	group 2
	Artocarpus lacucha	native	0.484	no	yes	group 2
	Ficus altissima	native	0.443^{G}	no	yes	not valuated
	Ficus benghalensis	native	0.494	no	yes	not valuated
	Ficus benjamina	native	0.459	no	yes	not valuated
	Ficus microcarpa	native	0.412^{G}	no	yes	not valuated
	Ficus racemosa	native	0.388^{G}	yes	yes	not valuated
	Ficus religiosa	native	0.443	no	yes	not valuated
	Ficus rumphii	native	0.401	no	yes	not valuated
	Streblus asper	native	0.622	no	yes	not valuated
Moringaceae	*Moringa oleifera*	non-native	0.262	yes	no	not valuated
Muntingiaceae	*Muntingia calabura*	non-native	0.300	yes	no	not valuated
Myrtaceae	*Callistemon viminalis*	non-native	0.689	no	no	not valuated
	Eucalyptus globulus	non-native	0.722	no	no	not valuated
	Syzygium cumini	native	0.673	yes	yes	group 2
	Syzygium malaccense	native	0.562	yes	yes	not valuated
	Syzygium samarangense	native	0.649	yes	yes	not valuated
Nyctaginaceae	*Pisonia grandis*	non-native	0.344^{G}	no	yes	not valuated
Oxalidaceae	*Averrhoa carambola*	non-native	0.577	yes	no	not valuated
Pandanaceae	*Pandanus pacificus*	non-native	0.331	no	no	not valuated
	Pandanus tectorius	non-native	0.331	no	no	not valuated
Phyllanthaceae	*Phyllanthus acidus*	non-native	0.600	yes	yes	not valuated
	Phyllanthus emblica	native	0.636	yes	yes	not valuated
Polygonaceae	*Coccoloba uvifera*	non-native	0.700	no	no	not valuated
Rhamnaceae	*Ziziphus mauritiana*	non-native	0.618	yes	yes	not valuated
Rhizophoraceae	*Bruguiera gymnorhiza*	native	0.740	no	no	not valuated
	Rhizophora apiculata	native	0.843	no	no	group 1
	Rhizophora mucronata	native	0.814	no	no	group 2
Rubiaceae	*Mitragyna diversifolia*	native	0.550	no	no	not valuated

	Morinda citrifolia	native	0.630	yes	yes	not valuated
	Nauclea orientalis	native	0.483	no	no	not valuated
Rutaceae	*Aegle mamelos*	non-native	0.826	yes	no	group 3
	Citrus maxima	native	0.740	yes	no	not valuated
	Limonia acidissima	non-native	0.840	yes	no	not valuated
	Murraya paniculata	native	0.871	no	no	not valuated
Salicaceae	*Salix babylonica*	non-native	0.420	no	no	not valuated
Sapindaceae	*Arfeuillea arborescens*	native	0.695^{F}	no	no	not valuated
	Dimocarpus longan	non-native	0.700	yes	no	not valuated
	Lepisanthes rubiginosa	native	0.630	no	no	not valuated
	Litchi chinensis	native	0.854	yes	no	group 2
Sapotaceae	*Manilkara achras*	non-native	0.885	yes	yes	not valuated
	Manilkara hexandra	native	1.060	no	yes	group 2
	Mimusops elengi	native	0.849	no	yes	group 2
Tiliaceae	*Schoutenia glomerata*	native	0.733^{G}	no	no	not valuated
Verbenaceae	*Citharexylum spinosum*	non-native	0.700	no	no	not valuated
Zygophyllaceae	*Guaiacum officinale*	non-native	1.177	no	no	not valuated

Table S4.2: AICc values of generalised linear models for species richness metrics with % impervious surface cover (linear and quadratic models) comparing between models fitted using Poisson error structure (log link) and Gaussian error structure (identity link).

Response variable	Location	AICc (linear model)		AICc (quadratic model)	
		Gaussian	Poisson	Gaussian	Poisson
Total species richness	Randomised	**871.38**	1000.69	**873.39**	1002.46
	Woodland	**897.36**	956.87	**897.97**	956.07
Native species richness	Randomised	**700.19**	700.00	**702.29**	702.05
	Woodland	**810.38**	898.35	**810.57**	896.45
Non-native species richness	Randomised	**717.62**	748.18	**719.47**	749.69
	Woodland	**708.78**	724.75	**710.68**	726.69

Table S4.3: Moran's I test results of residuals from glm models for measures of species richness with impervious surface (linear and quadratic models). Models with significant spatial autocorrelation detected in the residuals are shown in bold.

Response variable	Location	Moran's I test (linear model)		Moran's I test (quadratic model)	
		Observed	*P*	Observed	*P*
Total species richness	Randomised	**0.039**	**0.003**	**0.040**	**0.003**
	Woodland	-0.023	0.340	-0.024	0.315
Native species richness	Randomised	**0.032**	**0.014**	**0.032**	**0.014**
	Woodland	-0.017	0.546	-0.018	0.523
Non-native species richness	Randomised	0.013	0.216	0.015	0.176
	Woodland	-0.031	0.145	-0.032	0.138

Table S4.4: Comparison of coefficients and standard errors of species richness metrics at the randomised points (for which Moran's I values are statistically significant) as a function of percentage impervious surface cover (linear and quadratic models) with and without taking spatial correlation structure into account using a generalised linear mixed model approach.

Response variable	Model	Model type	Intercept	%impervious surface (Linear term)		%impervious surface (Quadratic term)	
				Coeff ± SE	*P*	Coeff ± SE	*P*
Total species richness	Linear	Non-spatial	6.323 ± 0.688	-0.012 ± 0.013	0.346		
		Spatial	6.508 ± 0.714	-0.015 ± 0.013	0.241		
	Quadratic	Non-spatial	6.563 ± 1.004	-0.027 ± 0.049	0.577	$1.6e^{-4} \pm 4.9e^{-4}$	0.743
		Spatial	6.542 ± 1.017	-0.018 ± 0.050	0.725	$2.5e^{-5} \pm 0.001$	0.962
Native species richness	Linear	Non-spatial	3.086 ± 0.389	-0.006 ± 0.007	0.391		
		Spatial	3.086 ± 0.386	-0.006 ± 0.007	0.386		
	Quadratic	Non-spatial	3.142 ± 0.568	-0.010 ± 0.028	0.726	$3.8e^{-5} \pm 2.8e^{-4}$	0.893
		Spatial	3.142 ± 0.562	-0.010 ± 0.028	0.723	$3.8e^{-5} \pm 2.8e^{-4}$	0.891

Table S4.5: Moran’s I test results of residuals from glm models of carbon storage, human food production, biodiversity support, and economic value of urban trees, as a function of percentage impervious surface cover (linear and quadratic models). Models with significant spatial autocorrelation detected in the residuals are in bold.

Response variable	Location	Moran’s I test (linear model)		Moran’s I test (quadratic model)	
		Observed	*P*	Observed	*P*
Total CS	Randomised	**0.025**	**0.041**	**0.025**	**0.044**
	Woodland	0.012	0.257	0.011	0.295
CS of native trees	Randomised	-0.009	0.880	-0.009	0.878
	Woodland	-2.6e^{-4}	0.693	-0.003	0.818
CS of non-native trees	Randomised	**0.029**	**0.022**	**0.029**	**0.023**
	Woodland	0.011	0.274	0.011	0.276
Total HFP	Randomised	**0.038**	**0.003**	**0.037**	**0.004**
	Woodland	**0.036**	**0.007**	**0.037**	**0.006**
HFP of native trees	Randomised	**0.022**	**0.016**	**0.021**	**0.019**
	Woodland	**0.033**	**0.015**	**0.035**	**0.013**
HFP of non-native trees	Randomised	**0.029**	**0.018**	**0.028**	**0.020**
	Woodland	**0.037**	**0.006**	**0.037**	**0.006**
Total BDS	Randomised	-0.008	0.910	-0.009	0.881
	Woodland	-0.018	0.501	-0.021	0.410
BDS of native trees	Randomised	-0.011	0.711	-0.012	0.690
	Woodland	-0.023	0.323	-0.027	0.227
BDS of non-native trees	Randomised	0.006	0.374	0.006	0.391
	Woodland	-0.010	0.845	-0.010	0.839
Total ECV	Randomised	-0.009	0.900	0.019	0.102
	Woodland	0.016	0.169	0.016	0.175
ECV of native trees	Randomised	-0.015	0.592	-0.017	0.482
	Woodland	0.011	0.276	0.010	0.307
ECV of non-native trees	Randomised	-0.013	0.632	-0.015	0.537
	Woodland	-0.020	0.416	-0.019	0.421

Table S4.6: Comparison of parameter coefficients and standard errors in models for ecosystem service provision as a function of percentage impervious surface cover (linear and quadratic models) in models with and without taking spatial correlation into account (using generalised linear mixed model approach). Results are presented for all ecosystem service models for which Moran's I values indicate significant spatial autocorrelation, i.e. (a) carbon storage, and (b) human food production.

a)

Response variable	Model	Model type	Intercept	%impervious surface (Linear term)		%impervious surface (Quadratic term)	
				Coeff ± SE	*P*	Coeff ± SE	*P*
Total CS at the randomised points	Linear	Non-spatial	12.449 ± 1.518	-0.045 ± 0.028	0.110		
		Spatial	13.110 ± 1.638	-0.061 ± 0.030	0.041		
	Quadratic	Non-spatial	12.119 ± 2.216	-0.023 ± 0.108	0.832	-2.3e^{-4} ± 0.001	0.838
		Spatial	12.119 ± 2.193	-0.023 ± 0.107	0.830	-2.3e^{-4} ± 0.001	0.836
CS of non-native trees at the randomised points	Linear	Non-spatial	9.950 ± 1.159	-0.051 ± 0.021	0.016		
		Spatial	10.265 ± 1.245	-0.060 ± 0.023	0.008		
	Quadratic	Non-spatial	9.852 ± 1.692	-0.045 ± 0.083	0.588	-1.0e^{-4} ± 0.001	0.937
		Spatial	9.852 ± 1.675	-0.045 ± 0.082	0.583	-1.0e^{-4} ± 0.001	0.936

b) HFP models that were spatially autocorrelated

Response variable	Model	Model type	Intercept	%impervious surface (Linear term)		%impervious surface (Quadratic term)	
				Coeff ± SE	*P*	Coeff ± SE	*P*
Total HFP at the randomised points	Linear	Non-spatial	3.881 ± 0.656	-0.029 ± 0.012	0.017		
		Spatial	4.155 ± 0.713	-0.033 ± 0.013	0.011		
	Quadratic	Non-spatial	4.036 ± 0.958	-0.039 ± 0.047	0.408	$1.1e^{-4}$ ± $4.8e^{-4}$	0.824
		Spatial	3.736 ± 1.019	-0.005 ± 0.050	0.916	$3.0e^{-4}$ ± 0.001	0.563
Total HFP at the woodland points	Linear	Non-spatial	9.622 ± 2.022	-0.059 ± 0.037	0.108		
		Spatial	8.586 ± 2.366	-0.039 ± 0.040	0.322		
	Quadratic	Non-spatial	9.196 ± 2.965	-0.032 ± 0.145	0.827	$-2.9e^{-4}$ ± 0.001	0.844
		Spatial	6.898 ± 3.108	0.073 ± 0.139	0.600	-0.001 ± 0.001	0.401
HFP of native trees at the randomised points	Linear	Non-spatial	0.415 ± 0.113	-0.004 ± 0.002	0.082		
		Spatial	0.415 ± 0.112	-0.004 ± 0.002	0.078		
	Quadratic	Non-spatial	0.251 ± 0.164	0.007 ± 0.008	0.379	$-1.1e^{-4}$ ± $1.0e^{-4}$	0.170
		Spatial	0.251 ± 0.162	0.007 ± 0.008	0.373	$-1.1e^{-4}$ ± $1.0e^{-4}$	0.163
HFP of native trees at the woodland points	Linear	Non-spatial	0.460 ± 0.152	0.002 ± 0.003	0.558		
		Spatial	0.549 ± 0.171	$2.8e^{-4}$ ± 0.003	0.927		
	Quadratic	Non-spatial	0.497 ± 0.223	-0.001 ± 0.011	0.941	$2.5e^{-5}$ ± $1.1e^{-4}$	0.818
		Spatial	0.637 ± 0.235	-0.005 ± 0.011	0.620	$6.1e^{-5}$ ± $1.1e^{-4}$	0.587
HFP of non-native trees at the randomised points	Linear	Non-spatial	3.585 ± 0.637	-0.026 ± 0.012	0.026		
		Spatial	3.771 ± 0.691	-0.031 ± 0.013	0.014		
	Quadratic	Non-spatial	3.905 ± 0.929	-0.047 ± 0.045	0.303	$2.2e^{-4}$ ± $4.6e^{-4}$	0.636
		Spatial	3.355 ± 0.978	-0.003 ± 0.047	0.945	$-3.0e^{-4}$ ± $4.9e^{-4}$	0.545
HFP of non-native trees at the woodland points	Linear	Non-spatial	9.162 ± 2.018	-0.061 ± 0.037	0.098		
		Spatial	7.976 ± 2.367	-0.038 ± 0.040	0.332		
	Quadratic	Non-spatial	8.699 ± 2.959	-0.031 ± 0.145	0.831	$-3.1e^{-4}$ ± 0.001	0.830
		Spatial	6.158 ± 3.107	0.082 ± 0.139	0.553	-0.001 ± 0.001	0.365

Table S4.7: Moran I's test results of residuals from generalised linear models of carbon storage (CS), human food potential (HFP), biodiversity support (BDS), and economic value (ECV) as a function of tree species richness and percentage impervious surface cover. Separate models are run that use data on total and native species richness (including linear and quadratic models). Models with significant spatial autocorrelation detected in the residuals are in bold.

Response variable	Location	Total species richness				Native species richness			
		Linear model		Quadratic model		Linear model		Quadratic model	
		Moran's I value	*P*	Moran's I value	*P*	Moran's I value	*P*	Moran's I value	*P*
CS	Randomised	-0.010	0.814	-0.017	0.502	-0.021	0.344	-0.020	0.374
	Woodland	0.014	0.206	0.019	0.124	0.016	0.173	0.022	0.083
HFP	Randomised	0.010	0.257	0.010	0.255	0.021	0.069	0.018	0.097
	Woodland	**0.038**	**0.005**	**0.041**	**0.003**	**0.038**	**0.006**	**0.040**	**0.003**
BDS	Randomised	-0.010	0.787	-0.013	0.642	-0.010	0.814	-0.012	0.681
	Woodland	-0.014	0.664	0.005	0.483	-0.022	0.368	-0.020	0.423
ECV	Randomised	-0.005	0.930	-0.008	0.942	-0.018	0.453	-0.018	0.459
	Woodland	0.020	0.101	0.025	0.055	0.022	0.085	0.018	0.131

Table S4.8: Comparison of coefficients and standard errors of models for total HFP at the woodland points with percentage impervious surface cover and tree species richness (including linear and quadratic terms) with and without taking spatial correlation structure into account by using generalised linear mixed model approach (nlme package) with exponential covariance structure.

Response variable	Model	Model type	Intercept	% impervious surface		Tree species richness Linear term		Tree species richness Quadratic term	
				Coeff ± SE	*P*	Coeff ± SE	*P*	Coeff ± SE	*P*
HFP at the woodland points	Linear	Non-spatial	15.152 ± 3.985	-0.043 ± 0.038	0.255	-2.985 ± 1.857	0.110		
		Spatial	11.505 ± 3.887	-0.037 ± 0.039	0.350	-1.441 ± 1.534	0.347		
	Quadratic	Non-spatial	24.105 ± 8.748	-0.042 ± 0.038	0.269	-13.014 ± 8.921	0.147	2.538 ± 2.208	0.252
		Spatial	15.043 ± 7.056	-0.035 ± 0.040	0.381	-5.453 ± 6.830	0.425	1.020 ± 1.690	0.546

Table 4.9: List of tree species found in this study arranged by total number of individuals across all surveyed locations.

Scientific name	Number of individuals			% occurrence			Mean DBH (cm)			Aboveground biomass (t/ha)		
	Randomised	Woodland	Total	Randomised	Woodland	Total	Randomised	Woodland	Total	Randomised	Woodland	Total
Cocos nucifera	249	790	1039	16.00	21.33	29.33	31.76	33.42	33.02	116.43	473.72	590.15
Leucaena leucocephala	88	599	687	22.00	68.00	70.67	28.13	27.18	27.30	37.65	226.48	264.13
Mangifera indica	403	279	682	42.67	38.67	60.00	27.89	28.49	28.13	101.08	78.65	179.72
Pithecellobium dulce	80	337	417	24.00	54.67	64.67	33.01	32.04	32.22	57.88	235.80	293.68
Pterocarpus indicus	112	264	376	25.33	38.67	50.00	34.27	38.79	37.45	83.52	289.39	372.91
Acacia auriculiformis	59	268	327	12.00	40.00	46.00	34.20	35.98	35.66	51.90	255.72	307.63
Albizia saman	51	187	238	16.00	30.00	38.00	72.86	74.55	74.18	224.18	885.88	1110.06
Peltophorum pterocarpum	109	110	219	9.33	13.33	20.67	34.33	37.55	35.94	73.79	90.72	164.52
Swietenia macrophylla	63	123	186	9.33	11.33	19.33	30.30	30.75	30.60	29.07	59.22	88.29
Tamarindus indica	64	121	185	26.00	40.67	52.67	30.32	30.32	30.32	58.33	109.67	168.00
Alstonia scholaris	59	121	180	19.33	17.33	32.67	32.82	40.01	37.66	24.70	87.75	112.44
Terminalia catappa	44	121	165	14.67	28.67	38.67	35.75	42.00	40.33	31.40	122.53	153.92
Tabebuia rosea	54	98	152	12.00	22.00	30.00	35.43	40.05	38.41	34.61	86.59	121.20
Ficus benjamina	38	89	127	13.33	30.67	39.33	61.73	63.07	62.67	150.03	280.07	430.10
Cassia fistula	76	49	125	23.33	14.67	34.67	27.43	26.82	27.19	36.23	21.82	58.06
Combretum quadrangulare	16	105	121	4.00	20.00	23.33	31.17	30.03	30.18	11.27	69.39	80.66

Cerbera odollam	41	73	114	8.67	14.67	20.67	26.24	27.42	26.99	4.46	8.44	12.90
Millingtonia hortensis	49	54	103	14.00	12.67	22.00	26.97	28.86	27.96	18.49	24.01	42.50
Sonneratia caseolaris	38	63	101	4.67	9.33	10.00	42.08	50.30	47.21	35.59	93.45	129.03
Delonix regia	36	57	93	10.67	18.67	24.67	43.10	52.47	48.84	46.42	124.83	171.26
Eucalyptus globulus	11	80	91	2.67	6.67	8.67	34.03	28.93	29.55	9.96	46.45	56.41
Ficus religiosa	36	55	91	14.00	16.00	28.00	63.21	61.54	62.20	140.25	161.21	301.46
Muntingia calabura	25	62	87	10.67	17.33	24.67	26.00	26.28	26.20	2.73	6.79	9.52
Azadirachta indica	29	54	83	13.33	22.00	29.33	28.14	28.01	28.06	13.44	24.32	37.77
Avicennia alba	34	41	75	3.33	4.67	6.00	34.38	42.38	38.75	27.00	50.51	77.51
Lagerstroemia floribunda	11	62	73	4.67	12.00	16.00	27.20	28.18	28.03	4.06	24.79	28.85
Terminalia ivorensis	45	17	62	9.33	8.67	17.33	26.07	26.04	26.06	11.32	4.51	15.83
Syzygium cumini	16	45	61	8.67	20.00	26.67	31.73	33.18	32.80	10.75	34.23	44.97
Artocarpus heterophyllus	35	24	59	14.67	10.00	23.33	26.55	29.30	27.67	8.82	7.72	16.54
Tectona grandis	7	51	58	4.00	10.67	14.67	29.10	32.78	32.34	3.55	35.40	38.95
Dolichandrone serrulata	31	20	51	5.33	7.33	12.67	26.62	27.38	26.92	8.02	5.69	13.71
Lagerstroemia loudonii	20	26	46	7.33	12.00	16.67	29.09	38.72	34.53	10.27	30.08	40.34
Nauclea orientalis	24	22	46	3.33	2.67	6.00	26.75	31.08	28.82	6.83	9.41	16.24
Mimusops elengi	6	38	44	4.00	10.67	14.00	25.55	26.60	26.46	1.67	11.21	12.88

Monoon longifolium var. pendula	34	7	41	4.00	2.00	5.33	25.91	26.47	26.00	12.18	2.68	14.86
Casuarina equisetifolia	11	28	39	2.00	2.67	4.67	27.87	31.34	30.36	6.22	21.29	27.51
Senna siamea	5	34	39	3.33	11.33	14.00	28.46	27.18	27.35	1.40	10.74	12.14
Albizia procera	13	24	37	2.00	6.67	8.00	34.21	33.93	34.02	8.19	16.04	24.23
Sandoricum koetjape	12	25	37	7.33	9.33	15.33	29.05	32.78	31.57	4.08	12.23	16.30
Moringa oleifera	18	18	36	10.00	9.33	19.33	28.06	27.48	27.77	2.29	2.12	4.40
Elaeocarpus hygrophilus	10	21	31	4.00	6.67	10.00	31.71	28.00	29.19	4.36	6.08	10.44
Lagerstroemia speciosa	8	21	29	3.33	6.00	9.33	29.58	29.88	29.80	3.92	10.89	14.81
Ficus benghalensis	7	21	28	4.67	10.67	13.33	76.99	67.48	69.86	50.50	79.15	129.66
Albizia lebbekoides	5	22	27	2.00	2.67	4.67	31.96	35.67	34.98	3.02	18.09	21.11
Tabebuia argentea	16	11	27	4.00	4.00	7.33	26.97	25.56	26.40	4.50	3.15	7.66
Casuarina junghuhniana	11	15	26	2.00	1.33	2.67	29.52	29.20	29.33	9.43	11.16	20.58
Streblus asper	6	20	26	3.33	8.00	10.00	25.94	26.16	26.11	1.29	4.39	5.68
Avicennia marina	11	13	24	2.00	2.00	3.33	39.50	38.81	39.13	13.51	15.15	28.66
Erythrina fusca	3	21	24	1.33	7.33	8.67	38.83	31.50	32.42	1.23	4.88	6.11
Crateva religiosa	3	16	19	1.33	4.67	6.00	30.24	31.20	31.05	1.21	7.17	8.38
Spondias pinnata	5	13	18	3.33	6.67	10.00	36.09	34.69	35.08	1.95	4.62	6.58
Syzygium malaccense	9	9	18	4.00	6.00	8.67	27.75	26.97	27.36	1.98	1.87	3.85

Calophyllum inophyllum	1	16	17	0.67	4.00	4.67	25.27	30.40	30.10	0.19	6.68	6.87
Couroupita guianensis	8	8	16	3.33	3.33	6.67	34.57	30.12	32.35	4.52	3.17	7.69
Dipterocarpus alatus	1	15	16	0.67	4.67	5.33	28.33	44.44	43.43	0.27	22.55	22.82
Phyllanthus acidus	14	2	16	8.00	1.33	9.33	25.98	28.63	26.31	2.64	0.38	3.02
Dimocarpus longan	3	12	15	2.00	6.67	8.00	28.99	31.74	31.19	1.58	7.75	9.33
Thespesia populnea	6	9	15	2.67	3.33	4.67	26.37	28.49	27.64	1.21	2.96	4.17
Hibiscus tiliaceus	0	14	14	0.00	5.33	5.33	0.00	26.15	26.15	0.00	1.94	1.94
Borassus flabellifer	2	11	13	0.67	4.67	5.33	29.76	30.07	30.02	1.49	9.16	10.65
Ficus racemosa	5	8	13	2.00	2.67	4.67	48.28	28.17	35.90	7.90	2.34	10.24
Litchi chinensis	7	6	13	1.33	2.00	3.33	27.24	31.31	29.12	2.47	2.87	5.34
Roystonea regia	7	5	12	2.00	2.67	4.67	34.29	50.17	40.90	3.87	6.78	10.65
Albizia odoratissima	2	9	11	1.33	2.67	4.00	31.87	29.21	29.70	1.15	4.86	6.00
Shorea roxburghii	2	9	11	0.67	1.33	2.00	29.92	38.09	36.61	1.16	9.80	10.96
Michelia champaca	7	3	10	3.33	2.00	5.33	25.90	26.31	26.03	1.19	0.56	1.75
Rhizophora mucronata	4	6	10	1.33	2.00	2.67	25.62	25.84	25.75	0.96	1.40	2.36
Spathodea campanulata	4	6	10	2.67	2.00	4.67	27.62	32.39	30.48	1.12	2.04	3.16
Diospyros mollis	0	9	9	0.00	4.67	4.67	0.00	35.07	35.07	0.00	7.62	7.62
Ficus altissima	1	8	9	0.67	4.00	4.67	78.30	46.09	49.67	4.26	11.69	15.95
Bruguiera gymnorhiza	5	3	8	2.00	2.00	3.33	27.69	27.59	27.65	2.05	1.11	3.17

Butea monosperma	5	3	8	1.33	1.33	2.00	31.08	39.11	34.09	1.37	2.07	3.44
Ficus microcarpa	4	4	8	2.67	2.67	5.33	84.49	54.94	69.72	19.85	6.58	26.42
Pandanus pacificus	0	8	8	0.00	2.00	2.00	0.00	54.56	54.56	0.00	6.21	6.21
Pisonia grandis	6	2	8	4.00	1.33	5.33	27.57	25.76	27.12	0.79	0.24	1.03
Syzygium samarangense	5	3	8	3.33	2.00	5.33	26.84	27.90	27.24	1.15	0.75	1.90
Cassia bakeriana	2	5	7	1.33	3.33	4.67	25.78	29.55	28.48	0.65	2.62	3.27
Cochlospermum religiosum	1	6	7	0.67	2.00	2.67	26.10	37.61	35.97	0.13	1.67	1.81
Plumeria rubra	6	1	7	4.00	0.67	4.67	26.52	30.56	27.10	0.99	0.26	1.25
Rhizophora apiculata	2	5	7	0.67	0.67	1.33	26.42	26.32	26.35	0.46	1.29	1.74
Swietenia mahagoni	7	0	7	0.67	0.00	0.67	46.87	0.00	46.87	7.08	0.00	7.08
Sterculia foetida	1	6	7	0.67	3.33	3.33	34.38	38.99	38.33	0.54	4.82	5.36
Albizia lebbeck	5	1	6	2.67	0.67	3.33	41.00	40.11	40.85	5.73	1.00	6.72
Acacia mangium	5	1	6	1.33	0.67	2.00	34.82	47.11	36.87	3.01	1.17	4.18
Cananga odorata	0	6	6	0.00	2.67	2.67	0.00	49.13	49.13	0.00	6.09	6.09
Citharexylum spinosum	5	1	6	3.33	0.67	4.00	26.16	25.46	26.05	0.49	0.13	0.61
Gliricidia sepium	2	4	6	1.33	2.67	3.33	32.57	39.95	37.49	1.30	4.22	5.52
Tabebuia pallida	0	6	6	0.00	2.67	2.67	0.00	28.44	28.44	0.00	1.69	1.69
Wodyetia bifurcata	6	0	6	0.67	0.00	0.67	25.20	0.00	25.20	0.87	0.00	0.87
Artocarpus altilis	1	4	5	0.67	2.00	2.67	31.55	27.06	27.96	0.25	0.76	1.01

Averrhoa carambola	2	3	5	1.33	2.00	3.33	28.27	28.62	28.48	0.70	0.97	1.67
Brownea ariza	1	4	5	0.67	1.33	2.00	27.08	28.98	28.60	0.47	2.15	2.62
Citrus maxima	0	5	5	0.00	0.67	0.67	0.00	32.59	32.59	0.00	1.72	1.72
Elaeis guineensis	0	5	5	0.00	0.67	0.67	0.00	34.12	34.12	0.00	2.10	2.10
Michelia alba	2	3	5	1.33	2.00	3.33	25.43	25.36	25.39	0.34	0.44	0.78
Manilkara hexandra	1	4	5	0.67	1.33	1.33	26.10	28.07	27.68	0.56	3.17	3.72
Plumeria alba	3	2	5	1.33	1.33	2.67	29.10	28.04	28.68	0.88	0.72	1.61
Phyllocarpus septentrionalis	2	3	5	1.33	2.00	3.33	50.45	34.48	40.87	3.98	2.27	6.26
Pterocarpus macrocarpus	0	5	5	0.00	2.00	2.00	0.00	36.28	36.28	0.00	4.55	4.55
Phoenix roebelenii	1	4	5	0.67	0.67	1.33	30.00	37.40	35.92	0.32	2.06	2.38
Arfeuillea arborescens	0	4	4	0.00	0.67	0.67	0.00	26.42	26.42	0.00	1.25	1.25
Aegle mamelos	1	3	4	0.67	2.00	2.67	25.46	27.99	27.36	0.42	1.56	1.98
Avicennia officinalis	2	2	4	0.67	0.67	0.67	26.26	55.45	40.85	0.77	6.77	7.54
Afzelia xylocarpa	0	4	4	0.00	1.33	1.33	0.00	30.64	30.64	0.00	2.68	2.68
Erythrina variegata	2	2	4	1.33	0.67	2.00	25.93	32.23	29.08	0.17	0.32	0.48
Lagerstroemia macrocarpa	2	2	4	1.33	0.67	2.00	26.35	27.22	26.78	0.68	0.78	1.46
Monoon longifolium var. longifolium	3	1	4	2.00	0.67	2.67	26.21	25.78	26.10	0.78	0.24	1.02
Pandanus tectorius	2	2	4	0.67	1.33	1.33	50.17	46.61	48.39	0.91	1.08	1.99

Xylocarpus granatum	4	0	4	1.33	0.00	1.33	27.61	0.00	27.61	1.27	0.00	1.27
Xylia xylocarpa	0	4	4	0.00	0.67	0.67	0.00	30.10	30.10	0.00	2.25	2.25
Bauhinia purpurea	1	2	3	0.67	0.67	1.33	25.46	26.90	26.42	0.24	0.53	0.77
Ceiba pentandra	0	3	3	0.00	0.67	0.67	0.00	34.06	34.06	0.00	1.05	1.05
Coccoloba uvifera	1	2	3	0.67	0.67	1.33	31.74	30.08	30.63	0.55	0.95	1.50
Callistemon viminalis	3	0	3	0.67	0.00	0.67	30.65	0.00	30.65	1.62	0.00	1.62
Diospyros decandra	2	1	3	0.67	0.67	1.33	26.10	28.33	26.84	0.83	0.41	1.23
Gustavia gracillima	3	0	3	0.67	0.00	0.67	29.58	0.00	29.58	0.38	0.00	0.38
Morinda citrifolia	2	1	3	1.33	0.67	2.00	25.07	26.84	25.66	0.44	0.18	0.61
Oroxylum indicum	2	1	3	1.33	0.67	2.00	26.74	27.37	26.95	0.31	0.20	0.51
Radermachera sinica	3	0	3	2.00	0.00	2.00	25.27	0.00	25.27	1.01	0.00	1.01
Schoutenia glomerata	0	3	3	0.00	0.67	0.67	0.00	25.89	25.89	0.00	0.83	0.83
Schefflera actinophylla	0	3	3	0.00	0.67	0.67	0.00	26.68	26.68	0.00	0.49	0.49
Abrus precatorius	0	2	2	0.00	1.33	1.33	0.00	32.71	32.71	0.00	1.56	1.56
Araucaria cookii	0	2	2	0.00	0.67	0.67	0.00	42.97	42.97	0.00	1.88	1.88
Barringtonia racemosa	0	2	2	0.00	0.67	0.67	0.00	25.94	25.94	0.00	0.33	0.33
Bombax ceiba	0	2	2	0.00	0.67	0.67	0.00	30.24	30.24	0.00	0.45	0.45
Cassia grandis	1	1	2	0.67	0.67	1.33	26.10	26.10	26.10	0.37	0.35	0.72
Durio zibethinus	0	2	2	0.00	0.67	0.67	0.00	27.69	27.69	0.00	0.41	0.41

Excoecaria indica	0	2	2	0.00	0.67	0.67	0.00	26.42	26.42	0.00	0.75	0.75
Garcinia schomburgkiana	0	2	2	0.00	1.33	1.33	0.00	25.31	25.31	0.00	0.58	0.58
Guaiacum officinale	1	1	2	0.67	0.67	1.33	27.80	26.74	27.27	0.36	0.54	0.90
Hopea odorata	0	2	2	0.00	1.33	1.33	0.00	40.27	40.27	0.00	2.54	2.54
Phyllanthus emblica	0	2	2	0.00	0.67	0.67	0.00	41.17	41.17	0.00	1.83	1.83
Ziziphus mauritiana	1	1	2	0.67	0.67	1.33	25.78	29.39	27.59	0.21	0.21	0.42
Adenanthera pavonina	0	1	1	0.00	0.67	0.67	0.00	44.88	44.88	0.00	1.41	1.41
Aglaia edulis	0	1	1	0.00	0.67	0.67	0.00	26.42	26.42	0.00	0.35	0.35
Artocarpus lacucha	0	1	1	0.00	0.67	0.67	0.00	27.37	27.37	0.00	0.23	0.23
Barringtonia acutangula	1	0	1	0.67	0.00	0.67	28.76	0.00	28.76	0.17	0.00	0.17
Cerbera manghas	1	0	1	0.67	0.00	0.67	25.78	0.00	25.78	0.14	0.00	0.14
Crescentia cujete	0	1	1	0.00	0.67	0.67	0.00	31.33	31.33	0.00	0.10	0.10
Cordia sebestena	1	0	1	0.67	0.00	0.67	27.84	0.00	27.84	0.28	0.00	0.28
Chukrasia tabularis	1	0	1	0.67	0.00	0.67	26.10	0.00	26.10	0.24	0.00	0.24
Caesalpinia coriaria	1	0	1	0.67	0.00	0.67	25.79	0.00	25.79	0.46	0.00	0.46
Dalbergia cochinchinensis	0	1	1	0.00	0.67	0.67	0.00	26.10	26.10	0.00	0.46	0.46
Dillenia indica	0	1	1	0.00	0.67	0.67	0.00	25.15	25.15	0.00	0.23	0.23
Ficus rumphii	0	1	1	0.00	0.67	0.67	0.00	43.39	43.39	0.00	0.86	0.86
Hura crepitans	0	1	1	0.00	0.67	0.67	0.00	78.62	78.62	0.00	3.69	3.69

Hydnocarpus anthelminthicus	0	1	1	0.00	0.67	0.67	0.00	27.37	27.37	0.00	0.30	0.30
Jacaranda filicifolia	1	0	1	0.67	0.00	0.67	26.87	0.00	26.87	0.17	0.00	0.17
Kopsia arborea	0	1	1	0.00	0.67	0.67	0.00	25.46	25.46	0.00	0.14	0.14
Limonia acidissima	0	1	1	0.00	0.67	0.67	0.00	25.78	25.78	0.00	0.43	0.43
Lepisanthes rubiginosa	0	1	1	0.00	0.67	0.67	0.00	25.78	25.78	0.00	0.33	0.33
Memecylon edule	0	1	1	0.00	0.67	0.67	0.00	26.74	26.74	0.00	0.32	0.32
Millettia brandisiana	0	1	1	0.00	0.67	0.67	0.00	27.37	27.37	0.00	0.35	0.35
Millettia leucantha	0	1	1	0.00	0.67	0.67	0.00	29.60	29.60	0.00	0.64	0.64
Manilkara achras	1	0	1	0.67	0.00	0.67	27.52	0.00	27.52	0.34	0.00	0.34
Murraya paniculata	1	0	1	0.67	0.00	0.67	26.40	0.00	26.40	0.24	0.00	0.24
Mitragyna diversifolia	0	1	1	0.00	0.67	0.67	0.00	32.82	32.82	0.00	0.42	0.42
Peltophorum dasyrrhachis	0	1	1	0.00	0.67	0.67	0.00	50.29	50.29	0.00	2.28	2.28
Pterospermum littorale	0	1	1	0.00	0.67	0.67	0.00	25.78	25.78	0.00	0.22	0.22
Salix babylonica	1	0	1	0.67	0.00	0.67	26.10	0.00	26.10	0.15	0.00	0.15
Terminalia chebula	0	1	1	0.00	0.67	0.67	0.00	27.28	27.28	0.00	0.32	0.32
Vatica diospyroides	0	1	1	0.00	0.67	0.67	0.00	27.06	27.06	0.00	0.23	0.23

Table S4.10: Number of species contributing to ecosystem service provision, mean service provision from all, native, and non-native species, tests of differences between native and non-native species' service provision (Matched-paired t-test for carbon storage at the randomised points and economic value at the woodland points, and Wilcoxon paired test for other variables), and the identity of species with the greatest contribution to each ecosystem service.

Location type	Cumulative number of species contributing		Service provision from all species		Service provision from native species		Service provision from non-native species		Test of differences (native & non-native service provision)		Species with the greatest contribution		
	Total	% native	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Test statistic*	*P*	Scientific name	Occupancy	Contribution
Carbon storage (t/ha) – 162 species (61.11% native)													
Randomised	119	55.46%	10.36 ± 0.79	0 – 51.30	2.82 ± 0.40	0 – 42.50	7.54 ± 0.61	0 – 38.57	-7.181	$3.1e^{-11}$	*Mangifera indica*	42.67%	10.19%
Woodland	147	63.95%	25.14 ± 1.37	4.03 – 86.69	6.07 ± 0.55	0 – 36.13	19.07 ± 1.18	0 – 84.29	0.806	$<2.2e^{-16}$	*Samanea saman*	30.00%	13.44%
Biomass of species contributing to human food production (t/ha) – 31 species (48.39% native)													
Randomised	25	44.00%	2.60 ± 0.35	0 – 26.65	0.24 ± 0.06	0 – 7.31	2.36 ± 0.33	0 – 25.66	0.683	$<2.2e^{-16}$	*Cocos nucifera*	16.00%	29.81%
Woodland	30	50.00%	6.71 ± 1.03	0 – 75.67	0.53 ± 0.08	0 – 4.63	6.18 ± 1.03	0 – 75.67	0.774	$<2.2e^{-16}$	*Cocos nucifera*	21.33%	47.10%
Biomass of species contributing to biodiversity support (t/ha) – 42 species (69.05% native)													
Randomised	32	62.50%	3.55 ± 0.70	0 – 84.11	2.89 ± 0.70	0 – 83.86	0.66 ± 0.10	0 – 9.06	0.272	0.001	*Ficus benjamina*	13.33%	28.15%
Woodland	40	70.00%	6.81 ± 0.64	0 – 37.08	5.08 ± 0.62	0 – 31.04	1.74 ± 0.19	0 – 15.71	0.279	0.001	*Ficus benjamina*	30.67%	27.41%
Economic value (£) – 43 species (74.42% native)													
Randomised	33	69.70%	643.38 ± 77.63	0 – 6,276.56	338.52 ± 48.00	0 – 3,089.50	295.44 ± 57.14	0 – 6276.56	0.174	0.033	*Samanea saman*	16.00%	26.92%
Woodland	42	73.81%	2,281.55 ± 242.12	0 – 15,283.70	1,204.07 ± 169.15	0 – 12,908.40	898.66 ± 139.02	0 – 11483.67	1.502	0.135	*Samanea saman*	30.00%	30.45%

* *t* value (for matched-paired t-test) or *Z* value (for Wilcoxon test)

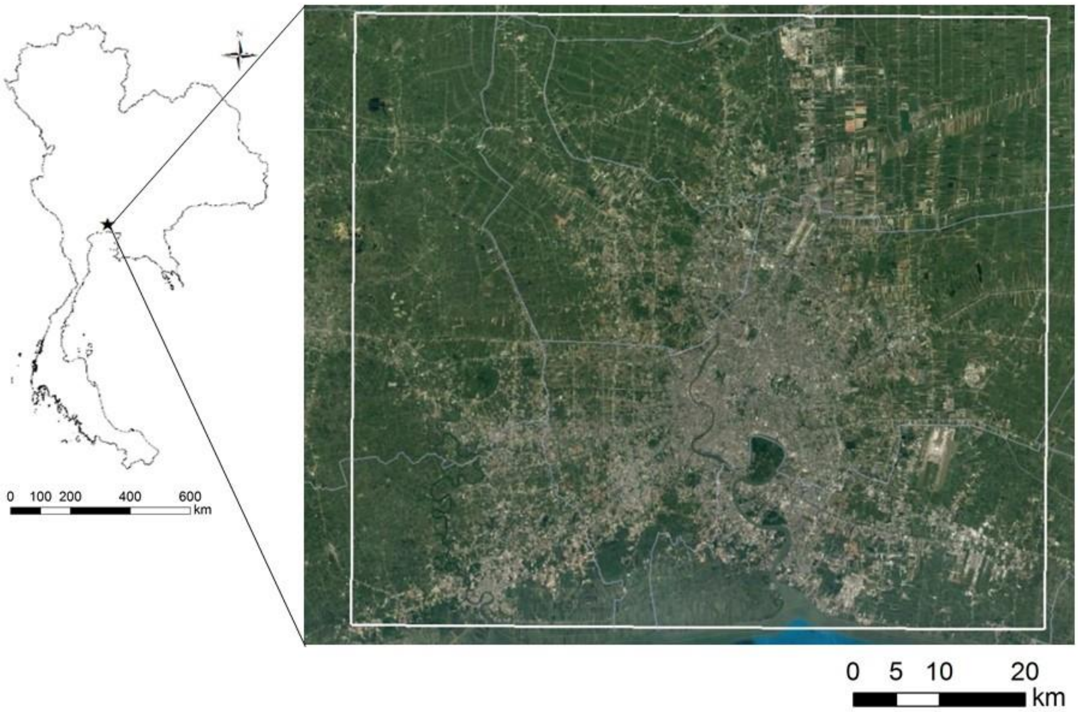


Figure S4.1: Map of Thailand showing the location of Bangkok and an inset map of the Bangkok region (using Google Earth's aerial imagery taken in 2018). The rectangle with grey border represents the 70 km × 80 km area delimiting our study region.

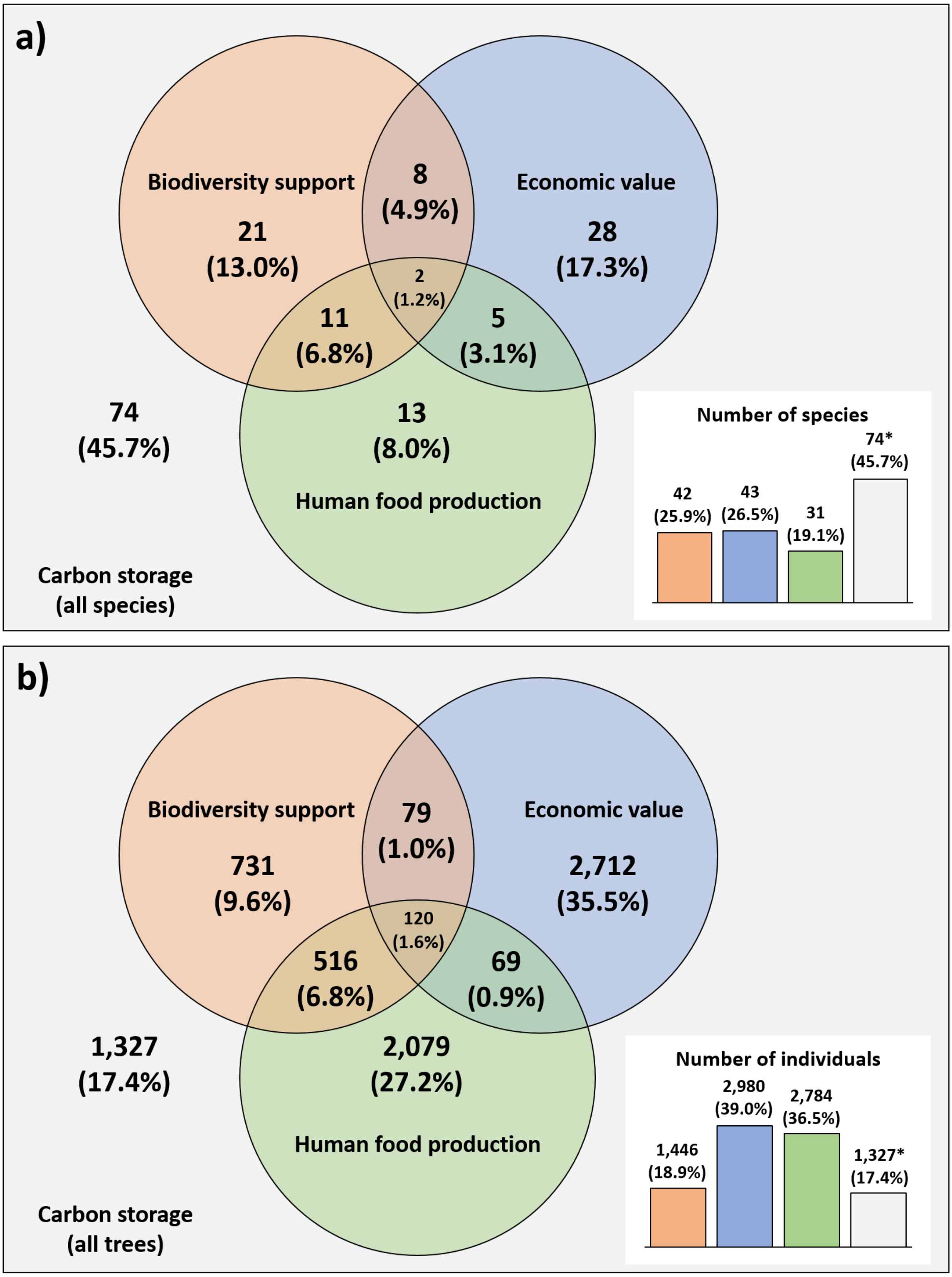


Figure S4.2: Cumulative number and percentage (in parentheses) of a) species and b) individuals that contribute to, at least, one of our focal ecosystem service, including carbon storage (grey), human food production (green), biodiversity support (red), and economic value (blue). Bar charts show total number of species and individuals that contribute to each ecosystem service except grey bars represent those only contribute to carbon storage.

CHAPTER FIVE

Avian species richness and tropical urbanization gradients — effects of woodland retention and human disturbance

(revisions have been requested by the journal Ecological Applications)

Abstract

Urbanization impacts land cover dynamics and biodiversity loss. In temperate regions avian species richness-urbanization intensity relationships typically exhibit unimodal patterns, with peak richness at intermediate urbanization levels. In tropical regions, the form of such relationships and the extent to which they are moderated by patches of semi-natural habitat are unclear. We address these questions in Bangkok, Thailand — one of the largest and most rapidly expanding tropical megacities. We use repeated point count surveys at a random location, and the largest available woodland patch, in 150 1 km × 1 km grid cells selected along the urbanization gradient. Woodland patches support higher species richness than paired randomized locations (except for non-natives), and avian species richness declines linearly with increasing urbanization intensity. The contrast with unimodal patterns in temperate regions is probably driven by divergent patterns of habitat heterogeneity along tropical and temperate urbanization gradients. Moreover, we provide novel evidence that retaining patches of urban woodland moderates adverse impacts of urbanization on avian species richness. For most species groups, the benefits of woodland increase as urbanization intensifies, even though such woodland patches are typically very small. Avian species richness in woodland patches is maximized, and less similar to that in randomized locations, when woodland patches are larger and visited by fewer people. Assemblages of forest dependent species, that provide additional ecological functions, also have higher richness, and are less similar to those in randomized locations, in patches of woodland with higher tree species richness and biomass. Finally, woodland proximity correlates positively with species richness in randomized sites, and such assemblages more closely resemble those of woodland sites. Our work highlights four strategies for tropical urban bird conservation: i) conserving woodland and other semi-natural habitats across the urbanization gradient regardless of patch size, ii) improving the quality of existing woodland by increasing tree density and diversity, iii) creating additional woodland that is well distributed throughout the urban area to minimize effects of habitat isolation and iv) reducing human disturbance, especially in areas of the highest habitat quality, whilst ensuring that the benefits of connecting people to nature are realized in other locations.

Key words: avian assemblage, cities, exotic species, habitat creation, habitat fragmentation, habitat restoration, spatial configuration, species turnover

5.1 Introduction

Urbanization generates marked landscape alteration, and is a key driver of environmental changes (Bren D'Amour, 2016; Deng *et al*., 2015; Wei, 2014) and biodiversity loss (*Aronson et al*., 2014; Rebelo *et al*., 2011; Sol *et al*., 2014). Species vary in their ability to cope with landscape alteration induced by urbanization and accompanying selection pressures, which increase in magnitude along the urbanization gradient (Isaksson, 2018; Johnson *et al*., 2015; Grimm *et al*., 2008). Specialist species are thus most likely to be absent from urban areas and typically exhibit the greatest declines in population densities (Callaghan *et al*., 2019; Evans et al., 2010). Consequently, intensively urbanized locations support a limited set of native species than less urbanized locations, contributing to biotic homogenization (Colleony *et al*., 2020; McKinney and Lockwood, 1999; Zeeman *et al*., 2017).

The precise pattern in which species richness changes along urbanization gradients is, however, rather variable across taxonomic groups and geographical locations (McKinney, 2008). Amongst birds, for example, in temperate regions species richness tends to exhibit a unimodal/hump-shaped pattern along urbanization gradients with maximum species richness in sub-urban areas with intermediate levels of urbanization intensity (Blair, 2004, Crooks et al., 2004; Tratalos *et al*., 2007; Luck and Smallbone, 2010; McKinney, 2002; Smith and Wacob, 2006; Vignoli *et al*., 2013). Such patterns are usually attributed to greater habitat diversity in sub-urban locations that promote local species richness, even though some specialists are excluded from such locations (Blair and Johnson, 2008; McKinney, 2002; Tratalos *et al*., 2007). In contrast, in tropical regions avian species richness may decline in a linear manner along urbanization gradients (Bhatt and Joshi, 2011; Reis *et al*., 2012; Leveau *et al*., 2017), but hump-shaped patterns have also been reported (Leveau, 2019) and more studies from tropical regions are required (Marzulff, 2001; Marzulff, 2017). The mechanisms generating linear declines in species richness in tropical regions (Chamberlain *et al*., 2017; Leveau *et al*., 2017; Reis *et al*., 2012), rather than hump-shaped curves, are unclear but may be due to differences in urban form and landscape characteristics with less urbanized locations in tropical regions containing more semi-natural habitat and less intensively managed agricultural land than those in temperate regions.

Regardless of the precise pattern of declines in species richness, it is clear that intensely urbanized locations have lower biodiversity than locations that are less urbanized (Sol *et al*., 2014). These lower levels of biodiversity in urbanized locations have a number of important consequences for conservation including the direct loss of biodiversity (McDonald *et al.*, 2008; McDonald *et al*., 2013; Sodhi *et al*., 2010), and reduced opportunities for city dwellers to engage with nature which can deliver well-being benefits (Coldwell and Evans, 2018; Schebella et al., 2019) and increase their appreciation of the natural world and support for conservation (Clergeau et al., 2001; Coldwell and Evans, 2017; Lo and Jim, 2010). Urban areas with higher levels of biodiversity may also generate more ecosystem services, e.g. food provision (Orsini *et al*., 2014; Speak *et al*., 2015), pollination (Baldock *et al*., 2019), carbon sequestration by urban trees (Agbelade *et al*., 2020), etc. There is thus considerable interest in how to increase biodiversity in urban environments.

Whilst urban bird diversity is positively related with the size of urban green areas (Kaushik *et al*., 2020; La Sorte *et al*., 2020) options for enhancing urban biodiversity by increasing the amount of urban green-space in currently urbanized locations are typically limited and expensive, although there is some potential for retro-fitting green-walls and roofs (Belcher *et al*., 2019; Collins *et al*., 2017; Orsini *et al*., 2014; Wang *et al*., 2017) or directly converting impervious surfaces to green-space (Qian *et al*., 2015). Cost-effective opportunities to enhance urban biodiversity are more likely to arise through improving the quality of existing green-space by changing management practices, or replacing types of green-space that support limited amounts of biodiversity with habitat types that support a wider range of species (Aronson *et al*., 2017; Threlfall *et al*., 2017). Such habitat replacement schemes often focus on enhancing the environmental quality of urban grasslands through converting intensely mown grassland to systems that resemble species rich meadows (Norton *et al*. 2019). Woodland areas also play a major role in retaining biodiversity in urban areas, especially for avian biodiversity (Melles *et al*., 2003; Pellissier *et al*., 2012; Plummer *et al*., 2020). Observed positive correlations between woodland cover and biodiversity may simply arise primarily because woodland increases at the expense of the amount of urban land, i.e. higher biodiversity in areas with more woodland simply due to lower levels of urbanization in such locations. Alternatively, increasing the amount of woodland in highly urbanized areas could mitigate some of the adverse impacts of urbanization on biodiversity — in which case the form of the relationships between biodiversity and urbanization intensity would be modified by the amount of woodland cover. We are not aware of any tests of such moderating impacts of urban woodland, but their occurrence would point to the potential effectiveness of increasing woodland cover in urban areas through a habitat restoration/creation schemes that could promote higher levels of avian biodiversity within towns and cities.

The quality of urban woodlands is likely to play a role in their impact on urban bird assemblages. More mature woodlands with larger trees are likely to provide more resources, such as fruit or phytophagous insects, due to allometric relationships and a greater diversity of resources, for example cavities that are required as nest sites are more likely to occur exclusively in larger older trees. A greater diversity of resources may also be provided by woodlands with a greater mix of tree species, and due to inter-specific variation in flowering and fruiting times, may provide greater stability of resources. Whilst more studies are required it is thus notable that urban avian species richness responds positively to the density (Barth *et al*., 2015; Fontana *et al*., 2011), richness (Jankovski *et al*., 2013; Paker *et al*., 2014), and size of trees (MacGregor-Fors, 2008; Stagoll *et al*., 2012) in urban woodlands. Landscape factors are also likely to play a role in determining the composition of avian assemblages in urban woodlands as woodland specialists may be more reluctant to travel through the urban matrix to cross gaps between woodland patches (Watson *et al*. 2005). Finally, evidence is also starting to accumulate that human disturbance can adversely impact avian territory establishment and species richness in woodlands (Bötsch *et al*., 2017), and some studies also report such effects in urban locations (e.g. MacGregor-Fors and Schondube, 2011).

Our study has four core objectives. We first quantify the form of the relationship between avian species richness and urbanization intensity across a tropical megacity and test the hypothesis that in tropical regions avian biodiversity declines linearly with urbanization intensity, rather than exhibiting the unimodal pattern typically exhibited in temperate regions. Second, we test if woodland cover along the urbanization gradient can modify the form of these relationships; we do so by comparing how species richness along the urbanization gradient changes when sampling locations with typical conditions for a given urbanization intensity (randomly selected locations) and when sampling nearby woodland patches embedded within the same urban matrix. We then test how characteristics of the sampling locations (i.e. size of the wooded patch, distance to the nearest woodland, level of human disturbance, tree species richness, tree biomass, and biomass of large trees) influence avian species richness, and the turnover in species composition between randomly selected and wooded locations. Our results inform understanding of urbanization in tropical regions on biodiversity, and the potential of urban woodland to minimize adverse impacts, and how to design such woodlands to maximize biodiversity benefits.

5.2 Methods

We use a southeast Asian case study (Bangkok, Thailand) as much of the urban development in this region has occurred in its biodiversity hotspots (as defined by Myers *et al*. (2000)), driving considerable biodiversity loss (Hughes, 2017; Sodhi *et al*., 2004), and future urbanization is predicted to follow a similar pattern (Seto *et al*., 2012). Bangkok provides a particularly suitable case study as it is one of the most rapidly urbanizing megacities in this region, and globally (Estoque and Murayama, 2015; Srivanit *et al*., 2012, Song *et al*., 2021).

Study area

This study was conducted in the urban area of Bangkok, defined as the 2 km × 2 km cells with at least 25% impervious surface cover (following Bonnington *et al*. (2014)). To determine the boundaries of this region we first delimited a 5,600 km^2 area (1,400 2 km × 2 km cells) that was centered on Metropolitan Bangkok and the surrounding provinces (Fig. S5.1). Using high resolution Google Earth's imagery taken during 2017 to 2018 and following Evans *et al*. (2009), we estimated the percentage of each 2 km × 2 km grid cell that comprised impervious surfaces using 100 uniformly distributed sampling points within each grid cell. This delimited a study region of 2,628 km^2 (Fig. 5.1).

Selecting survey sampling points

For each 1 km × 1 km grid cell within our sampling region we calculated the percentage land cover for each of nine categories (impervious surface cover, trees, grassland, rice fields, salt pans, green roofs, bare ground, construction site and water body) using our sampling grid (see *Study area*). We then classified each 1km x 1km grid cell within the study region into one of ten categories of urbanization intensity based on their percentage vegetation cover (0–10%, 11–20%, …, 91–100%) with more urbanized locations having less vegetation cover. We then used random stratification to select 15 1 km × 1 km grid cells within each green area category, resulting in a total of 150 sampling cells spread along a gradient of urbanization intensity. Two sampling points were located within each grid cell. The first sampling point

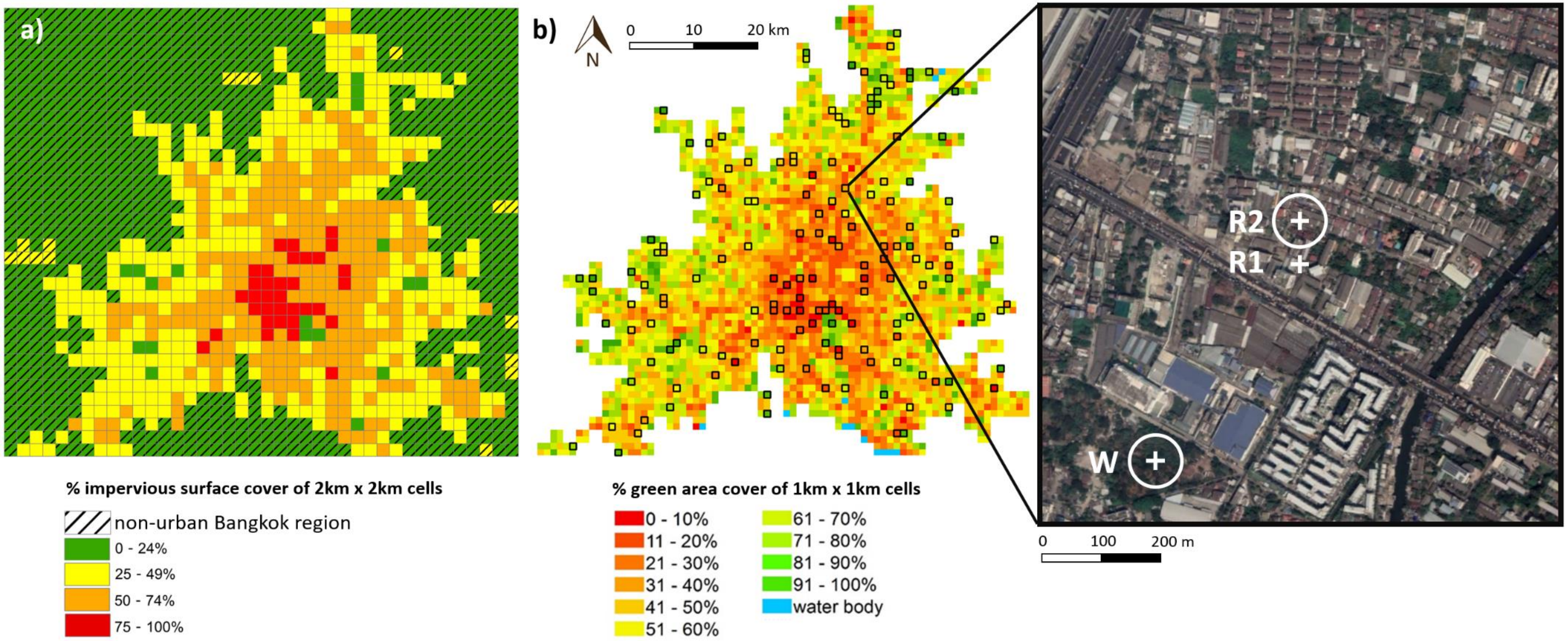


Figure 5.1: a) land cover map of the Bangkok study region showing percentage impervious surface cover of 2 km × 2 km grid cells used to define the study region. Grid cells with ≥25% impervious surface cover that were isolated from the main urban region were considered to be part of other urban settlements. Cells that had <25% impervious surface cover were considered to be non-urban unless they were completely surrounded by urban cells, b) the percentage green-space cover of 1 km × 1 km grid cells across the urban study region with grid cells outlined in black representing the 150 cells selected for sampling using random stratification across each categories of green-space (15 sampling grid cells each). The inset map shows an example 1 km × 1 km grid cell with locations of the randomized plot (R2), which is located at the nearest accessible point to the north of the grid cell's centre (R1) which is inaccessible, and the woodland sampling plot (W) which is located in the largest area of woodland within the focal grid cell. White circles show point counts' 50 m sampling radii.

(referred to as the randomized plot) was located at the center of each randomly selected grid cell and thus represents typical conditions of grid cells at similar levels of urbanization intensity. When the center of a grid cell was inaccessible, we used the nearest accessible location (Fig. 5.1b). The second sampling point was located at the center of the largest accessible patch of trees/woodland (referred to as the woodland plot). Comparing the avian assemblages across these two types of sampling locations enables us to assess if woodland cover modifies the effects of urbanization intensity on tropical urban avian biodiversity.

Field surveys

Bird surveys were conducted using 15-minute point counts with a 50m survey radius. All birds heard or seen during the point count were recorded to species. Surveys took place from 6:30 am and stopped at noon. A rangefinder (Viking Compact Laser Rangefinder) was used when necessary to ensure that detected birds were within the 50 m radius of the survey point. To capture seasonal variation, each sampling point was visited 3 times during March to July 2018 (first visit 12th March to 28th April; second visit 2nd May to 11th June; third visit 12th June to 25th July). The first visit captures the period when wintering and passage migrants are present in the Bangkok region, whilst the second two visits overlap with the breeding season of most species in the region. Within each sampling period survey locations were visited in an order that was unbiased with regard to their urbanization intensity.

The number of people detected in the sampling area during each point count was recorded to generate an index of human disturbance (calculated as mean number of people across three visits). The abundance of most resources provided by trees, such as fruits, flowers, or phytophagous insects, is largely controlled by tree biomass and thus larger trees contribute disproportionately. All trees within the radius of each point count with at least 25 cm diameter-at-breast-height (DBH) were identified to species, and their DBH and height recorded. Large trees were defined as those with ≥ 70 cm DBH (following Slik *et al.* (2013)). We then calculated the aboveground biomass of surveyed trees using allometric equations from Chave *et al.* (2005), with wood density data obtained from Global Wood Density Database (Zanne *et al.*, 2009), and scaled to tonnes/ha to provide an index of the density of tree biomass within each point count area.

Each bird species was classified as native or non-native to Bangkok area (based on Round & Gardner (2008)), by its seasonal occurrence status (resident, passage migrant, breeding visitor, and non-breeding visitor (based on Round & Gardner (2008)) and forest dependency status (based on BirdLife international (2019)). Species with 'high forest-dependency' are forest specialists that mainly occur in undisturbed forests and are rarely found in degraded forest habitats, 'medium forest-dependent' species are mainly found in undisturbed forest but also regularly occur in degraded forest habitat such as forest edge and secondary forest, and 'low forest-dependent' species are mostly generalists and well adapt to live and breed in disturbed habitats (Buchanan *et al*., 2008; Buchanan *et al*., 2011). We classified species defined by BirdLife as 'does not normally occur in forest' and 'low forest dependent species' as non-forest dependent species, and included species defined by BirdLife as 'medium forest dependent species' as forest dependent species (no species with a high forest dependency were detected in our surveys).

Landscape scale data

We obtained data on percentage impervious surface and tree cover for each 1 km × 1 km grid cell from our landcover classifications (described above). Urban woodland patches were defined as areas with delimited by the area of contiguous tree canopy cover that were at least 0.02 ha in area. Their size was measured by delimiting the edge of continuous tree canopy cover and measuring the resultant area using Google Earth (Google Earth Pro v7.3.2). The straight-line distance between the randomized and woodland survey points, and the distance between the randomized point and the edge of the nearest woodland patch was measured using ruler tools in Google Earth.

Table 5.1: Description of predictor variables that were used in multiple regression models for bird species richness and species turnover (Jaccard's dissimilarity index) of bird community in woodland and randomized sampling plot. x̄ represents mean values for impervious surface percentage and distance from randomized plot to the sampled woodland and median for the predictors with natural log transformation (used to reduce the skew in predictor distributions).

Predictor variables	Units	x̄	Range	Transformation
Landscape scale				
% impervious surface cover of grid cell	%	46.86	0 - 96.00	-
Distance from the randomized plot to the nearest woodland	m	15.00	0 - 445.00	ln (x + 1)
Distance from the randomized plot to the sampled woodland	m	245.00	5.00 - 540.00	-
Size of the sampled woodland	ha	1.14	0.11 - 87.71	ln (x)
Point count scale (randomized point)				
Mean number of humans	people	12.40	1 - 121.67	ln (x)
Tree species richness	species	6.00	0 - 22.00	ln (x + 1)
Total aboveground tree biomass	t/ha	7.99	0 - 89.89	ln (x + 1)
Aboveground tree biomass of large trees	t/ha	0	0 - 82.41	ln (x + 1)
Point count scale (woodland point)				
Mean number of humans	people	1.67	1 - 89.67	ln (x)
Tree species richness	species	9.00	1.00 - 30.00	ln (x)
Total aboveground tree biomass	t/ha	29.83	2.86 - 144.92	ln (x)
Aboveground tree biomass of large trees	t/ha	0	0 - 103.98	ln (x + 1)
Point count scale (absolute difference between locations)				
Mean number of humans	people	4.33	0 -118.67	ln (x + 1)
Tree species richness	species	5.00	0 - 24.00	ln (x + 1)
Total aboveground tree biomass	t/ha	15.19	0.36 - 136.36	ln (x)
Aboveground tree biomass of large trees	t/ha	2.34	0 - 103.98	ln (x + 1)

Data analyses

All analyses were performed using R version 3.4.2 (R-studio Team, 2015). To meet our first objective of testing if species richness declines linearly with increasing urbanization intensity, or peaks at intermediate levels of urbanization intensity we model species richness as a function of impervious surface cover using linear and quadratic terms. Models were constructed separately for randomized and woodland points, and for total species richness, native species richness, non-native species richness, resident species richness, non-breeding migrant species richness, non-forest species, and forest-dependent species. We tested if Poisson or Gaussian error structures provided a better fit based on models' AICc values (Table S5.1). We *a priori* determined that evidence for a quadratic relationship would be provided if the AICc value of the quadratic model was ≥2 AICc points lower than the linear model, and the *P* value of the quadratic term was statistically significant. In all models, the model (or partial) r^2 values were calculated as variance-function-based r^2 using the rsq package which employs the methodology described by Zhang (2017).

To assess the impacts of woodland habitat on species richness we first conducted a matched paired t-test of species richness in the wooded and randomized survey locations within each grid cell. We then assessed if the impact of urbanization intensity on species richness is modified by woodland cover we modelled species richness as a function of impervious surface percentage, location type (i.e. randomized or woodland plot), and grid cell ID (random effect) and the interaction term between impervious surface percentage and location type (i.e. randomized or woodland plot) to assess. Three grid cells where the randomized points were located within the grid cell's largest woodland were excluded from this analysis. Models were constructed with the lme4 package and we again tested if Poisson or Gaussian error structures provided a better fit based on models' AICc values (Table S5.2). We fitted models with Gaussian error structure and identity link for total species richness, native species richness, non-native species richness, resident species richness, and forest-dependent species richness and with Poisson error structure and log link for non-breeding migrant species richness, and non-forest species richness.

Moran's I tests (ape package) to quantify spatial autocorrelation in response variables did not detected any significant spatial autocorrelation ($P < 0.05$) in species richness metrics from the randomized plots. In the wooded plots some species richness metrics exhibited statistically significant spatial autocorrelation, but Moran's I values were consistently low (≤ 0.022; Table S5.3). Moreover, parameter estimates in models that did not take spatial correlation structure into account were extremely similar to those in models that took spatial autocorrelation into account (Table S5.4) and we thus only report results from non-spatial models in the main manuscript.

We assessed factors influencing bird species richness by performing multiple regression analyses for bird species richness with landscape characteristics and ecological attributes of the wooded habitat, separately for randomized and woodland locations. We did so by using a full model approach based on the advocacy of Whittingham *et al*. (2016). Bird species richness at the randomized locations was modelled with percentage impervious surface cover of the grid cell, distance to the nearest woodland, mean number of humans, tree species richness, total aboveground tree biomass, and aboveground tree biomass of large trees (Table 5.1). Equivalent set of predictors was used to predict bird species richness at the woodland locations, with exception being using size of the sampled woodland instead of distance to the nearest woodland. We fitted models with Gaussian error structure and identity link for total species richness, native species richness, non-native species richness, resident species richness, and forest-dependent species richness and with Poisson error structure and log link for non-breeding migrant species richness, and non-forest species richness — selecting error structures that generated the best fit to the data based on AICc values (Table S5.5).

Use of the 'vif' function in the car package (Fox and Weisberg 2019) revealed that none of our species richness models were unduly influenced by collinearity (Variance Inflation Factors (VIFs) were consistently below the threshold above which collinearity becomes as concern; VIF > 10 (Dorman *et al*., 2013); Table S5.6). Moran's I tests detected significant autocorrelation in some models for species richness with habitat features, but the Moran's I values were again consistently low (≤ 0.033; Table S5.7). Comparison between models with and without taking spatial correlation structure into account revealed a very limited differences in coefficient estimates and standard errors and we thus only report results from non-spatial models in the main manuscript (Table S5.8, Table S5.9).

To further understand how patches of woodland influence species composition of urban bird communities along the urbanization gradient, we quantified differences in community composition between the randomized and woodland survey points using Jaccard's dissimilarity index (1 - Jaccard's similarity index; Chase and Leibold 2002). We calculated Jaccard's dissimilarity index for total species richness, native species richness, resident species richness, and forest dependency categories, but not non-native species and non-breeding migrants as few species within each of these group were recorded in total (non-native species — 5 species; non-breeding migrants — 36 species) and at individual point count locations (non-native species: randomized point median = 2 (range 0–3), woodland point median = 2 (range 0–3); non-breeding migrants: randomized point median = 0 (range 0–4), woodland point median = 1 (range 0–6); Fig. 5.2). Dissimilarity indices were then modelled, again using a full model approach, as a function of landscape scale variables and measures of 'environmental roughness' (*sensu* Gaston *et al*. (2007)) i.e. the difference in environmental conditions between the two sampling locations. The complete list of predictors variables is percentage impervious surface cover (within the 1 km grid cell that the pair of points is located), distance from randomized point to the nearest woodland, distance from randomized point to the sampled woodland, size of the sampled woodland), absolute difference in mean number of humans, absolute difference in tree species richness, and absolute difference in total aboveground tree biomass (Table 5.1). Variance Inflation Factors (VIFs) for species turnover models were again consistently lower than the threshold indicating no influence of multi-collinearity among our predictors in species turnover models (Table S5.6). Moran's I tests did not detect significant autocorrelation for our measures of Jaccard's dissimilarity (Table S5.10).

5.3 Results

General description of the avifauna

A total of 142 bird species were detected across the 300 point count locations during three visits between March and July 2018. These comprised 99 residents, 36 non-breeding visitors, 5 passage migrants, and 2 breeding visitors (Table S5.11). The vast majority of species are native to the Bangkok area (137 species; 96.5%) with only five species (3.5%) being locally non-native (Zebra Dove *Geopelia striata*; native to southern Thailand, Alexandrine Parakeet *Palaeornis eupatria*; native to north-western and western Thailand) or nationally non-native

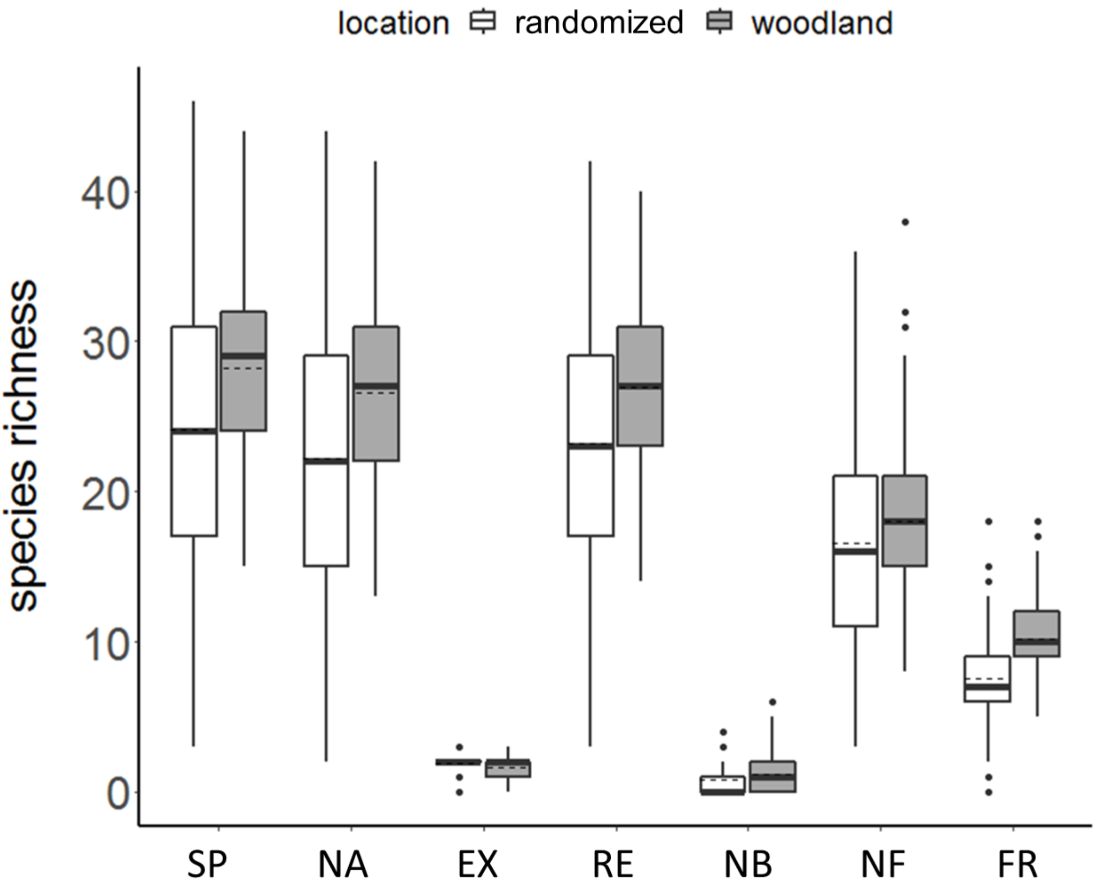
(Rock Pigeon *Columbia livia*, Java Sparrow *Lonchura oryzivora*, and Rose-ringed Parakeet *Alexandrinus krameri*). Whilst two of these species are of global conservation concern, they had very low rates of occurrence (Alexandrine Parakeet *Palaeornis eupatria* — near-threatened, 1.3% of grid cells; Java Sparrow *Lonchura oryzivora* — endangered, 1.3% of grid cells; BirdLife international, 2019), as did Rose-ringed parakeet (2% of grid cells), contrasting with the much more widespread Rock Pigeon (91.3% of grid cells) and Zebra Dove (100% of grid cells). Non-forest dependent species comprised 71.1% (101 species) of the detected species, with forest-dependent species comprising the remaining 28.9% (41 species).

Shape of species richness-urbanization intensity relationships

For all our species richness metrics the quadratic models never met our criteria of having a delta AICc value ≤ 2 relative to the linear model, and a statistically significant quadratic term (Table 5.2). Whilst both criteria were close to being met in the model of resident species richness at woodland locations the plot of predicted values follows a trajectory of slowly accelerating loss of species at more urbanized locations with no evidence for a unimodal relationship with species richness peaking at intermediate levels of urbanization intensity (Fig. S5.2). All other species groupings (total species, native species, resident species, non-breeding visitor, non-forest species, and forest-dependent species) exhibited linear declines in species richness as urbanization intensity increased (Table 5.2; Figure 5.3), with the exception of non-native species richness which exhibited a slight linear increase as urban intensification increased (Table 5.2; Figure 5.3c).

Comparison of woodland and randomized points

Species richness was significantly higher in wooded than randomized point counts for all species groups, except for non-native species which exhibited significantly higher richness in the randomized points (Fig. 5.2). Moreover, the interaction between type of point count (randomized or woodland) and urbanization intensity was significant in models of the species richness-urbanization intensity relationship for almost all species groups. Interaction terms were not significant in models of non-breeding visitors and forest dependent species which thus exhibited similar patterns of decline in richness along the urbanization gradient in randomized and wooded point count locations (Table 5.3). When interaction terms were significant, as urbanization intensity increased species richness almost invariably declined more slowly in wooded locations than randomly selected ones; consequently, the gap in species richness between randomized and wooded locations became larger as urbanization intensity increased (Table 5.3; Fig. 5.3). The opposite pattern was exhibited by non-native species, with the difference in richness between randomized and woodland points narrowing as urbanization intensity increased (Table 5.3; Fig. 5.3c).



t	8.052	8.59	-5.294	7.703	4.159	3.329	10.669
P	$2.62e^{-13}$	$1.21e^{-14}$	$4.30e^{-7}$	$1.87e^{-12}$	$5.44e^{-5}$	0.001	$<2.2e^{-16}$

Figure 5.2: Total species richness (SP), native species richness (NA), non-native species richness (EX), resident species richness (RE), non-breeding species richness (NB), non-forest species richness (NF), and forest-dependent species richness (FR) in randomized (white bars) and woodland (grey bars) plots. Thick solid horizontal lines represent median species richness, interquartile boxes represent middle 50% (25th to 75th percentile) of the data, and dashed lines represent mean species richness, whiskers represent 25% ranges for the bottom and top of the data values, and dots represent outliers. Below table shows results from matched-paired t-tests comparing observed species richness cumulated over three visits to randomized and woodland point counts in the same 1 km × 1 km grid cell (n = 147 as three grid cells in which the randomized point fell within the largest woodland patch were excluded).

Table 5.2: Relationships between avian species richness and percentage impervious surface cover comparing between linear model and quadratic model. Asterisks indicate models fitted with Poisson error structure (log link) and the rests were fitted with Gaussian error structure (Identity link).

Response variable	Location type	Linear model			Quadratic model				
		AICc	Coeff ± SE Linear term	*P* Linear term	AICc	Coeff ± SE Linear term	*P* Linear term	Coeff ± SE Quadratic term	*P* Quadratic term
Total species richness	Randomized	945.74	-0.210 ± 0.016	$<2.2e^{-16}$	947.81	-0.223 ± 0.063	0.001	$1.3e^{-4} \pm 0.001$	0.838
	Woodland	869.90	-0.150 ± 0.013	$<2.2e^{-16}$	870.82	-0.099 ± 0.049	0.044	-0.001 ± 0.001	0.280
Native species richness	Randomized	950.31	-0.213 ± 0.016	$<2.2e^{-16}$	952.05	-0.232 ± 0.064	$3.9e^{-4}$	$2.00e^{-4} \pm 0.001$	0.759
	Woodland	877.67	-0.158 ± 0.013	$<2.2e^{-16}$	878.62	-0.107 ± 0.050	0.035	-0.001 ± 0.001	0.286
Non-native species richness	Randomized	133.14	0.002 ± 0.001	0.039	133.79	0.007 ± 0.004	0.092	$-5.1e^{-5} \pm 4.3e^{-5}$	0.232
	Woodland	269.24	0.008 ± 0.002	$5.4e^{-6}$	271.34	0.007 ± 0.007	0.270	$7.0e^{-6} \pm 6.7e^{-5}$	0.917
Resident species richness	Randomized	920.96	-0.192 ± 0.015	$<2.2e^{-16}$	923.03	-0.181 ± 0.058	0.002	$-1.17e^{-4} \pm 0.001$	0.842
	Woodland	854.07	-0.132 ± 0.012	$<2.2e^{-16}$	852.47	-0.047 ± 0.046	0.309	$-0.001 \pm 4.7e^{-4}$	0.057
Non-breeding visitor species richness	Randomized*	341.08	-0.021 ± 0.004	$8.9e^{-9}$	343.14	-0.022 ± 0.012	0.070	$1.8e^{-5} \pm 1.4e^{-4}$	0.900
	Woodland*	415.86	-0.013 ± 0.003	$1.9e^{-6}$	415.77	-0.027 ± 0.010	0.005	$1.6e^{-4} \pm 1.1e^{-4}$	0.137
Non-forest species richness	Randomized*	878.02	-0.010 ± 0.035	$<2.2e^{-16}$	879.43	-0.008 ± 0.003	0.004	$-2.4e^{-5} \pm 2.9e^{-5}$	0.412
	Woodland*	852.06	-0.006 ± 0.001	$<2.2e^{-16}$	853.50	-0.004 ± 0.003	0.137	$-2.2e^{-5} \pm 2.7e^{-5}$	0.427
Forest-dependent species richness	Randomized*	738.17	-0.007 ± 0.001	$2.0e^{-10}$	738.20	-0.001 ± 0.004	0.760	$6.1e^{-5} \pm 4.3e^{-5}$	0.154
	Woodland	698.11	-0.046 ± 0.007	$1.1e^{-9}$	697.44	-0.002 ± 0.027	0.938	$4.6e^{-4} \pm 2.8e^{-4}$	0.100

Table 5.3: Coefficients and standard errors of the linear mixed models with Gaussian error structure for total bird species richness, native species richness, non-native species richness, resident species richness, and forest-dependent species richness and generalized linear mixed models with Poisson error structure for non-breeding visitor species richness and non-forest species richness as response of impervious surface percentage (fix effect) and its interaction term with location type (fix effect), and grid ID as random effect. Significant effects ($P< 0.05$) were shown in bold. Asterisks indicate models performed with Poisson error structure.

Response variables	intercept	Fixed effects		
		% impervious surface	Location type	Interaction term
Total species	34.079 ± 0.798	**-0.211 ± 0.014** **($P < 2.2e^{-16}$)**	1.302 ± 0.951 ($P = 0.173$)	**0.060 ± 0.017** **($P = 0.001$)**
Native species	32.317 ± 0.813	**-0.214 ± 0.015** **($P < 2.2e^{-16}$)**	1.824 ± 0.959 ($P = 0.059$)	**0.054 ± 0.017** **($P = 0.002$)**
Non-native species	1.762 ± 0.078	0.003 ± 0.001 ($P = 0.070$)	**-0.522 ± 0.100** **($P = 5.0e^{-7}$)**	**0.005 ± 0.002** **($P = 0.005$)**
Resident species	32.336 ± 0.741	**-0.194 ± 0.013** **($P < 2.2e^{-16}$)**	0.861 ± 0.890 ($P = 0.335$)	**0.060 ± 0.016** **($P = 2.7e^{-4}$)**
Non-breeding visitor*	0.543 ± 0.157	**-0.020 ± 0.004** **($P = 4.03e^{-8}$)**	0.185 ± 0.194 ($P = 0.342$)	0.007 ± 0.005 ($P = 0.137$)
Non-forest dependent species*	3.239 ± 0.040	**-0.010 ± 0.001** **($P < 2.2e^{-16}$)**	-0.080 ± 0.050 ($P = 0.107$)	**0.004 ± 0.001** **($P = 7.1e^{-5}$)**
Forest dependent species	9.834 ± 0.412	**-0.048 ± 0.007** **($P = 4.9e^{-10}$)**	**2.461 ± 0.483** **($P = 1.1e^{-6}$)**	0.004 ± 0.009 ($P = 0.620$)

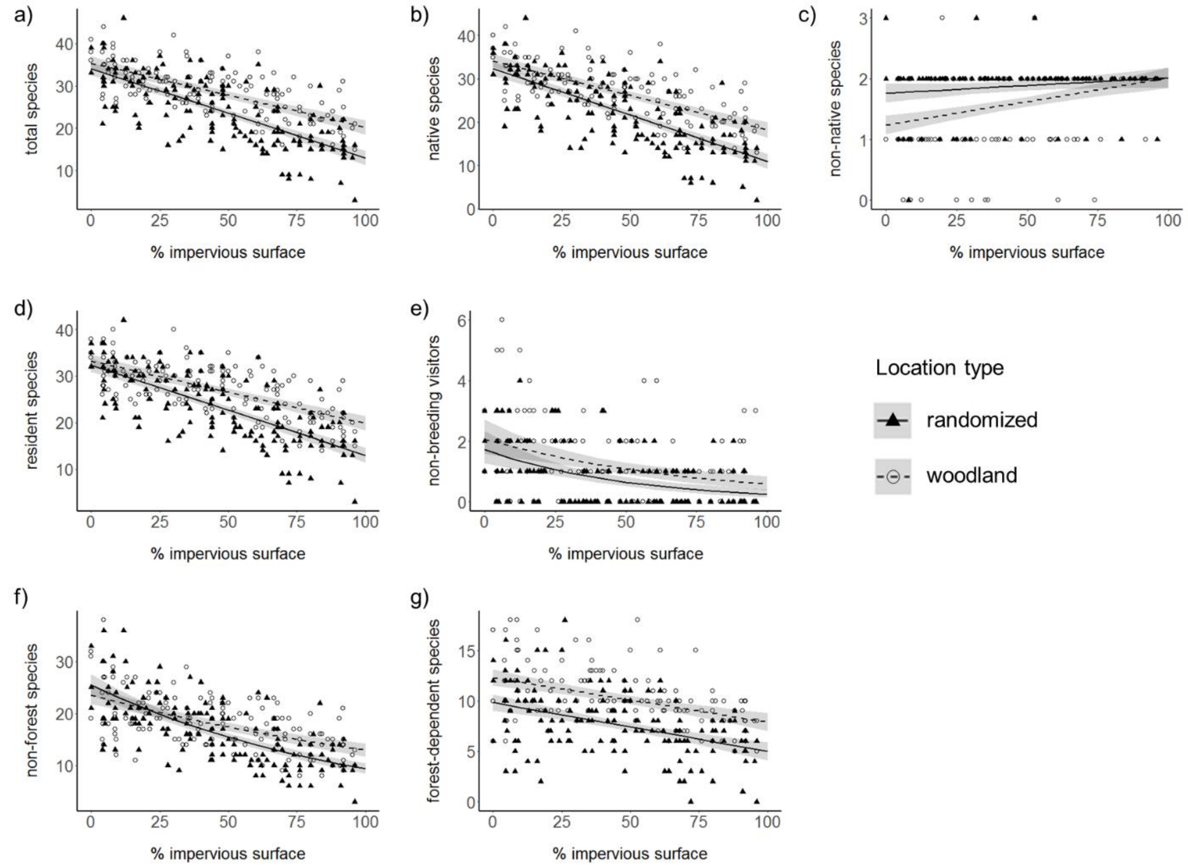


Figure 5.3: Bird species richness; (a) total species richness, (b) native species richness, (c) non-native species richness, (d) resident species richness, (e) non-breeding visitor species richness, (f) non-forest species richness, and (g) forest-dependent species richness as function of % impervious surface comparing between randomized plot (filled triangle and solid line) and woodland plot (open circle with dashed line). Fitted lines indicate predicted values from linear mixed model with Gaussian error structure (a-d, g) and generalised linear mixed model with Poisson error structure (e, f) with shades representing confident interval (see Table 5.3).

Factors associated with bird species richness in randomized locations

We modelled our suite of species richness metrics as functions of percentage impervious surface cover, distance to the nearest woodland, mean number of humans, tree species richness, total aboveground tree biomass, and aboveground biomass of large trees. Our model of non-native species richness had very limited explanatory power and our full model did not contain any statistically significant predictors (Table 5.4). Explanatory power for all our other species richness models was substantially higher, and percentage impervious surface cover and mean number of humans were consistently negatively associated with species richness (Table 5.4). The richness of forest dependent species was negatively with distance to the nearest woodland, and positively associated with tree species richness and above ground tree biomass (Table 5.4). Tree biomass was also positively associated with total species richness, native species richness and resident species richness (Table 5.4).

Factors associated with bird species richness in woodland locations

We modelled our suite of species richness metrics as functions of percentage impervious surface cover, size of the woodland, mean number of humans, tree species richness, total aboveground tree biomass, and aboveground biomass of large trees. Our models explained between approximately 15% and 60% of the variation in our response variables, with a noticeable improvement in explanatory capacity for non-native species richness relative to that in the randomized points (Table 5.5). Again, the percentage of impervious surface was negatively correlated with species richness for all our species groups except non-native species richness, for which there was a marginally significant positive effect (Table 5.5). The mean number of humans at the point count locations was negatively associated with species richness for all species groups except non-native species, for which there was a significant positive effect, and non-breeding visitors (no significant effect; Table 5.5). The number of forest dependent species was positively correlated with the size of the sampled woodland, tree species richness and above ground tree biomass (Table 5.5). The only other significant effects were negative impacts of woodland size on the number of non-native species and negative effects of tree species richness on non-forest species (Table 5.5).

Factors associated with community dissimilarity between randomized and wooded locations

Models of the dissimilarity in species composition between the randomized and wooded points for all bird species, natives, residents and non-forest species all contained the same suite of significant predictors. Jaccard's dissimilarity indices increased in less urbanized grid cells, and when distance to the nearest woodland was greater, the sampled woodland was larger and there was a greater difference in mean numbers of people recorded at the two locations (Table 5.6). These models explained between approximately 18% and 25% of the variation in Jaccard's dissimilarity indices. Dissimilarity in species composition of forest dependent species assemblages increased significantly with distance to the nearest woodland and the difference in tree species richness between the randomized and wooded locations – with the model also explaining approximately one quarter of the variation in the dissimilarity index (Table 5.6). No other predictor variables were significantly associated with the Jaccard's dissimilarity indices of any of our focal avian assemblages.

Table 5.4: Multiple regression models of bird species richness in randomized plots as function of % impervious surface, mean number of humans (log-transformed), tree species richness (log-transformed), total aboveground tree biomass (log-transformed), and aboveground biomass of large trees (log-transformed). Significant predictors (*P*<0.05) were shown in bold. Asterisks indicate models fitted using Poisson error structures.

Response variable	Predictor											
	% impervious surface		Distance to the nearest woodland		Mean number of humans		Tree species richness		Total aboveground tree biomass		Aboveground biomass of large trees	
	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*
Total species (% r^2 = 71.19)	**-0.098 ± 0.019 (16.01)**	**$6.2e^{-7}$**	0.109 ± 0.291 (0.10)	0.710	**-3.150 ± 0.397 (30.62)**	**$5.3e^{-13}$**	-0.752 ± 0.829 (0.44)	0.427	**2.226 ± 0.829 (4.80)**	**0.008**	-0.537 ± 0.490 (0.83)	0.275
Native species (% r^2 = 71.00)	**-0.100 ± 0.019 (15.88)**	**$6.9e^{-7}$**	0.125 ± 0.296 (0.12)	0.674	**-3.209 ± 0.404 (30.66)**	**$5.1e^{-13}$**	-0.675 ± 0.961 (0.34)	0.484	**2.175 ± 0.843 (4.45)**	**0.011**	-0.501 ± 0.499 (0.70)	0.317
Non-native species (% r^2 = 6.46)	0.001 ± 0.002 (0.40)	0.452	-0.016 ± 0.026 (0.27)	0.534	0.059 ± 0.036 (1.88)	0.100	-0.078 ± 0.085 (0.58)	0.361	0.051 ± 0.074 (0.32)	0.497	-0.036 ± 0.044 (0.46)	0.416
Resident species (% r^2 = 71.98)	**-0.088 ± 0.017 (15.70)**	**$8.1e^{-7}$**	0.036 ± 0.263 (0.01)	0.892	**-2.920 ± 0.359 (31.65)**	**$1.8e^{-13}$**	-0.431 ± 0.854 (0.18)	0.615	**1.931 ± 0.750 (4.43)**	**0.011**	-0.407 ± 0.444 (0.58)	0.361
Non-breeding visitors* (% r^2 = 25.49)	**-0.012 ± 0.005 (5.68)**	**0.015**	0.010 ± 0.074 (0.00)	0.893	**-0.255 ± 0.110 (3.87)**	**0.021**	-0.281 ± 0.237 (1.09)	0.236	0.187 ± 0.200 (0.60)	0.349	-0.095 ± 0.121 (0.26)	0.434
Non-forest species* (% r^2 = 64.94)	**-0.004 ± 0.001 (14.86)**	**$1.6e^{-5}$**	0.025 ± 0.016 (3.08)	0.115	**-0.166 ± 0.023 (25.60)**	**$3.8e^{-13}$**	-0.089 ± 0.052 (2.17)	0.085	0.084 ± 0.045 (2.27)	0.060	-0.023 ± 0.027 (0.41)	0.387
Forest-dependent species (% r^2 = 65.44)	**-0.022 ± 0.008 (5.16)**	**0.006**	**-0.373 ± 0.123 (6.08)**	**0.003**	**-0.591 ± 0.167 (8.05)**	**0.001**	**0.998 ± 0.398 (4.22)**	**0.013**	**0.773 ± 0.349 (3.32)**	**0.028**	-0.184 ± 0.207 (0.55)	0.375

Table 5.5: Multiple regression models of bird species richness in woodland plots as function of % impervious surface, size of the woodland (log-transformed), mean number of humans (log-transformed), tree species richness (log-transformed), total aboveground tree biomass (log-transformed), and aboveground biomass of large trees (log-transformed). Significant predictors ($P<0.05$) were shown in bold. Asterisks indicate models fitted using Poisson error structure.

Response variable	Predictor											
	% impervious surface		Size of sampled woodland		Mean number of humans		Tree species richness		Total aboveground tree biomass		Aboveground biomass of large trees	
	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*
Total species (% r^2 = 59.44)	**-0.107 ± 0.014** **(28.48)**	**4.8e^{-12}**	0.314 ± 0.349 (0.56)	0.370	**-2.180 ± 0.439** **(14.71)**	**1.9e^{-6}**	-0.740 ± 0.648 (0.91)	0.255	0.087 ± 0.604 (0.01)	0.886	0.163 ± 0.307 (0.20)	0.597
Native species (% r^2 = 61.80)	**-0.110 ± 0.014** **(29.25)**	**1.4e^{-12}**	0.477 ± 0.352 (1.27)	0.178	**-2.334 ± 0.443** **(16.27)**	**4.9e^{-7}**	-0.827 ± 0.653 (1.11)	0.208	0.240 ± 0.609 (0.11)	0.694	0.157 ± 0.310 (0.18)	0.615
Non-native species (% r^2 = 29.29)	0.003 ± 0.002 (1.64)	0.122	**-0.164 ± 0.047** **(7.66)**	**0.001**	**0.155 ± 0.060** **(4.48)**	**0.011**	0.086 ± 0.088 (0.66)	0.329	-0.153 ± 0.082 (2.38)	0.064	0.006 ± 0.042 (0.02)	0.881
Resident species (% r^2 = 57.42)	**-0.089 ± 0.013** **(23.61)**	**4.2e^{-10}**	0.201 ± 0.327 (0.26)	0.539	**-2.244 ± 0.411** **(17.23)**	**2.1e^{-7}**	-0.582 ± 0.607 (0.64)	0.339	0.012 ± 0.565 (3.41e^{-4})	0.982	0.125± 0.288 (0.13)	0.666
Non-breeding visitors* (% r^2 = 16.75)	**-0.013 ± 0.003** **(9.76)**	**1.7e^{-4}**	0.093 ± 0.072 (1.08)	0.197	0.034 ± 0.106 (0.00)	0.748	-0.035 ± 0.144 (0.00)	0.805	0.094 ± 0.131 (0.22)	0.472	0.009 ± 0.068 (0.05)	0.894
Non-forest species* (% r^2 = 50.91)	**-0.004 ± 0.001** **(19.72)**	**4.9e^{-7}**	-0.024 ± 0.021 (2.53)	0.251	**-0.098 ± 0.029** **(9.05)**	**0.001**	**-0.080 ± 0.038** **(3.88)**	**0.034**	-0.068 ± 0.035 (4.19)	0.052	0.023 ± 0.019 (0.85)	0.211
Forest-dependent species (% r^2 = 54.77)	**-0.027 ± 0.007** **(9.77)**	**1.3e^{-4}**	**0.837 ± 0.168** **(14.82)**	**1.7e^{-6}**	**-0.737 ± 0.211** **(7.86)**	**0.001**	**0.865 ± 0.311** **(5.12)**	**0.006**	**1.258 ± 0.290** **(11.62)**	**2.7e^{-5}**	-0.242 ± 0.148 (1.84)	0.104

Table 5.6: Multiple regression models of Jaccard dissimilarity index (%) for total bird species, native species, resident species, non-forest species and forest dependent species in two sampling location (randomized and woodland plots) as function of % impervious surface, distance from random plot to the nearest woodland (log-transformed) and to the sampled woodland, size of the sampled woodland, and absolute differences in habitat characteristics (number of humans (log-transformed), tree species richness (log-transformed), total aboveground tree biomass (log-transformed), and aboveground biomass of large trees (log-transformed)). Significant predictors (*P*<0.05) were shown in bold. Non-native species and non-breeding migrant species categories were excluded from the analysis due to insufficient detection at each site.

Response variables	Predictor															
	% impervious surface		Distance to nearest woodland		Distance to sampled woodland		Size of sampled woodland		Difference in number of humans		Difference in tree species richness		Difference in total AGB		Difference in AGB of large trees	
	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*	Coeff ± SE (% partial r^2)	*P*
Total species (% r^2 = 24.40)	**-0.151 ± 0.043 (8.08)**	**0.001**	**2.533 ± 0.547 (13.78)**	**6.3e^{-6}**	-3.26e^{-4}±0.007 (1.5e^{-3})	0.964	**2.908 ± 1.045 (5.31)**	**0.006**	**3.485 ± 0.965 (8.63)**	**4.2e^{-4}**	1.686 ± 1.331 (1.15)	0.207	-0.907 ± 0.892 (0.74)	0.311	0.252 ± 0.692 (0.10)	0.716
Native species (% r^2 = 25.74)	**-0.132 ± 0.044 (6.19)**	**0.003**	**2.526 ± 0.548 (13.36)**	**9.0e^{-6}**	3.10e^{-4} ± 0.007 (1.29e^{-3})	0.966	**2.584 ± 1.062 (4.12)**	**0.016**	**4.035 ± 0.980 (10.93)**	**6.6e^{-5}**	2.381 ± 1.352 (2.20)	0.080	-0.971 ± 0.906 (0.83)	0.285	0.107 ± 0.703 (0.02)	0.880
Resident species (% r^2 = 24.63)	**-0.149 ± 0.044 (7.58)**	**0.001**	**2.645 ± 0.554 (14.17)**	**4.6e^{-6}**	0.002 ± 0.007 (0.04)	0.805	**2.713 ± 1.075 (4.41)**	**0.013**	**3.693 ± 0.992 (9.12)**	**2.9e^{-4}**	1.821 ± 1.368 (1.27)	0.185	-1.274 ± 0.917 (1.38)	0.167	0.367 ± 0.711 (0.19)	0.607
Non-forest species (% r^2 = 17.38)	**-0.166 ± 0.047 (8.24)**	**0.001**	**1.425 ± 0.587 (4.10)**	**0.016**	4.67e^{-4} ± 0.008 (2.6e^{-3})	0.953	**2.998 ± 1.138 (4.79)**	**0.009**	**3.895 ± 1.051 (9.05)**	**3.0e^{-4}**	-0.027 ± 1.449 (2.5e^{-4})	0.985	-1.643 ± 0.971 (2.03)	0.093	0.539 ± 0.753 (0.37)	0.475
Forest-dependent species (% r^2 = 24.04)	-0.128 ± 0.071 (2.34)	0.071	**4.772 ± 0.880 (17.55)**	**2.6e^{-7}**	-0.001 ± 0.012 (0.01)	0.899	3.011 ± 1.707 (2.20)	0.080	2.547 ± 1.576 (1.86)	0.108	**5.126 ± 2.173 (3.87)**	**0.020**	0.546 ± 1.456 (0.10)	0.709	0.013 ± 1.130 (1.0e^{-4})	0.991

5.4 Discussion

Importance of urban areas — forest dependent species and migrants

We did not detect any highly forest-dependent species, i.e. specialists that mainly occur in undisturbed forests and are rarely found in degraded forest habitats (as defined by BirdLife International (2019)), but documented 41 (28.9 %) species with medium forest-dependency, those that are mainly found in undisturbed forest but also occur in forest edge and secondary forest. Many of these species were fairly widespread throughout our focal grid cells, being detected in at least one quarter of them, Pink-necked Green Pigeon *Treron vernans,* Brown-throated Sunbird *Anthreptes malacensis* and Lineated Barbet *Megalaima lineata* (see Table S5.11 for more examples). Their presence within our study region demonstrate that a wide range of relatively specialized species can occur in urbanized regions helping to maintain a range of ecological functions such as pollination (Brown-throated Sunbird *Anthreptes malacensis*) and seed-dispersal (frugivores such as Pink-necked Green Pigeon *Treron vernans* and Lineated Barbet *Megalaima lineata*). We also detected 36 non-breeding migrant species (25.4 % of our total) confirming the importance of considering urban areas when developing strategies to maintain bird migration along the East Asian-Australasian flyway (BirdLife international, 2015; Yong *et al*., 2015). In combination, these findings underscore that urban areas must be considered when setting regional and global conservation agendas (Ives *et al*., 2006).

Dominance of native species

Urban assemblages, including avian ones, are often considered to include a high proportion of established non-native species (Lazarina *et al*., 2020; Marzluff, 2001). Yet, only a small proportion of species detected in our surveys (5 of the 142 recorded species, 3.5%) were non-native to the Bangkok region, and of these only two species were widespread (Rock pigeon *Columba livia* and Zebra Dove *Geopelia striata* both occurred in over 90% of our grid cells). This is particularly surprising given that Bangkok is a major centre for the captive bird trade (Chng and Eaton, 2016; Round, 1990), which is often assumed to increase the risk of accidental introductions (Reino *et al*., 2017). Notably, however, some of the widespread native species that we detected are widely considered to be dominant competitors that are non-native invasive species in other regions, examples include the Common Myna

Acridotheres tristis (94.7 % occupancy; Colleony *et al*., 2020), Scaly-breasted Munia *Lonchura punctulata* (80.0 % occupancy; Conn *et al*., 2017), and Red turtle Dove *Streptopelia tranquebarica* (82.7 % occupancy; Yeo and Chia, 2010). Inter-specific competition can play a key role in structuring urban bird communities (Martin and Bonier, 2018). It is thus possible that the competitive abilities of these native species limit the extent to which non-native species have been able to become established in Bangkok. Such factors may contribute to the low occupancy rates of three of the five non-native species detected in our survey (Rose-ringed Parakeet *Alexandrinus krameri*, Alexandrine Parakeet *Palaeornis eupatria*, and Java Sparrow *Lonchura oryzivora*), especially as some of these are much more widespread in parts of their non-native ranges, such as Rose-ringed Parakeet *Alexandrinus krameri* (Pârâu *et al*., 2016). The later species is regarded as one of the 100 worst alien species in Europe (Brochier *et al*., 2010) and may in future expand throughout the Bangkok region threatening native cavity nesting species as is thought to be the case elsewhere in the Rose-ringed Parakeet's non-native range (Strubbe and Matthysen, 2009). Finally, and despite the low number of non-native species, we found that the richness of non-native species increased along the urbanization intensity gradient, contrasting with declines in species richness for all other groups, thus providing some support for the current perception that urban areas favour non-native species (Lazarina *et al*., 2020).

The form of tropical species richness-urbanization intensity relationships

In temperate regions, avian species richness typically follows a hump-shaped pattern along the urbanization intensity gradient, with richness peaking at intermediate levels of urbanization (Blair, 2004; Smith and Wacob, 2006; Vignoli *et al*., 2013). We found no evidence for such patterns in our tropical cases study, with richness of all species groups (except non-native species) peaking in the least urbanized parts of our urbanization gradient, and almost invariably declined in a linear manner as urbanization increased. Such linear species richness-urbanization intensity patterns have been documented in the relatively small number of similar studies conducted in urban regions, although not all have formally tested for alternative patterns (Chamberlain *et al*., 2017; Filloy *et al*., 2019; Leveau *et al*., 2017; Reis *et al*., 2012). Whilst our sampling gradient did not extend into natural habitats (i.e. Khao Yai National Park, approximately 100 km from Bangkok centre) doing so is unlikely to generate a unimodal richness-urban intensity gradient due to the extremely high avian richness of this location (Round *et al*., 2011) and we consider that the contrasting form of these relationships between tropical and temperate regions is likely to be a general pattern. In temperate regions habitat diversity often peaks at intermediate levels of urbanization intensity whilst the rural landscape is intensively used and consequently contains limited habitat heterogeneity, and this is considered to be the major mechanism driving the unimodal richness pattern (Tratalos *et al*., 2007). The negative linear pattern observed in our tropical case study might thus be generated by a high diversity of habitats in the least urbanized parts of our gradient (i.e. interspersing of semi-natural wetland, rice fields, orchards, and patches of secondary woodland etc.), with habitat diversity gradually declining as urbanization increases. This might be a general driver of linear declines in species richness along urbanization gradients in tropical locations. In addition, it is plausible albeit not unequivocal that tropical regions contain a greater proportion of specialized species (Belmaker *et al*., 2012; Cirtwill *et al*., 2015). Such a macroecological pattern could also contribute to the contrasting patterns between tropical and temperate species richness-urbanization intensity gradients. As urbanization selects against specialized species (Callaghan *et al*., 2019; Evans *et al*., 2010) assemblages with a greater proportion of specialists are less likely to exhibit peaks in richness at intermediate levels of urbanization.

Moderating effects of woodland on the impacts of urbanization

Woodland survey points had higher species richness than the randomized points for almost all species groups. This is unsurprising given that other studies have demonstrated the importance of woodland in urban environments for enhancing the diversity of bird communities (Ferenc *et al*., 2014; Filloy *et al*., 2019; Pellissier *et al*., 2012). Our results regarding the impact of woodland on the richness of urban bird assemblages, however, go beyond confirming results of earlier studies in two important aspects. First, we find that non-native species are an exception to this rule, and have lower species richness at the woodland points. This suggests that maintaining patches of more natural vegetation in urban environment could reduce the extent to which urban environments are prone to invasion by non-native avian species. Second, we assess how woodland patches moderate changes in species richness along the urbanization gradient. For those species groups that decline in richness in response to urbanization we typically find shallower declines in species richness along the urbanization gradient at the woodland points. Consequently, the greatest gains in species richness from adding patches of woodland to the environment occur in the most urbanized sites. This has important implications for policies regarding habitat protection and restoration in urban environments as even small patches of woodland (mean woodland size in our most urbanized grid cells, i.e. 90-100% impervious surface cover, was 0.38 ± 0.21 (s.e.) ha (median = 0.13 ha) can deliver biodiversity benefits in intensely urbanized locations. This contrasts with the traditional dogma that small patches of natural habitat are likely to have little biodiversity value, although this view has recently been challenged (Wintle *et al*., 2019). Whilst woodland did not moderate the effect of urbanization intensity on the richness of non-breeding migrants and forest dependent species, the beneficial impacts of woodland were maintained across the urbanization gradient — further suggesting that small patches of woodland surrounded by a highly urbanized matrix can provide biodiversity benefits. Such locations often represent the only greenspace in such areas and are thus the last chance for conserving their remaining bird diversity (Savard *et al*., 2000; Soanes and Lentini, 2019). Larger patches of green space, especially of more natural vegetation types, should though not be ignored in urban conservation initiatives (see section *Effects of spatial configuration and ecological characteristics of woodland patches*).

Human disturbance

Positive influences of human disturbance on non-native species richness is probably driven by responses of two widespread non-native commensal species (i.e. feral pigeon and zebra dove) that largely rely on human derived food resources (Round and Gardner, 2008). The richness of all other groups, except non-breeding visitors in the woodland locations which exhibited no significant association, declined as human disturbance increased. This was the predictor variable with the greatest explanatory power at the randomized points, and was the second most influential predictor variable at the wooded points. A small number of other studies have also reported negative impacts of human disturbance on urban bird assemblages (Jasmani *et al*., 2017; Kang *et al*., 2015), yet discussions of conservation actions in urban settings tend to focus on altering habitat types and management practices rather than grappling with human disturbance issues (e.g. Aronson *et al*., 2017). Our results thus expose a trade-off between the desire to manage urban green-spaces in a manner that maximizes biodiversity and increasing residents’ exposure to nature, which is likely to enhance their appreciation of biodiversity and desire to protect it (Coldwell and Evans, 2017), alongside gaining wellbeing benefits (Taylor and Hochuli, 2015) — but at the risk of reducing avian biodiversity.

Effects of spatial configuration and ecological characteristics of woodland patches

Randomized survey points that were further away from woodland had lower numbers of forest dependent species, but not species in other groups. Turnover in the composition of bird assemblages between paired randomized and woodland points also increased when randomized points were further away from woodland. It is thus clear that close spatial proximity of woodland enables woodland specialists and, to a lesser extent, other species that utilize woodland to occupy the urban matrix. This is probably because the willingness to travel across the urban matrix varies between species, with forest-dependent species particularly reluctant to cross gaps between suitable habitat patches (Watson *et al*., 2005). Larger woodlands increased the richness of forest dependent species, and increased the turnover in species composition (relative to random points) for all species groups. This highlights that larger urban woodlands support a relatively unique assemblage of species and thus play an important role in maximizing urban avian diversity (La Sorte *et al*., 2020).

Tree species richness and above ground biomass positively influenced the richness of forest dependent species in both the randomized and woodland survey locations, with above ground biomass also promoting higher richness of a number of other groups in the randomized points. Notably, the difference in tree species richness between the randomized and wooded points was positively associated with the turnover in species composition between these points. Our results thus suggest that woodland patches with a more diverse tree flora and high aboveground biomass are likely to be most important in enhancing urban avian diversity. Our results thus provide evidence-based guidelines that urban woodland creation schemes should seek to plant a wide range of tree species, at relatively high densities. Whilst we found no explicit evidence that particularly large trees provided additional benefits this is perhaps a reflection of their rarity in the urban landscape, with just 2.9% of trees meeting our definition of large trees DBH ≥ 70 cm, and we do advocate that all large trees are protected within urban landscapes for their biodiversity benefits. Indeed, their rarity may partially explain why we did not detect any highly forest dependent species in our surveys.

5.5 Conclusions and recommendations

Our study makes a number of important contributions to assessments of the factors influencing urban bird assemblages and how to manage these regions to optimize biodiversity. Our study adds to the growing but limited evidence base that tropical avian assemblages appear to exhibit linear declines in richness along the urbanization gradient, contrasting with temperate regions' unimodal patterns with richness peaking at intermediate urbanization intensities. Potential mechanisms driving this contrast are contrasting changes in habitat heterogeneity along tropical and temperature urbanization gradients, and greater proportions of specialized species that are sensitive to urbanization in tropical regions. Moreover, we provide novel evidence that retaining patches of urban woodland can mitigate some of the adverse effects of the intensity of urbanization on species richness — and for many species groups the benefits of woodland patches increase as urbanization intensifies even though such woodland patches are typically very small. We suggest four main recommendations for bird conservation in tropical urban regions: *i) conserving* semi-natural habitats and areas with high levels of habitat diversity, *ii) improving* the quality of wooded habitats to maximize the capacity of woodland to support avian biodiversity by increasing tree density and species diversity, *iii) creating* more woodland across the urbanization gradient, including in highly urbanized locations, even small wooded patches will be beneficial and the additional woodland should be well distributed throughout the urban area to minimize the effects of habitat isolation, and *iv) managing human disturbance* in some areas, especially those of high habitat quality, to minimize adverse effects on urban bird populations whilst ensuring the benefits of connecting people to nature are realized in other locations.

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5.7 Supplementary materials

Table S5.1: Akaike Information Criterion values adjusted for small sample size (AICc) of generalised linear models for bird species richness with % impervious surface cover (linear and quadratic models) comparing between model fitted using Poisson error structure (log link) and Gaussian error structure (identity link).

Response variable	Location type	AICc (linear model)		AICc (quadratic model)	
		Poisson	Gaussian	Poisson	Gaussian
Total species richness	Randomized	960.20	**945.74**	960.19	**947.81**
	Woodland	881.20	**869.90**	880.82	**870.82**
Native species richness	Randomized	973.52	**950.31**	973.10	**952.33**
	Woodland	884.99	**877.67**	884.01	**878.62**
Non-native species richness	Randomized	398.21	**133.14**	396.62	**133.79**
	Woodland	391.62	**269.24**	393.70	**271.34**
Resident species richness	Randomized	933.79	**920.96**	932.96	**923.03**
	Woodland	868.65	**854.07**	866.39	**852.47**
Non-breeding visitor species richness	Randomized	**341.08**	400.97	**343.14**	400.53
	Woodland	**415.86**	462.19	**415.77**	459.38
Non-forest species richness	Randomized	**878.02**	890.23	**879.43**	891.75
	Woodland	**852.06**	863.23	**853.50**	865.32
Forest-dependent species richness	Randomized	**738.17**	738.39	**738.20**	739.75
	Woodland	709.36	**698.11**	709.02	**697.44**

Table S5.2: Akaike Information Criterion values adjusted for small sample size (AICc) of generalised linear models for bird species richness with ecological features comparing between model fitted using Poisson error structure (log link) and Gaussian error structure (identity link).

Response variable	Location type	AICc	
		Poisson	Gaussian
Total species richness	Randomized	888.96	**882.91**
	Woodland	869.67	**847.57**
Native species richness	Randomized	892.56	**888.20**
	Woodland	867.24	**869.67**
Non-native species richness	Randomized	406.42	**159.63**
	Woodland	396.31	**249.14**
Resident species richness	Randomized	868.36	**852.79**
	Woodland	856.45	**827.93**
Non-breeding visitor species richness	Randomized	**341.12**	401.64
	Woodland	**423.02**	469.40
Non-forest species richness	Randomized	**825.77**	845.74
	Woodland	**825.74**	833.17
Forest-dependent species richness	Randomized	660.92	**632.83**
	Woodland	684.30	**627.74**

Table S5.3: Moran's I test results of generalised linear models for bird species richness with % impervious surface cover (linear and quadratic models) in randomized and woodland plots. Models with significant spatial autocorrelation were shown in bold.

Response variable	Location	Model	Moran's I test	
			observed	*P*
Total species richness	Randomized	Linear	-0.005	0.605
		quadratic	-0.005	0.574
	Woodland	**Linear**	**-0.016**	**0.016**
		quadratic	**-0.015**	**0.028**
Native species richness	Randomized	Linear	-0.008	0.785
		quadratic	-0.007	0.839
	Woodland	Linear	-0.008	0.785
		quadratic	-0.011	0.230
Non-native species richness	Randomized	Linear	-0.008	0.824
		quadratic	-0.006	0.929
	Woodland	**Linear**	**-0.020**	$\mathbf{3.22e^{-4}}$
		quadratic	**-0.020**	$\mathbf{3.28e^{-4}}$
Resident species richness	Randomized	Linear	-0.003	0.393
		quadratic	-0.004	0.413
	Woodland	**Linear**	**-0.019**	**0.002**
		quadratic	**-0.016**	**0.011**
Non-breeding visitor species richness	Randomized	Linear*	-0.006	0.904
		Quadratic*	-0.006	0.891
	Woodland	Linear*	-0.009	0.554
		Quadratic*	-0.008	0.680
Non-forest species richness	Randomized	Linear*	-0.004	0.495
		Quadratic*	-0.005	0.564
	Woodland	**Linear***	**-0.022**	$\mathbf{2.99e^{-5}}$
		Quadratic*	**-0.018**	$\mathbf{4.16e^{-5}}$
Forest-dependent species richness	Randomized	Linear*	-0.006	0.901
		Quadratic*	-0.008	0.758
	Woodland	Linear	-0.011	0.266
		quadratic	-0.010	0.355

Table S5.4: Comparison of coefficients and standard errors of species richness models in woodland plot as function of impervious surface percentage (linear and quadratic models) with and without taking spatial correlation structure into account by using generalised linear mixed model approach. Models were fitted with Gaussian error structure (identity link) for total species richness, non-native species richness, and resident species richness, and with Poisson error structure (log link) for non-forest species richness.

Response variable	Model type	Linear model			Quadratic model				
		Intercept	Coeff ± SE	*P*	Intercept	Coeff ± SE (linear term)	*P* (linear term)	Coeff ± SE (quadratic term)	*P* (quadratic term)
Total species richness	Spatial	34.916 ± 0.770	-0.139 ± 0.014	$<2e^{-16}$	34.716 ± 1.042	-0.125 ± 0.050	0.014	$-1.60e^{-4} \pm 0.001$	0.763
	Non-spatial	35.323 ± 0.685	-0.150 ± 0.013	$<2e^{-16}$	34.539 ± 0.995	-0.099 ± 0.049	0.044	$-0.001 \pm 4.955e^{-4}$	0.280
Non-native species richness	Spatial	1.213 ± 0.092	0.008 ± 0.002	$<2e^{-16}$	1.223 ± 0.135	0.007 ± 0.007	0.270	$7.00e^{-6} \pm 6.71e^{-5}$	0.917
	Non-spatial	1.213 ± 0.092	0.008 ± 0.002	$5.39e^{-6}$	1.223 ± 0.135	0.007 ± 0.007	0.270	$6.98e^{-6} \pm 6.71e^{-5}$	0.917
Resident species richness	Spatial	32.536 ± 0.768	-0.114 ± 0.013	$<2e^{-16}$	31.900 ± 0.997	-0.069 ± 0.047	0.147	$-0.001 \pm 4.90e^{-4}$	0.298
	Non-spatial	33.119 ± 0.649	-0.132 ± 0.012	$<2e^{-16}$	31.813 ± 0.936	-0.047 ± 0.046	0.309	$-0.001 \pm 4.66e^{-4}$	0.057
Non-forest species richness	Spatial	3.115 ± 0.042	-0.005 ± 0.001	$<2e^{-16}$	3.117 ± 0.053	-0.005 ± 0.003	0.064	$2.00e^{-6} \pm 2.74e^{-5}$	0.943
	Non-spatial	3.151 ± 0.035	-0.006 ± 0.001	$<2e^{-16}$	3.122 ± 0.050	-0.004 ± 0.003	0.137	$2.18e^{-5} \pm 2.74e^{-5}$	0.427

Table S5.5: Akaike Information Criterion values adjusted for small sample size (AICc) of generalised linear mixed models for bird species richness with % impervious surface cover and its interaction term with typ of sampling point (randomized and woodland points) comparing between model fitted using Poisson error structure (log link) and Gaussian error structure (identity link). The results from the better fitted models (shown in bold) were reported in Table 5.3.

Response variable	AICc	
	Poisson model	Gaussian model
Total species richness	1803.58	**1778.18**
Native species richness	1813.94	**1787.65**
Non-native species richness	777.06	**420.07**
Resident species richness	1766.54	**1735.34**
Non-breeding migrant species richness	**740.28**	841.30
Non-forest species richness	**1681.70**	1698.16
Forest-dependent species richness	1414.55	**1387.43**

Table S5.6: Variance Inflation Factors (VIFs) values of multiple regression models for bird species richness with landscape and ecological attributes (separately for randomized and woodland plots), and species turnover (Jaccard's dissimilarity index; JDI) of bird community in randomized and woodland locations revealed no multicollinearity amongst our models (VIF < 10).

Predictor variables	VIFs
Bird species richness at the randomized locations	
% impervious surface cover of grid cell	2.131
Distance from randomized plot to the nearest woodland	1.996
Mean number of humans	2.136
Tree species richness	4.159
Total aboveground tree biomass	6.343
Aboveground tree biomass of large trees	1.965
Bird species richness at the woodland locations	
% impervious surface cover of grid cell	1.549
Size of the sampled woodland	1.314
Mean number of humans	1.591
Tree species richness	1.331
Total aboveground tree biomass	2.044
Aboveground tree biomass of large trees	1.805
Species turnover (JDI) between randomized and woodland locations	
% impervious surface cover of grid cell	1.928
Distance from randomized plot to the nearest woodland	1.152
Distance from randomized plot to the sampled woodland	1.062
Size of the sampled woodland	1.289
Absolute difference in mean number of humans	1.892
Absolute difference in tree species richness	1.154
Absolute difference in total aboveground tree biomass	1.248
Absolute difference in aboveground tree biomass of large trees	1.194

Table S5.7: Moran's I test results of multiple regression models for bird species richness with landscape characteristics and ecological features (Table 5.1 in the main manuscript) in randomized and woodland plots. Models with significant spatial autocorrelation were shown in bold.

Response variable	Location	Moran's I test	
		observed	*P*
Total species richness	**Randomized**	**0.021**	**0.011**
	Woodland	**0.027**	**0.002**
Native species richness	**Randomized**	**0.033**	**2.75e^{-4}**
	Woodland	**0.019**	**0.015**
Non-native species richness	Randomized	0.003	0.380
	Woodland	**0.029**	**0.001**
Resident species richness	**Randomized**	**0.017**	**0.031**
	Woodland	**0.024**	**0.004**
Non-breeding visitor species richness	**Randomized***	**-0.016**	**0.037**
	Woodland*	0.006	0.251
Non-forest species richness	Randomized*	-0.011	0.094
	Woodland*	**0.028**	**0.001**
Forest-dependent species richness	Randomized	-0.012	0.603
	Woodland	-0.001	0.621

Table S5.8: Comparison of coefficients and standard errors of species richness in randomized plot as function of ecological features (Table 5.1 in the main manuscript) with and without taking spatial correlation structure into account by using generalised linear mixed model approach. Models were fitted with Gaussian error structure (identity link) for total species richness, native species richness, resident species richness, and forest-dependent species richness and with Poisson error structure (log link) for non-breeding visitor species richness.

Response variable	Model type	% Impervious surface		Size of sampled woodland		Mean number of humans		Tree species richness		Total aboveground tree biomass		Aboveground biomass of large trees	
		Coeff ± SE	*P*	Coeff ± SE	*P*	Coeff ± SE	*P*	Coeff ± SE	*P*	Coeff ± SE	*P*	Coeff ± SE	*P*
Total species richness	Spatial	-0.097 ± 0.019	$<2.2e^{-16}$	0.106 ± 0.289	0.714	-3.162 ± 0.396	$<2.2e^{-16}$	-0.812 ± 0.946	0.392	2.295 ± 0.932	0.007	-0.597 ± 0.493	0.228
	Non-spatial	-0.098 ± 0.019	$6.17e^{-7}$	0.109 ± 0.291	0.710	-3.150 ± 0.397	$5.29e^{-13}$	-0.752 ± 0.944	0.427	2.226 ± 0.829	0.008	-0.537 ± 0.490	0.276
Native species richness	Spatial	-0.099 ± 0.019	$<2.2e^{-16}$	0.122 ± 0.295	0.680	-3.221 ± 0.403	$<2.2e^{-16}$	-0.733 ± 0.963	0.448	2.242 ± 0.847	0.009	-0.559 ± 0.501	0.267
	Non-spatial	-0.100 ± 0.019	$6.88e^{-7}$	0.125 ± 0.296	0.673	-3.209 ± 0.404	$5.06e^{13}$	-0.675 ± 0.961	0.484	2.175 ± 0.843	0.011	-0.501 ± 0.499	0.317
Resident species richness	Spatial	-0.087 ± 0.017	$<2.2e^{-16}$	0.034 ± 0.263	0.896	-2.924 ± 0.359	$<2.2e^{-16}$	-0.461 ± 0.856	0.591	1.967 ± 0.752	0.010	-0.435 ± 0.445	0.330
	Non-spatial	-0.088 ± 0.017	$8.05e^{-7}$	0.036 ± 0.263	0.892	-2.920 ± 0.359	$1.79e^{-13}$	-0.431 ± 0.854	0.615	1.931 ± 0.750	0.011	-0.407 ± 0.444	0.361
Non-breeding visitor species richness	Spatial	-0.012 ± 0.005	0.018	0.010 ± 0.074	0.897	-0.258 ± 0.110	0.021	-0.288 ± 0.237	0.227	0.194 ± 0.200	0.333	-0.103 ± 0.122	0.398
	Non-spatial	-0.012 ± 0.005	0.015	0.010 ± 0.074	0.893	-0.255 ± 0.110	0.021	-0.281 ± 0.237	0.236	0.187 ± 0.200	0.349	-0.095 ± 0.121	0.211

Table S5.9: Comparison of coefficients and standard errors of species richness in woodland plots as function of woodland features (Table 1 in the main manuscript) with and without taking spatial correlation structure into account by using generalised linear mixed model approach. Models were fitted with Gaussian error structure (identity link) for total species richness, native species richness, resident species richness, and forest-dependent species richness and with Poisson error structure (log link) for non-breeding visitor species richness.

Response variable	Model type	% Impervious surface		Size of sampled woodland		Mean number of humans		Tree species richness		Total aboveground tree biomass		Aboveground biomass of large trees	
		Coeff ± SE	*P*	Coeff ± SE	*P*	Coeff ± SE	*P*	Coeff ± SE	*P*	Coeff ± SE	*P*	Coeff ± SE	*P*
Total species richness	Spatial	-0.098 ± 0.015	$<2.2e^{-16}$	0.332 ± 0.339	0.329	-2.124 ± 0.422	$<2.2e^{-16}$	-0.977 ± 0.631	0.124	0.463 ± 0.583	0.429	0.129 ± 0.296	0.663
	Non-spatial	-0.107 ± 0.014	$4.79e^{-12}$	0.314 ± 0.349	0.370	-2.180 ± 0.439	$1.93e^{-6}$	-0.740 ± 0.648	0.255	0.087 ± 0.604	0.886	0.163 ± 0.307	0.597
Native species richness	Spatial	-0.110 ± 0.014	$<2.2e^{-16}$	0.478 ± 0.352	0.177	-2.333 ± 0.443	$<2.2e^{-16}$	-0.825 ± 0.653	0.209	0.239 ± 0.609	0.696	0.157 ± 0.310	0.613
	Non-spatial	-0.110 ± 0.014	$2.18e^{-12}$	0.477 ± 0.352	0.178	-2.334 ± 0.443	$4.91e^{-7}$	-0.827 ± 0.653	0.208	0.240 ± 0.609	0.694	0.157 ± 0.310	0.615
Non -native species richness	Spatial	0.003 ± 0.002	0.123	-0.164 ± 0.047	0.001	0.155 ± 0.060	0.011	0.086 ± 0.088	0.329	-0.153 ± 0.082	0.064	0.006 ± 0.042	0.881
	Non-spatial	0.003 ± 0.002	0.122	-0.164 ± 0.047	0.001	0.155 ± 0.060	0.011	0.086 ± 0.088	0.329	-0.153 ± 0.082	0.064	0.006 ± 0.042	0.881
Resident species richness	Spatial	-0.089 ± 0.013	$<2.2e^{-16}$	0.201 ± 0.327	0.539	-2.244 ± 0.411	$<2.2e^{-16}$	-0.582 ± 0.607	0.339	0.012 ± 0.565	0.982	0.125 ± 0.288	0.666
	Non-spatial	-0.089 ± 0.013	$4.15e^{-10}$	0.201 ± 0.327	0.539	-2.244 ± 0.411	$2.08e^{-7}$	-0.582 ± 0.607	0.339	0.012 ± 0.565	0.982	0.125 ± 0.288	0.666
Non-forest species richness	Spatial	-0.004 ± 0.001	$<2.2e^{-16}$	-0.021 ± 0.017	0.235	-0.091 ± 0.023	$1.00e^{-4}$	-0.087 ± 0.032	0.006	-0.050 ± 0.029	0.083	0.024 ± 0.015	0.122
	Non-spatial	-0.004 ± 0.001	$4.93e^{-7}$	-0.024 ± 0.021	0.251	-0.098 ± 0.029	0.001	-0.080 ± 0.038	0.034	-0.068 ± 0.035	0.052	0.023 ± 0.019	0.211

Table S5.10: Moran's I test results for Jaccard's dissimilarity index with landscape characteristics and ecological features (Table 5.1 in the main manuscript) in randomized and woodland plots.

Response variable	Moran's I test	
	observed	*P*
Total species richness	-0.020	0.821
Native species richness	-0.023	0.867
Resident species richness	-0.017	0.769
Non-forest species richness	-0.010	0.577
Forest-dependent species richness	-0.009	0.561

Table S5.11 List of bird species detected in this study arranged by % occupancy (number of grid cell they were found). Classification as native or non-native species to Bangkok area is based on Round & Gardner (2008). Seasonal status (resident, passage migrant, breeding visitor, and non-breeding visitor species) is based on Round & Gardner (2008), and forest dependency status (low, medium, high forest dependency, and 'does not normally occur in forest') is based on Birdlife international (2019). For data analyses, we defined 'does not normally occur in forest' and 'low forest dependency' as 'non-forest species', and 'medium-' and 'high forest dependency' as 'forest dependent species'.

Scientific name	Native to Bangkok area	Seasonal status	Forest dependency	% occupancy		
				Randomized	Woodland	Total
Geopelia striata	introduced	resident	does not normally occur in forest	98.00	92.67	100.00
Dicaeum cruentatum	native	resident	medium	74.67	97.33	100.00
Rhipidura javanica	native	resident	medium	91.33	99.33	100.00
Pycnonotus conradi	native	resident	low	92.00	100.00	100.00
Copsychus saularis	native	resident	medium	94.00	98.00	99.33
Acridotheres grandis	native	resident	does not normally occur in forest	90.00	89.33	97.33
Megalaima haemacephala	native	resident	medium	71.33	95.33	97.33
Acridotheres tristis	native	resident	low	88.67	84.00	94.67
Pycnonotus goiavier	native	resident	low	76.67	85.33	94.67
Spilopelia chinensis	native	resident	medium	80.67	84.67	94.00
Passer montanus	native	resident	low	90.67	76.00	92.67
Columba livia	introduced	resident	does not normally occur in forest	87.33	62.67	91.33
Cinnyris jugularis	native	resident	low	58.00	83.33	90.00
Eudynamys scolopaceus	native	resident	medium	58.67	88.00	90.00
Apus nipalensis	native	resident	low	72.00	69.33	88.67

Scientific name	Native to Bangkok area	Seasonal status	Forest dependency	% occupancy		
				Randomized	Woodland	Total
Orthotomus sutorius	native	resident	low	50.67	80.00	86.00
Prinia inornata	native	resident	low	67.33	75.33	84.00
Aegithina tiphia	native	resident	medium	48.00	78.00	83.33
Streptopelia tranquebarica	native	resident	medium	74.67	70.67	82.67
Cacomantis merulinus	native	resident	low	52.67	69.33	80.67
Lonchura punctulata	native	resident	low	56.00	62.67	80.00
Anthreptes malacensis	native	resident	medium	45.33	69.33	80.00
Passer domesticus	native	resident	low	60.00	53.33	76.00
Amaurornis phoenicurus	native	resident	low	40.67	64.00	70.00
Centropus sinensis	native	resident	low	34.67	58.67	64.00
Coracias affinis	native	resident	low	36.00	50.00	62.00
Cypsiurus balasiensis	native	resident	low	35.33	43.33	61.33
Prinia flaviventris	native	resident	low	42.67	49.33	61.33
Ardeola speciosa	native	resident	low	32.00	41.33	52.67
Hirundo rustica	native	non-breeding visitor	does not normally occur in forest	30.00	26.67	45.33
Anastomus oscitans	native	resident	does not normally occur in forest	29.33	25.33	44.00
Dicrurus macrocercus	native	resident	does not normally occur in forest	24.67	33.33	44.00
Orthotomus atrogularis	native	resident	medium	14.67	28.67	34.67
Pericrocotus cinnamomeus	native	resident	medium	18.00	28.67	34.67

Scientific name	Native to Bangkok area	Seasonal status	Forest dependency	% occupancy		
				Randomized	Woodland	Total
Treron vernans	native	resident	medium	20.00	30.00	34.00
Corvus macrorhynchos	native	resident	medium	16.00	22.67	32.00
Egretta garzetta	native	resident	does not normally occur in forest	22.67	17.33	30.67
Ploceus philippinus	native	resident	low	18.67	19.33	28.67
Ardeola bacchus	native	non-breeding visitor	low	17.33	17.33	28.00
Megalaima lineata	native	resident	medium	12.67	22.00	27.33
Gracupica contra	native	resident	does not normally occur in forest	18.67	18.67	26.67
Muscicapa latirostris	native	non-breeding visitor	medium	6.67	23.33	26.67
Lonchura striata	native	resident	low	16.67	14.67	26.00
Vanellus indicus	native	resident	does not normally occur in forest	17.33	16.00	24.00
Dicrurus paradiseus	native	resident	medium	5.33	23.33	24.00
Aerodramus germani	native	resident	low	13.33	14.00	22.00
Gracupica nigricollis	native	resident	low	12.67	12.00	21.33
Ceuthmochares australis	native	resident	medium	6.00	16.00	20.00
Ploceus hypoxanthus	native	resident	low	14.00	9.33	19.33
Ixobrychus sinensis	native	resident	low	9.33	12.00	19.33
Microcarbo niger	native	resident	low	13.33	8.67	18.67
Butorides striata	native	resident	low	6.67	15.33	18.67
Pycnonotus jocosus	native	resident	low	7.33	10.00	16.67

Scientific name	Native to Bangkok area	Seasonal status	Forest dependency	% occupancy		
				Randomized	Woodland	Total
Todiramphus chloris	native	resident	medium	6.00	12.67	14.67
Artamus fuscus	native	resident	low	6.00	10.00	14.00
Passer flaveolus	native	resident	low	7.33	6.00	12.67
Nycticorax nycticorax	native	resident	low	4.00	10.67	12.67
Merops philippinus	native	resident	low	8.00	6.00	12.00
Cisticola juncidis	native	resident	does not normally occur in forest	6.67	8.67	12.00
Dendrocygna javanica	native	resident	low	8.00	6.00	11.33
Ardea alba	native	resident	does not normally occur in forest	6.00	7.33	11.33
Bubulcus ibis	native	resident	low	8.00	3.33	10.00
Himantopus himantopus	native	resident	does not normally occur in forest	8.00	4.67	10.00
Lanius cristatus	native	non-breeding visitor	low	4.67	5.33	10.00
Dicrurus leucophaeus	native	non-breeding visitor	low	1.33	10.00	9.33
Glareola maldivarum	native	breeding visitor	does not normally occur in forest	6.00	6.00	8.67
Halcyon pileata	native	non-breeding visitor	medium	1.33	7.33	8.67
Oriolus chinensis	native	non-breeding visitor	medium	2.67	7.33	8.67
Crypsirina temia	native	resident	medium	2.00	6.00	6.67
Ixobrychus flavicollis	native	breeding visitor	medium	3.33	3.33	6.00
Metopidius indicus	native	resident	does not normally occur in forest	4.67	4.00	6.00
Ardea purpurea	native	resident	low	3.33	2.00	5.33

Scientific name	Native to Bangkok area	Seasonal status	Forest dependency	% occupancy		
				Randomized	Woodland	Total
Halcyon smyrnensis	native	resident	low	1.33	4.00	5.33
Pelargopsis capensis	native	resident	medium	1.33	4.00	5.33
Centropus bengalensis	native	resident	does not normally occur in forest	0.67	4.67	5.33
Elanus axillaris	native	resident	does not normally occur in forest	3.33	1.33	4.67
Anthus rufulus	native	resident	does not normally occur in forest	3.33	2.00	4.67
Chlidonias hybrida	native	non-breeding visitor	does not normally occur in forest	4.00	2.00	4.67
Iduna aedon	native	non-breeding visitor	does not normally occur in forest	1.33	4.00	4.67
Sturnia malabarica	native	resident	low	2.00	2.67	4.00
Ardea intermedia	native	non-breeding visitor	low	2.67	2.67	4.00
Tachybaptus ruficollis	native	resident	does not normally occur in forest	2.67	0.67	3.33
Dendrocopos macei	native	resident	medium	2.00	1.33	3.33
Mycteria leucocephala	native	resident	does not normally occur in forest	1.33	2.00	3.33
Haliastur indus	native	resident	low	2.00	0.67	2.67
Ploceus manyar	native	resident	does not normally occur in forest	1.33	1.33	2.67
Phylloscopus tenellipes	native	non-breeding visitor	medium	1.33	0.67	2.00
Ficedula albicilla	native	non-breeding visitor	medium	1.33	0.67	2.00
Alexandrinus krameri	introduced	resident	medium	1.33	1.33	2.00
Pycnonotus aurigaster	native	resident	low	0.67	0.67	1.33
Phalacrocorax fuscicollis	native	resident	low	0.67	0.67	1.33

Scientific name	Native to Bangkok area	Seasonal status	Forest dependency	% occupancy		
				Randomized	Woodland	Total
Ficedula zanthopygia	native	passage migrant	medium	0.67	0.67	1.33
Palaeornis eupatria	introduced	resident	medium	0.67	0.67	1.33
Chroicocephalus brunnicephalus	native	non-breeding visitor	does not normally occur in forest	0.67	0.67	1.33
Acrocephalus bistrigiceps	native	non-breeding visitor	does not normally occur in forest	0.67	0.67	1.33
Sterna hirundo	native	non-breeding visitor	does not normally occur in forest	0.67	0.67	1.33
Acrocephalus orientalis	native	non-breeding visitor	does not normally occur in forest	0.67	0.67	1.33
Ixobrychus cinnamomeus	native	resident	low	1.33	0.67	1.33
Lonchura atricapilla	native	resident	does not normally occur in forest	1.33	0.67	1.33
Phylloscopus borealis	native	non-breeding visitor	low	0.00	1.33	1.33
Ardeola grayii	native	non-breeding visitor	low	0.00	1.33	1.33
Lanius schach	native	resident	low	0.00	1.33	1.33
Dendronanthus indicus	native	non-breeding visitor	medium	0.00	1.33	1.33
Eurystomus orientalis	native	non-breeding visitor	medium	0.00	1.33	1.33
Otus lettia	native	resident	medium	0.00	1.33	1.33
Athene brama	native	resident	does not normally occur in forest	0.00	1.33	1.33
Lonchura oryzivora	introduced	resident	does not normally occur in forest	0.00	1.33	1.33
Picus vittatus	native	resident	medium	1.33	0.00	1.33
Porphyrio porphyrio	native	resident	does not normally occur in forest	1.33	0.00	1.33
Turnix sylvaticus	native	resident	does not normally occur in forest	1.33	0.00	1.33

Scientific name	Native to Bangkok area	Seasonal status	Forest dependency	% occupancy		
				Randomized	Woodland	Total
Amaurornis cinerea	native	resident	low	0.67	0.67	0.67
Psittacula alexandri	native	resident	medium	0.67	0.67	0.67
Sturnia sinensis	native	non-breeding visitor	does not normally occur in forest	0.67	0.67	0.67
Terpsiphone paradisi	native	non-breeding visitor	low	0.00	0.67	0.67
Threskiornis melanocephalus	native	non-breeding visitor	low	0.00	0.67	0.67
Alcedo atthis	native	non-breeding visitor	low	0.00	0.67	0.67
Falco tinnunculus	native	non-breeding visitor	low	0.00	0.67	0.67
Phylloscopus fuscatus	native	non-breeding visitor	low	0.00	0.67	0.67
Anhinga melanogaster	native	resident	low	0.00	0.67	0.67
Pericrocotus divaricatus	native	non-breeding visitor	medium	0.00	0.67	0.67
Caprimulgus jotaka	native	non-breeding visitor	medium	0.00	0.67	0.67
Pitta moluccensis	native	passage migrant	medium	0.00	0.67	0.67
Lanius tigrinus	native	passage migrant	medium	0.00	0.67	0.67
Tringa totanus	native	non-breeding visitor	does not normally occur in forest	0.00	0.67	0.67
Tringa stagnatilis	native	non-breeding visitor	does not normally occur in forest	0.00	0.67	0.67
Riparia riparia	native	non-breeding visitor	does not normally occur in forest	0.00	0.67	0.67
Gorsachius melanolophus	native	resident	does not normally occur in forest	0.00	0.67	0.67
Hydrophasianus chirurgus	native	resident	does not normally occur in forest	0.00	0.67	0.67
Porzana fusca	native	resident	does not normally occur in forest	0.00	0.67	0.67

Scientific name	Native to Bangkok area	Seasonal status	Forest dependency	% occupancy		
				Randomized	Woodland	Total
Cecropis daurica	native	non-breeding visitor	low	0.67	0.00	0.67
Tringa glareola	native	non-breeding visitor	low	0.67	0.00	0.67
Agropsar sturninus	native	passage migrant	low	0.67	0.00	0.67
Turnix suscitator	native	resident	low	0.67	0.00	0.67
Ardea cinerea	native	resident	low	0.67	0.00	0.67
Caprimulgus macrurus	native	resident	low	0.67	0.00	0.67
Pernis ptilorhynchus	native	non-breeding visitor	medium	0.67	0.00	0.67
Ficedula mugimaki	native	passage migrant	medium	0.67	0.00	0.67
Gerygone sulphurea	native	resident	medium	0.67	0.00	0.67
Motacilla cinerea	native	non-breeding visitor	does not normally occur in forest	0.67	0.00	0.67
Motacilla flava	native	non-breeding visitor	does not normally occur in forest	0.67	0.00	0.67
Nettapus coromandelianus	native	resident	does not normally occur in forest	0.67	0.00	0.67
Gallicrex cinerea	native	resident	does not normally occur in forest	0.67	0.00	0.67

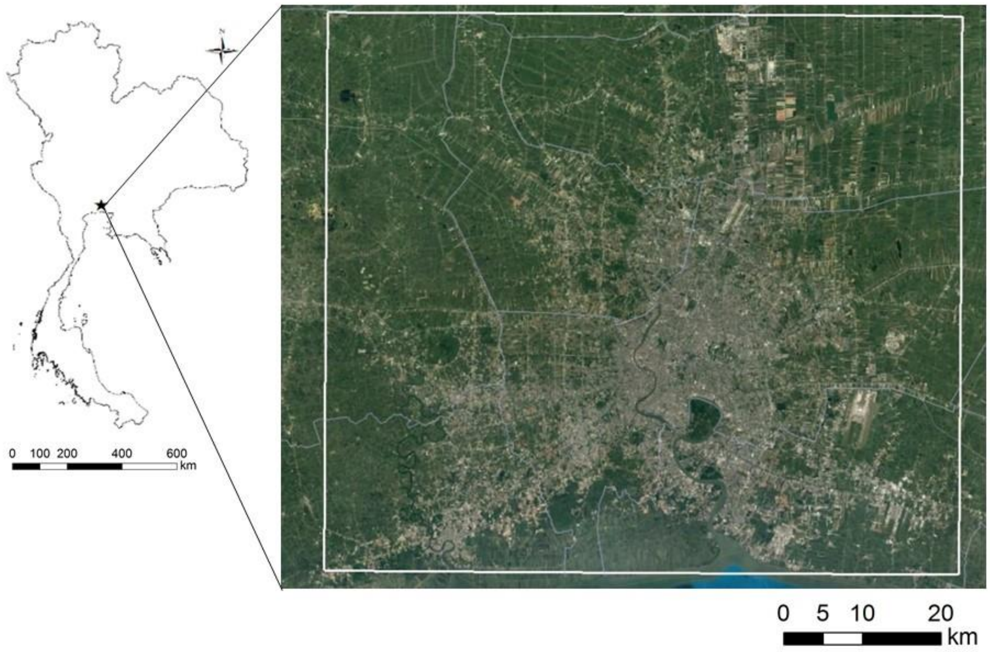

Figure S5.1: Map of Thailand showing the location of Bangkok and an inset map of the Bangkok region (using aerial imagery taken in March 2018). The rectangle with grey border delimits the 5,600 km^2 (70 km × 80 km rectangle) study region.

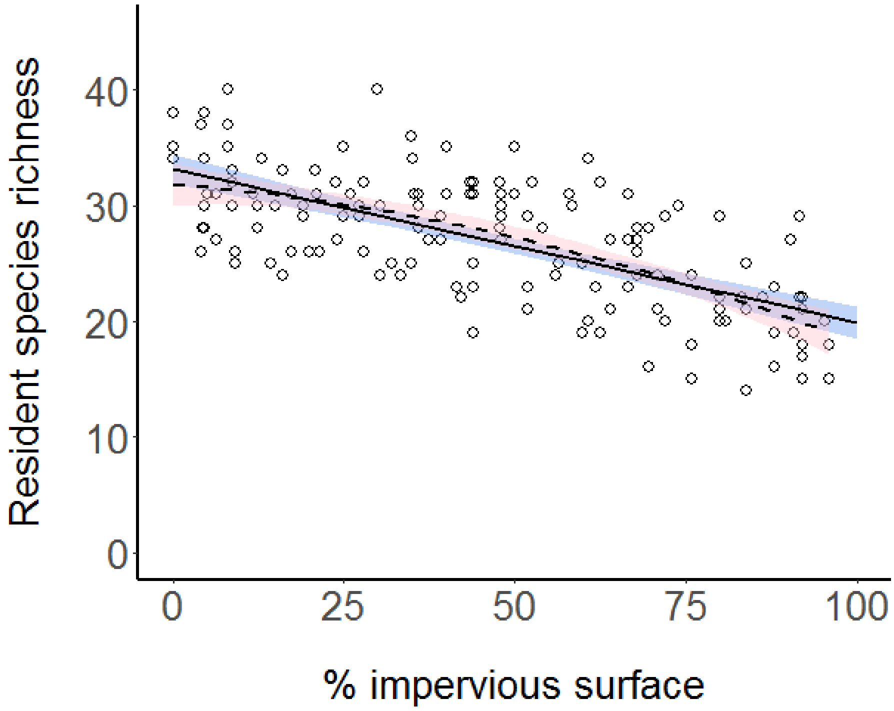

Figure S5.2: Urbanization gradient on resident species richness with fitted lines indicate predicted values comparing between linear model (solid line and blue shade) and quadratic model (dashed line and pink shade) and shades represent confident intervals.

CHAPTER SIX

General discussion

6.1 Bangkok urbanisation in the 21st century

This thesis investigates the impacts of urbanisation in Bangkok on landcover transformation during the 21st century and its implications for tropical urban biodiversity and ecosystem services. This focal Bangkok study region was delimited as 70 km × 80 km grid (5,600 km^2) covering Metropolitan Bangkok and parts of the surrounding provinces. During ~2004 to ~2018, Bangkok region has undergone intense urban development which resulted in an estimated ~487 km^2 of additional impervious surface cover and an estimated loss of ~540 km^2 of vegetation. These change are probably ultimately driven by the increase in the region's human population size from 9.6 million inhabitants in 2004 to 10.9 million in 2018. There was a significant increase of tree cover, potentially as a results of growth of street trees established as part of a planting program in the 1990s (Thaiutsa *et al*., 2008), which could provide some mitigation for urbanisation impacts on biodiversity and people (see section 6.5). This novel urban greenspace may not, however, provide equivalent ecosystem services and functions to the original vegetation cover (Wang *et al*., 2019). Nearly half of the sampling cells that were urbanised in ~2004 (equating to an area of ~761 km^2) experienced urban densification, in which total vegetation cover was reduced by approximately 18.1% (equating to an area of ~137.8 km^2) creating areas with some of the smallest amounts of vegetation. This thus challenges urban planners and policy makers promoting a compact city development approach (in order to reduce urban land expansion as it will in turn reduce the environmental quality in the densified urban areas.

6.2 Tropical cities as a biodiversity hotspot?

Bangkok is located within the Indo-Burma biodiversity hotspot (Myers *et al*., 2000). Despite a substantial number of 162 tree, 142 bird, and 4 small arboreal mammal species (from the squirrel and tree-shrew groups) detected during my study, these numbers of species were much lower than those in more natural settings (e.g. Khao Yai National Park: 204 tree species; Brockelman *et al*., 2011 and 329 bird species; Round *et al*., 2011, and 7 small arboreal mammal species; Brockelman *et al*., 2011). Similarly, bird and small arboreal mammal species richness in this study represent merely approximately one-third and half, respectively, of the larger species pool of the lower central plains of Thailand (412 bird species; Round and Gardner, 2008, and 7 small arboreal mammal species; Francis, 2017). Extremely low numbers of mammalian species in Bangkok may support the suggestion that mammals tend to be more susceptible to urbanisation than other taxa (McKinney, 2002). Unfortunately, there is a lack of previous survey that used the equivalent systematic sampling design to enable assessment of temporal changes in biodiversity due to the increasing urbanisation in the Bangkok region. The data that I collected does, however, provide a suitable base-line for future monitoring.

My results provide some clues that there is a considerable variation in the proportion of native/non-native species across taxonomic groups in a tropical urban ecosystem. Tree assemblages in Bangkok tend to be dominated by non-natives, which is consistent with results from several cities in temperate (e.g. Schlaepfer *et al*., 2020) and tropical regions (e.g. Nagendra and Gopal, 2011). This may relate to human planting choices towards their function and service provision towards people, especially towards trees that provide foods for people which is often a key consideration in tropical cities (e.g. Jaganmohan *et al*., 2012). On the other hand, the dominance of native avian and mammalian species detected in this study contrast to several studies from temperate regions that emphaise a high proportion of non-native species in the urban areas (e.g. for birds; Lazarina *et al*., 2020; Marzluff, 2001, for mammals; Müller *et al*., 2013). The dominance of native fauna may arise partially because some of these native species have a high competitive ability. Indeed, some of these species are highly invasive outside their native range [e.g. such as common myna *Acridotheres tristis* (e.g. Colleony *et al*., 2020), Scaly-breasted Munia *Lonchura punctulata* (e.g. Conn *et al*., 2017) and *Callosciurus* spp. (e.g. Adriaens *et* al., 2015; Oshida *et al*., 2007)] and may be able to outcompete and potential non-native species with similar ecological niches before they become established in urban Bangkok. Combination of non-native flora and native fauna in Bangkok's tropical urban ecosystem may also suggest that native faunal biodiversity can co-occur with a predominantly non-native flora, leading to further questions reagarding the validity of conservation policies that prioritise native vegetation. Further research that uses the data I collated to assess how bird and small arboreal mammal communities respond to the relative abundance of non-native tree species would be useful and shed further light on these questions.

Relatively few species detected in this study are species of conservation concern (i.e. IUCN red lists; Table S6.1), with 18 tree species (11.1% of the 162 species detected) and 6 bird species (4.2% of the 142 species detected). None of the mammalian species detected in this study are on IUCN red list, despite a detection of footprints of Smooth-coated Otter *Lutrogale perspicillata* (Vulnerable; de Silva *et al*., 2015) at one sampling site. These results suggest that potential of urban areas in a rapidly growing tropical mega-city to harbour species of conservation concern is generally limited**.** However, whilst most of species of conservation concern are extremely rare across all survey sites (13(72.2%) tree species and 5(83.3%) bird species of conservation concern were found in less than 5% of total sampling cells; Table S6.1), some species are surprisingly fairly common. These include, for example, endangered Burmese Rosewood *Pterocarpus indicus* (recorded in 50% of the total sampling cells; Table S6.1a) which it was also one of the most abundant street trees in Bangkok (Thaiutsa *et al*., 2008). This supports growing evidence that endangered species conservation can occur outside of species' native ranges (e.g. Sophonrat *et al*., 2019). However, continued urban expansion may further limit the conservation value of Bangkok for some of these species. As an example, the near-threatened Asian Golden Weaver *Plocues hypoxanthus* was detected in nearly 20% of sampling cells, substantial reduction of grassland cover, which is a vital habitat for this species and other grassland specialists that are not yet on the IUCN red lists, generates uncertainty regarding the ability of the Bangkok region to support such species in the future. Consequently, these findings highlight the importance of urban areas when setting regional and global conservation agendas (Ives *et al*., 2006), both in terms of assessment of species that tend to be eliminated as expansion of urban lands into their habitats and conservation outside species' native ranges.

6.3 Species richness along an urbanisation gradient in a tropical mega-city

My thesis contributes to the limited understanding of biodiversity patterns along an urbanisation gradient in the understudied tropical region of southeast Asia. The spatial pattern of biodiversity along Bangkok's urbanisation gradient did not follow the proposition that species richness peaks at the intermediate levels of urbanisation intensity that is typically the case in temperate regions (Crooks *et al*., 2004; McKinney, 2008; Vignoli *et al*., 2013). This supports the growing evidence indicating considerable variations in the shape of the relationships between species richness and urbanisation intensity when comparing tropical and temperate regions. Furthermore, the spatial species richness patterns observed in my study varied between taxa and do not always match those documented in other tropical cities. For example, tree species richness at the randomised survey points was maintained across the gradients, and exhibited a slight linear increase at the wooded locations. This contrasts with the unimodal pattern reported in Mexico cities (Ortega- Álvarez *et al*., 2011). Similarly, the linear decline of avian species richness along the urbanisation gradient in Bangkok may be consistent with some other tropical cities (e.g. Naintal (India) — Bhatt and Joshi, 2011; Palmas (Brazil) — Reis *et al*., 2012; Lapaz (Bolivia) and Osorno (Chile) — Leveau *et al*., 2017), but the unimodal pattern has also been reported (Leveau, 2019). Consequently, my results suggest that spatial pattern in species richness along the gradient of urbanisation intensity in the tropics tend to vary among locations and taxonomic groups rather than having a general pattern. My study provides evidence that could further understanding of the mechanisms underlining urbanisation impacts on biodiversity, which is crucial for effective design of urban planning policies to promote conservation.

6.4 Human disturbance and predation pressures

My study uncovers negative influences of human disturbance on avian species richness and squirrel abundance. This complicates urban management and planning decisions that attempt to balance i) reduction of human impacts to achieve biodiversity conservation goals and ii) enhancing residents’ access to urban greenspace to gain benefits from engaging with nature. However, there were also variations in animals’ response to human disturbance, i.e. species richness of non-native birds showed a positive relationship with number of humans and no significant relationship was detected with the abundance of Northern Tree-shrew *Tupaia belengeri* and Finlayson’s squirrels *Callosciurus finlaysonii*. This may provide some clues that some species have higher ability to tolerate human disturbance and take advantage from human subsidies, indicating influences of human disturbance on modifying species composition of urban wildlife assemblages by eliminating larger number of avoider species and facilitating a few exploiter species (*sensu* Blair, 1996).

Urbanisation profoundly alters predation pressure in a tropical mega-city by reducing indigenous predators and introducing free-ranging human companions such as cats *Felis catus* and dogs *Canis lupus familiaris*. Mammalian predators are more likely to be eliminated at the very beginning of the urbanisation process (McKinney, 2002), resulting in predators that were previously recorded in my study region, such as Jungle Cat *Felis chaus* (Gray *et al*., 2016) and Small Asian Mongoose *Herpestes javanicus* (Chutipong *et al*., 2016) now being absent or extremely rare. Rapters were also extremely rare, with only six species being detected in between 0.7%–4.7% of the total sampling grid cells during the study. This suggests that urban predation pressure in the Bangkok region is mainly contributed by free-ranging cats and dogs, as has been widely reported in other cities across the globe (e.g. for cats; Blancher, 2013; Loss and Marra, 2017, for dogs; Mella-Méndez *et al*., 2019; Soultan *et al*., In press). However, I found a limited evidence that these urban predation pressure can strongly adversely influence squirrel and tree-shrew population. However, there were marginally significant negative effects of free-ranging dogs on tree-shrew *T. belangeri* and Pallas's squirrel *C. erythraeus*. These results thus support to the growing but limited attention on such mammalian predators in the urban environment, especially in the tropical city such as Bangkok where the population size of feral dogs has risen rapidly due to the ineffective animal controls (Hemachudha, 2005; Kasempimolporn *et al*., 2011; Toukhsati *et al*., 2015). Further analyses on the impacts on other taxa (i.e. birds and reptiles) and experimental manipulation of feral population are thus required to minimise adverse impacts of tropical urban biodiversity and risks of transmission diseases (i.e. rabies — Hemachudha, 2005; Kasempimolporn *et al*., 2011).

6.5 Urban trees as a nature-based solution to improve quality of the urban environment

Although intense urbanisation in Bangkok has contributed to several environmental changes that reduce biodiversity and well-being of urban residents, the increase in tree cover in all areas except those undergoing densification suggests the potential to at least partially mitigate some of these urbanisation impacts. Whilst the importance of urban trees in improving urban environmental quality and sustainable urban development is now beyond question, it is interesting how these beneficial impacts are distributed across the urbanised landscape and the extent to which management and policies will help optimise and sustain their ecosystem service provision. My thesis suggests that the potential to retain wooded patches to support urban biodiversity is maximised in the highly urbanised locations (but see below for a discussion of recent trends). This biodiversity support function was emphasised in Chapter 5, which suggests the potential of woodland retention to enhance avian species richness was highest in the highly urbanised locations, although species richness still declined linearly as urbanisation increased. More importantly, my study also indicates that the proximity of randomly selected locations to the nearest wooded patch, rather than the largest patch of woodland within the grid cell, can enhance urban avian biodiversity. This thus suggests that, whilst opportunities to increase urban greenspace are limited by the availability and extremely high price of urban lands, retention of woodlands that are well-distributed, even if they small, will benefits urban avian assemblages.

Whilst my study used biomass of fruit trees as indicators of provisioning services of urban trees, such as human food production for people and for frugivorous birds, it may not sufficiently represent the actual contributions of urban trees to such ecosystem services. Firstly, environmental conditions in the urban areas are generally different from the natural conditions or the agricultural systems, which limit resource production. Further study that quantify the actual amount of ecosystem service provision (i.e. fruit abundance or biomass) is required to assess variation in production yield from urban fruit trees. Moreover, even if resources are produced they are not necessarily used — e.g. food produced in urban areas for people is often underutilised (Grafius *et al.*, 2020, personal observation), and in some urban areas there may be insufficient variety of abundance of birds to consume fruits or nots. Moreover, in some areas food provision of urban trees was dominated by relatively few species, indicating limited stability of food production throughout the year — limiting the potential benefits for specialists frugivores that require constant fruit supplies, and increasing the susceptibility of ecosystem services to future environmental instability. Management and implementation to optimise ecosystem service provision in urban areas thus needs to take into account not just the magnitude of ecosystem service provision but also accessibility, utilisation, and stability.

6.6 Congruence of the results and implications for urban planning and designs

The results from Chapters 3, 4 and 5 can be used to generate urban planning and design recommendations to improve urban biodiversity and ecosystem service provision. Achieving these twin goals is unlikely to be straightforward as the results from Chapter 4 indicate that native tree species richness is not strongly associated with the magnitude of some example ecosystem services provided by those trees. Similarly, when taking the divergent biodiversity metrics from each sampling location from each chapter (Chapter 3 — squirrel and tree-shrew abundance; Chapter 4 — tree species richness; Chapter 5 — bird species richness) and our measures of ecosystem service provision (from Chapter 4) we find negligible evidence for consistently strong positive associations between biodiversity and ecosystem service provision at either the random or woodland sampling points (Table S6.2). It is notable though that our biodiversity metrics do at least consistently significantly positively associate with carbon storage even if the strength of these relationships is somewhat limited (Table S6.2). We also find rather limited positive associations between our various biodiversity metrics (Table S6.2). Other studies report somewhat limited positive correlations between divergent biodiversity metrics due to taxonomic groups varying in their response to their habitat type and other landscape features (e.g. Grafius *et al*., 2019; Sattler *et al*., 2014), and between biodiversity and ecosystem service metrics (Harrison *et al*., 2016; Ziter, 2016). This highlights that one of the key challenges of managing urban areas is that optimal designs for one particular set of species or ecosystem services will inevitably be sub-optimal for other taxa or services. Urban green-sapce has long been recognised as multi-functional and the challenge is to find ways of changing its design that generate the optimal solution to balancing trade-offs between divergent biodiversity and ecosystem services outcomes. Even when positive correlations appear to arise between biodiversity metrics and ecosystem service provision these may not materialise in reality. As an example, we find a positive correlation between *Callosciurus erythraeus* abundance and human food production potential, but this could lead to a human-wildlife conflict especially in agricultural areas dominated by coconut farms and orchards. The form of perceived optimal solution will in part be dependent on the relative importance assigned to each of the biodiversity and ecosystem service outcome arising from urban design and planning decisions, which is ultimately a subjective decision.

6.7 What does the future hold for tropical urban ecosystems?

Recent growth in human population in the Bangkok region (from 9.4 million in 2000 to 10.9 million in 2020; Bangkok Metropolitan Administration, 2020) is projected to continue with the city expected to contain 11 million people by 2025 (Bangkok Metropolitan Administration; 2020). The adverse impacts that I document of urban expansion and densification are thus likely to continue, leading to further loss of ecosystem function and services. Although many of the adverse impacts of urbanisation on environmental quality and urban biodiversity can partially be mitigated by urban woodlands, these large wooded patches are under threatened by the ongoing urban development in this region. Contrasting with the patterns of increasing urban tree cover during ~2004 to ~2018 (see Chapter 2), 25 (16.7% of the total) of the sampled woodlands (i.e. those that were the largest patches of trees in the randomly selected grid cells) lost at least 80% of their wooded area between 2018 and 2021 — based on additional analysis of Google Earth imagery (Fig. 6.1). In most cases, these woodlands were replaced with impervious surface cover or transitioned to bare grand or construction site — suggesting that urban densification is continuing to impact woodland cover. Loss of these vital wooded areas will result in a further decline of ecosystem service provisioning, at least in terms of carbon storage potential, indicating unsustainable urban development in this region. Further work is needed to assess if particular types of woodland (e.g. those with a higher proportion of native species, or species with greater biodiversity support functions) are more likely to be lost than other woodland types.

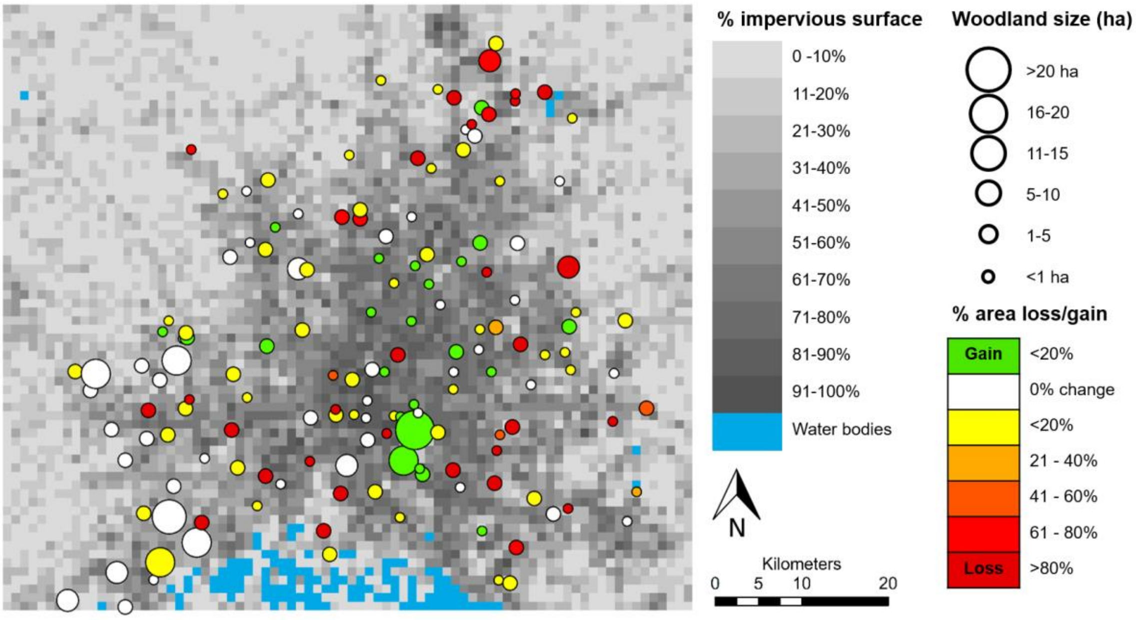

Figure 6.1: Landcover map of the Bangkok study region showing percentage impervious surface cover of the 5,600 1 km × 1 km grid cells in 2018 (shading) and the largest woodlands within each 150 1 km × 1 km randomly selected grid cells (circle) with size of the circle indicating woodland size (ha) and colour representing percentage of area lost during 2018 and 2021.

On the other hand, regulations that allow the use of trees as collateral for financial loans may help reduce tree removal and enhance tree planting particularly on private land. This may help reduce the dominance of non-native trees as over 90% of the eligible species in the current regulations are native to Thailand (BAAC, 2020). However, selection of these species was largely based on their timber value and, from the total 43 economic valuable species detected in this study, only 15 of them provide our focal ecosystem services (i.e. providing foods for people and frugivorous birds) other than contributing to carbon storage. There is thus a need to revise the eligible tree species based on their ecosystem service provisioning and resilience against future environmental instability — such as tree disease and climate change.

6.8 The next steps

Intense urbanisation is currently ongoing in the Bangkok region, with the impacts on landcover transformation varying between areas that are subject to expansion and densification processes. Whilst urbanisation intensity tends to have considerable impacts on biodiversity, especially for birds, there is a need to investigate the biodiversity consequences arising from different urbanisation processes (i.e. expansion and densification) using the current biodiversity and landcover classification data. Moreover, additional data collection in the next few years can enable analyses of temporal changes in biodiversity comparing between the effects of expansion and densification and also along the urbanisation gradient to further assess the ability of space-for-time substitution approach to predict changes in biodiversity in the Bangkok region. This will provide insights that inform urban planning decision to minimise urbanisation impacts on the region biodiversity.

Although my results underline the potential of woodland retention to moderate urbanisation impacts on avian biodiversity, this mitigation solution appear to be ineffective for non-breeding migratory species (see Chapter 5). Urbanisation in this region may thus interrupt migratory birds along the East Asian-Australasian flyway, which is of major conservation importance (BirdLife, 2015; Yong *et al.*, 2015). There is thus an urgent need for further research to explore urban habitat restoration mechanisms that can enhance the capacity of urban areas to support migratory species.

My study has underlined the potential of the current regulations that allow the use of tree as a valid collateral for financial loans to reduce tree removal and enhance tree planting in the urban areas. Long term empirical studies are required to asses i) if trees that are used as collateral are less likely to be removed compared to otherwise similar trees that are not used as collateral ii) if such a scheme can significantly stimulate tree planting, and iii) if resultant increases in tree cover from this scheme can modify species composition of urban tree assemblages in Bangkok by increasing the proportion of native trees.

Furthermore, my thesis supports evidence that human infrastructure (i.e. bridge) in urban Bangkok can increase the permeability of a geographic barrier separating two allopatric *Callosciurus* squirrel species and consequently induce hybridisation (i.e. Chao-Praya river; Boonkhaw *et al*., 2017). However, further studies that use genetic markers or sequencing to assess inter-specific gene flow is required. This is important both in terms of management to conserve genetic diversity and provision of better understanding of evolutionary processes in urban ecosystems.

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6.9 Supplementary materials

Table S6.1 Species of conservation concern for (a) trees and (b) birds detected in the Bangkok region in this study. Global IUCN Red List category follows IUCN (2021). For trees, species were indicated as native/non-native to Thailand based on Thai Plant Names (Smitinand, 2014), distribution maps from Plants of the World (POWO, 2019) and Agroforestree Database (Orwa *et al*., 2009). For birds, extent of occurrence (based on breeding/resident range with asterisk indicating non-breeding range) follows BirdLife (2019) and the native/non-native status to the Bangkok region follows Round and Gardner (2008). Occupancy (%) indicate occurrence of species in at least one sampling point in grid cell (either randomised or woodland point).

a) Trees

Scientific name	Global IUCN Red List category	Native to Thailand	Occupancy (%)
Pterocarpus indicus	Endangered	Native	50.00
Swietenia macrophylla	Vulnerable	Non-native	19.33
Terminalia ivorensis	Vulnerable	Non-native	17.33
Dimocarpus longan	Near-threatened	Non-native	8.00
Dipterocarpus alatus	Vulnerable	Native	5.33
Aegle mamelos	Near-threatened	Non-native	2.67
Pterocarpus macrocarpus	Endangered	Native	2.00
Shorea roxburghii	Vulnerable	Native	2.00
Afzelia xylocarpa	Endangered	Native	1.33
Guaiacum officinale	Endangered	Non-native	1.33
Hopea odorata	Vulnerable	Native	1.33
Aglaia edulis	Near-threatened	Native	0.67
Araucaria cookii	Endangered	Non-native	0.67
Dalbergia cochinchinensis	Vulnerable	Native	0.67
Gustavia gracillima	Vulnerable	Non-native	0.67
Pterospermum littorale	Endangered	Native	0.67
Swietenia mahagoni	Near-threatened	Non-native	0.67
Vatica diospyroides	Endangered	Native	0.67

b) Birds

Scientific name	Global IUCN Red List category	Native to Bangkok	Occupancy (%)	Extent of occurrence (1000 km^2)
Plocues hypoxanthus	Near-threatened	Native	19.33%	3400
Lonchura oryzivora	Endangered	Non-native	1.33%	148
Palaeornis eupatria	Near-threatened	Non-native	1.33%	8920
Anhinga melanogaster	Near-threatened	Native	0.67%	19400
Psittacula alexandri	Near-threatened	Native	0.67%	9400
Threskiornis melanochephalus	Near-threatened	Native	0.67%	22300, 17900*

Table S6.2 Correlations between response variables across three data chapters — i.e. squirrel and tree-shrew population (maximum abundance of *Tupaia belangeri* (TBP), *Callsciurus finlaysonii* (CFP), *C. erythraeus* (CEP), *C.* hybrid (CHP)), tree species richness (TSR), bird species richness (BSR), carbon storage of urban trees (t/ha; CBS), human food production potential of urban trees (t/ha; HFP), biodiversity supports of urban trees — i.e. biomass of fruit trees for frugivorous birds (t/ha; BDS), and economic value of urban trees (£; ECV). Asterisks indicate significant levels of the correlation (*P* < 0.001 ***; 0.01 **; 0.05 *).

	Pearson's correlation test results									
	Squirrel and tree-shrew abundance				Species richness		Ecosystem service provision			
	TBP	CFP	CEP	CHP	TSR	BSR	CBS	HFP	BDS	ECV
Randomised points										
TBP	-									
CFP	0.09	-								
CEP	0.32***	0.04	-							
CHP	0.24**	0.08	0.30***	-						
TSR	0.49***	0.25**	0.25**	0.18*	-					
BSR	0.31***	-0.07	0.27***	0.13	0.14	-				
CBS	0.50***	0.27***	0.33***	0.29***	0.69***	0.24**	-			
HFP	0.41***	0.08	0.43***	0.27**	0.41***	0.23**	0.54***	-		
BDS	0.05	0.15	-0.05	0.01	0.23**	-0.06	0.50***	0.07	-	
ECV	0.42***	0.24**	0.16	0.26**	0.50***	0.21**	0.64***	0.16*	0.02	-
Woodland points										
TBP	-									
CFP	0.19*	-								
CEP	0.22**	-0.31***	-							
CHP	0.03	-0.07	0.20*	-						
TSR	0.13	0.40***	-0.02	0.08	-					
BSR	0.07	-0.22**	0.22**	0.02	-0.30***	-				
CBS	0.23**	0.36***	0.17*	0.10	0.27***	-0.05	-			
HFP	0.21**	-0.16*	0.39***	0.07	-0.11	0.08	0.46***	-		
BDS	0.02	0.24**	-0.17*	0.02	0.37***	-0.19*	0.20*	-0.09	-	
ECV	0.09	0.58***	-0.18*	0.03	0.31***	-0.13	0.65***	-0.21**	0.09	-