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Species richness and ecosystem services of tree assemblages along an urbanisation gradient in a tropical mega-city: Consequences for urban design

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A B S T R A C T

We assess how tree species richness and ecosystem services vary along a tropical urbanisation gradient in a rapidly expanding mega-city (Bangkok, Thailand). We conduct tree surveys in 150 1 km cells selected by random stratification across an impervious surface cover gradient. 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 (production of food for frugivorous birds), and iv) economic value (assessed using regulations for using trees as collateral for financial loans). Surveys detected 162 species (99 natives) indicating substantial species loss relative to nearby natural forests. Despite this, and contrasting with typical patterns in temperate cities, tree species richness (including of natives) and ecosystem service provision is relatively stable across the urbanisation gradient. This finding has two important consequences. First, growing cities through high intensity developments that require less space may benefit regional biodiversity without compromising ecosystem services. Second, even the typically very small woodlands present in highly urbanised locations contribute to supporting biodiversity and providing ecosystem services; thus such woodlands require protection. Species richness is not strongly positively associated with most of our focal ecosystem services. Urban planners must therefore pay attention to both biodiversity and ecosystem services as these do not automatically accrue from each other, partly because non-native species contributed substantially to most ecosystem services except biodiversity support. Finally, trees provide substantial value as collateral for financial loans (averages of £643 ha at random locations and £2282 ha in wooded locations). Policies promoting such valuations may reduce tree removal and encourage tree planting, but the list of eligible species warrants revision to include additional species that enhance biodiversity support, ecosystem services, and resilience against future environmental instability.

1. Introduction

Trees are a key component of urban biodiversity that deliver numerous cultural, regulatory and provisioning ecosystem services that enhance urban residents' quality of life and support additional biodiversity. 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 contribute to provisioning services by providing 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 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).

Abbreviations: CS, Carbon storage; HFP, Human food production; BDS, Biodiversity support; ECV, Economic value.

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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 surfaces, i.e., buildings, roads, and other sealed surfaces, 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) how 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. This approach is a useful tool for understanding interactions between urban development and the structure and function of ecological systems that can inform urban planning and management (McDonnell and Hahs, 2008). We use these focal ecosystem services as examples of a range of ecological services and functions but acknowledge that other ecosystem services, especially cultural ones, are important in urban areas. 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 south-east Asia (Xu et al., 2019).

2. Methods

Our sampling design is explained in full in Thaweepworadej and Evans (In press).

2.1. Study area and selecting survey points

We delimited a 5600 km^2 area (1400 2 km × 2 km grid cells) centred on central Bangkok and covering the wider region (Fig. S1). The region started to urbanise in the 16th Century, and does not contain remnants of the original forest cover; all vegetation is planted or is secondary growth arising from natural regeneration. 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. 1a). We classified each 1 km × 1 km grid cell as one of ten urbanisation intensity bands based on percentage green-space 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-space category, resulting in a total of 150 sampling grid cells (Fig. 1b; this approach and use of different spatial scales to define an urban region and select grid cells follows Bonnington et al., 2014).

2.2. 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. 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

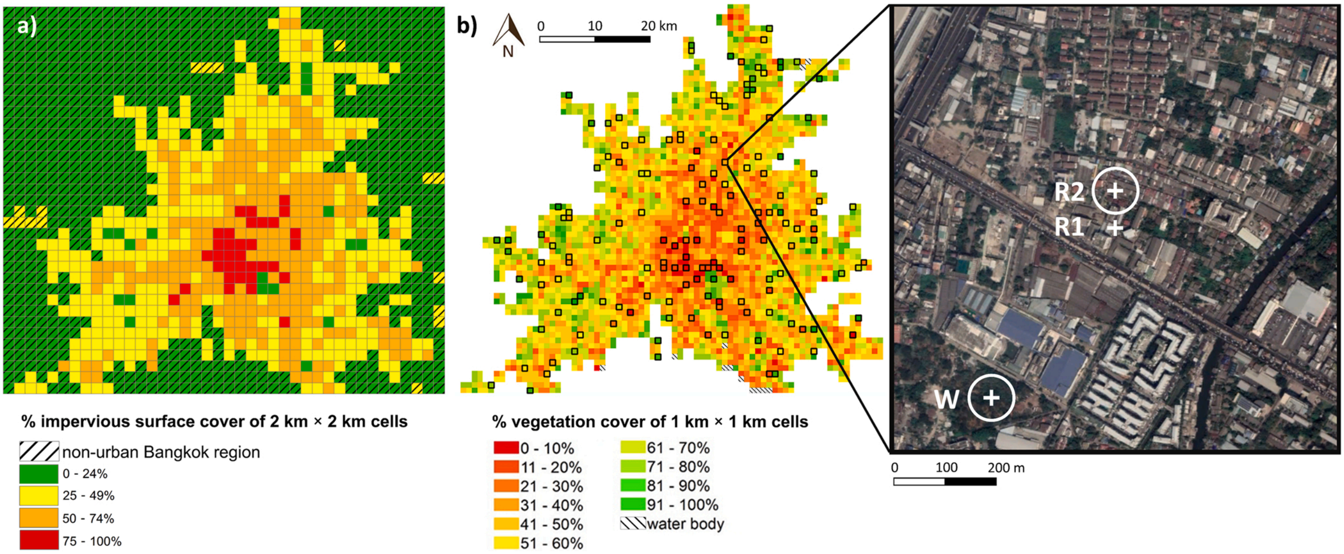

Fig. 1. a) land cover map of the Bangkok study region showing percentage impervious surface cover of 2 km × 2 km grid cells used to define the study region. Grid cells with ≥ 25% impervious surface cover that were isolated from the main urban region were considered to be part of other urban settlements. 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.

sampling point. There is a trade-off between the size threshold for incorporating trees into our surveys and the number of survey locations from which data can be obtained. Biomass is disproportionately accumulated in larger trees (Nowak, 1994), and in urban areas the number of trees within a given size category, or biomass stored within such trees, is positively correlated with the number of trees/biomass stored in trees in other smaller size categories (Morgenroth, Nowak, and Koeser, 2020). We thus sampled all trees located within this plot, i.e. their trunk's centre was within the plot, with a DBH ≥ 25 cm to generate an index of tree biomass across the urbanisation gradient. Trees were identified to species and their DBH recorded to the nearest 1 cm and height recorded to the nearest 0.1 m 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 S1).

2.3. *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 (Eq. 1 below) developed for tropical moist forests by Chave et al. (2005); this follows methods used in other tropical cities with similar climates to Bangkok (e.g., Khadanga and Jayakumar, 2018; Ngo et al., 2013):

$$\mathrm{AGB} = 0{\cdot}0509\rho\mathrm{DBH}^2\mathrm{H} \tag{1}$$

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 S1). 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), Eq. 2.

$$\mathrm{BGB} = 0{\cdot}489\mathrm{AGB}^{0.089} \tag{2}$$

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.

2.4. *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 S1), primarily fruits (e.g., mango *Mangifera indica*, tamarind *Tamarindus indica*) or seeds (i.e., coconut *Cocos nucifera* and tal palm *Borassus flabellifer*). The yield of such products is strongly correlated with tree size (Chapman et al., 1992) and we summed the AGB of focal species as an index of potential human food production (HFP).

2.5. *Biodiversity support function — frugivorous birds*

Our biodiversity support index focuses on birds as they are one of the most obvious forms of urban biodiversity to the general public with notable cultural value (Echeverri et al., 2021; Hedblom et al., 2017), and there is sufficient quality and quantity of data documenting the ability of tree species to provide food for 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).

2.6. 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 $V = 0.0002DBH^{2.3162}$ (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).

2.7. Data analysis

All analyses were performed using R version 4.1.2 (R Core Team, 2021).

We quantified how tree species richness changes along the urbanisation gradient using generalised linear models ('glm' function in *stats* package) 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 S2). 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 I's values were low (≤ 0.04) but significant ($P < 0.05$) in models of total and native species richness at the randomised points (Table S3). 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). 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 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 S5). 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 S6) 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 ecosystem 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 I's tests detected significant spatial autocorrelation in models for HFP with total and native species richness (Table S7). 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 S8), 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.

3. Results

3.1. Tree assemblage structure

Our surveys documented 7633 trees, from 162 species (99 natives) and 48 families (Table S1, S9). Most species were very rare with 113 represented by < 20 individuals (Table S9). 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, whilst white leadtree *Leucaena leucocephala* was the commonest species at the woodland points, both are non-natives (Table S1).

3.2. 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 1; Fig. 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 between 4.0% and 5.4%; Table 1; Fig. 2).

3.3. 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 S10). Total CS was not significantly associated with urbanisation intensity at randomised (Table 2) and woodland points (Table 3). CS in native species was positively, and linearly, associated with urbanisation intensity in the woodland points (Table 3; Fig. 3d), but not the randomised ones (Table 2). CS in non-native trees in the randomised points declined linearly with increasing urbanisation intensity (Table 2; Fig. 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

Table 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

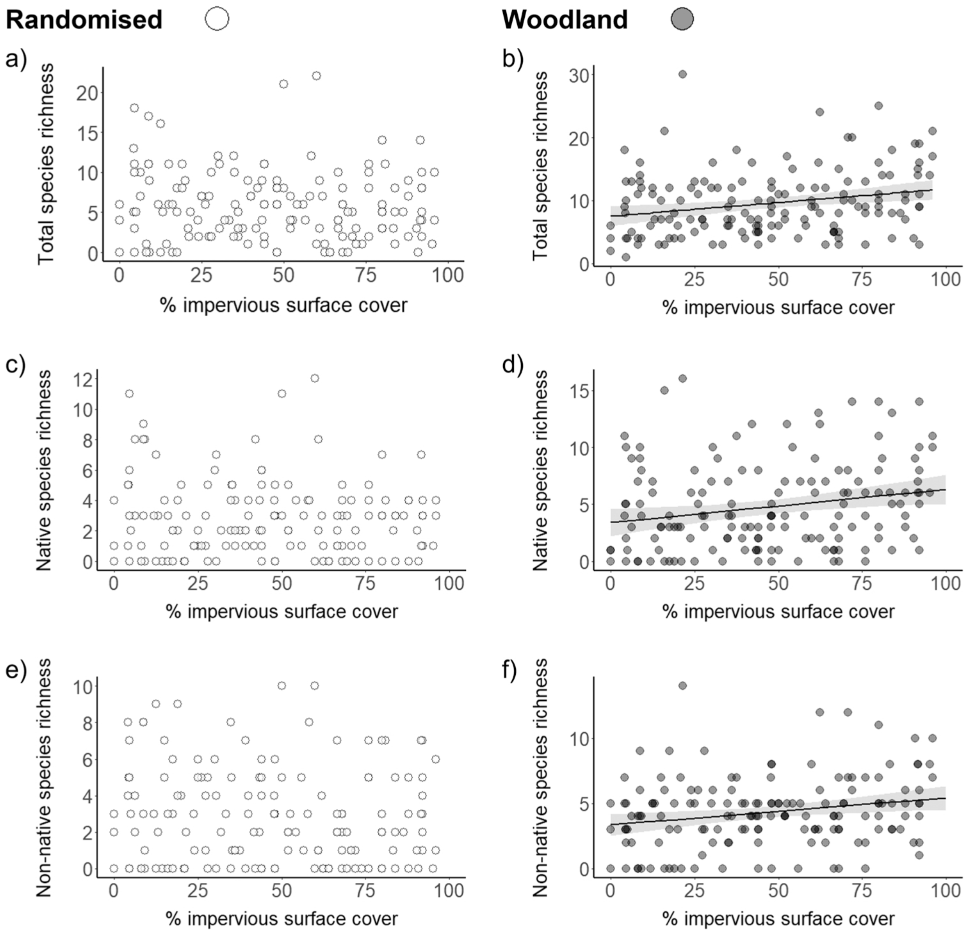

Fig. 2. Relationships between (a and b) total, (c and d) native, and (e and f) non-native species richness (respectively at the randomised and woodland points) and percentage impervious surface cover. Fitted lines indicate predicted values, with shading indicating 95% confidence intervals, from generalised linear models reported in Table 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.

contributing 92.2%; Table S10). Total HFP and that from non-native trees declined linearly with urbanisation intensity in the randomised points (Table 2; Fig. 3b, c), but was not significantly associated with urbanisation intensity at the woodland points (Table 3). HFP of native trees was not significantly associated with urbanisation intensity at either the randomised (Table 2) or woodland points (Table 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 S10). Total BDS was not significantly associated with urbanisation intensity at the randomised points (Table 2), but it increased linearly with urbanisation intensity at the woodland points (Table 3; Fig. 3e). BDS of native trees increased linearly with urbanisation intensity at the woodland points (Fig. 3f) but was not significantly associated with urbanisation intensity at the randomised points (Table 2). BDS of non-native trees was not significantly associated with urbanisation intensity in either the randomised (Table 2) or woodland points (Table 3).

Table 2
Ecosystem services metrics, i.e., carbon storage (CS; t/ha), human food production (HFP; t/ha), biodiversity support (BDS; t/ha), and economic 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	$-2.3e^{-4} \pm 0.001$	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	$-1.6e^{-4} \pm 0.001$	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	$-6.7e^{-5} \pm 0.001$	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	$1.1e^{-4} \pm 4.8e^{-4}$	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	$1.1e^{-4} \pm 8.1e^{-5}$	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	$2.2e^{-4} \pm 4.6e^{-4}$	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	$3.1e^{-4} \pm 0.003$	0.928		
	Quadratic	0.34	482.91	-0.009 ± 0.013	0.515	$9.5e^{-5} \pm 1.4e^{-4}$	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 3
Ecosystem services metrics, i.e., carbon storage (CS; t/ha), human food production (HFP; t/ha), biodiversity support (BDS; t/ha), and economic 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	$7.5e^{-5} \pm 0.002$	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	$-2.9e^{-4} \pm 0.001$	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	$-3.1e^{-4} \pm 0.001$	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

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 S10), whilst at the woodland points there was no significant difference in the contributions of native and non-native trees (Table S10). Total ECV was not significantly associated with urbanisation intensity at the randomised points (Table 2), but increased linearly with urbanisation intensity at the woodland points (Table 3; Fig. 3g). Similarly, ECV of native trees increased linearly with urbanisation intensity at the woodland points (Table 3; Fig. 3h) but was significantly associated with urbanisation intensity at the randomised ones (Table 2). There was no significant relationship between ECV of non-native trees and urbanisation intensity in either randomised

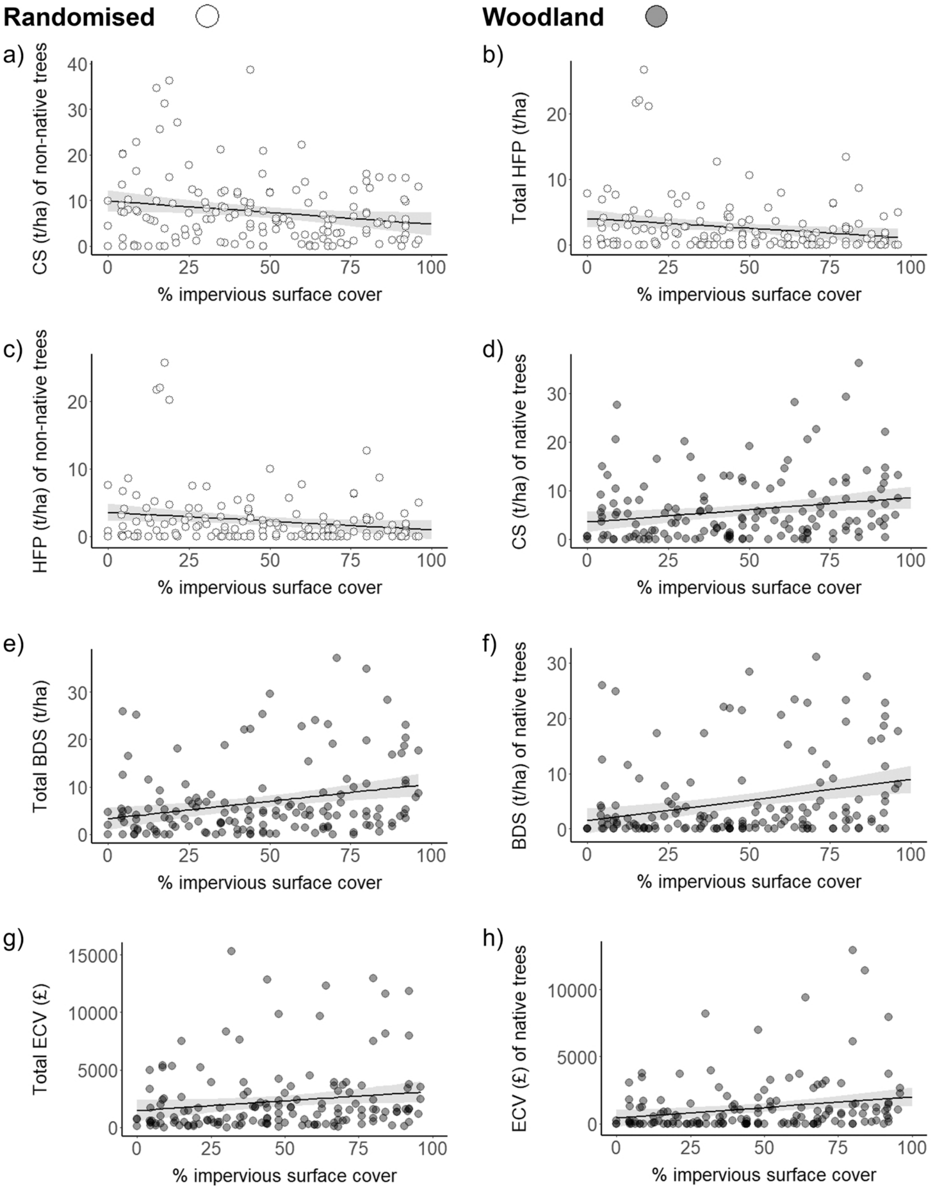

Fig. 3. Plots of significant relationships between ecosystem service provision (CS, carbon storage; HFP; human food production potential; BDS, biodiversity support; ECV, economic value) and percentage impervious surface cover at the randomised (white circles, a-c) and woodland points (grey circles, d-h). Fitted lines indicate predicted values and shading indicates 95% confidence interval derived from the generalised linear models in Table 2 (randomised points).

(Table 2) or woodland points (Table 3). In all relationships, explanatory power was consistently low (variance-function-based r^2 between 2.8% and 4.9%).

3.4. 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. 4a; variance-function-based partial r^2 40.7%) and linearly at the woodland points (Table 4, Fig. 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. 5a) and along an accelerating quadratic curve at woodland points (Table 5, Fig. 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. 4c), explaining c. 16.5% of the variation, whilst no significant relationship was detected at the woodland points (Table 4, Fig. 4d). HFP increased linearly with ln-transformed native species richness at the randomised points (Fig. 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 5, Fig. 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 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. 4a; variance-function-based partial r^2 4.7%) and woodland points (Table 4; Fig. 4f; variance-function-based partial r^2 12.1%). Similarly, BDS increased linearly with ln-transformed native species richness in both randomised (Fig. 5e) and woodland points

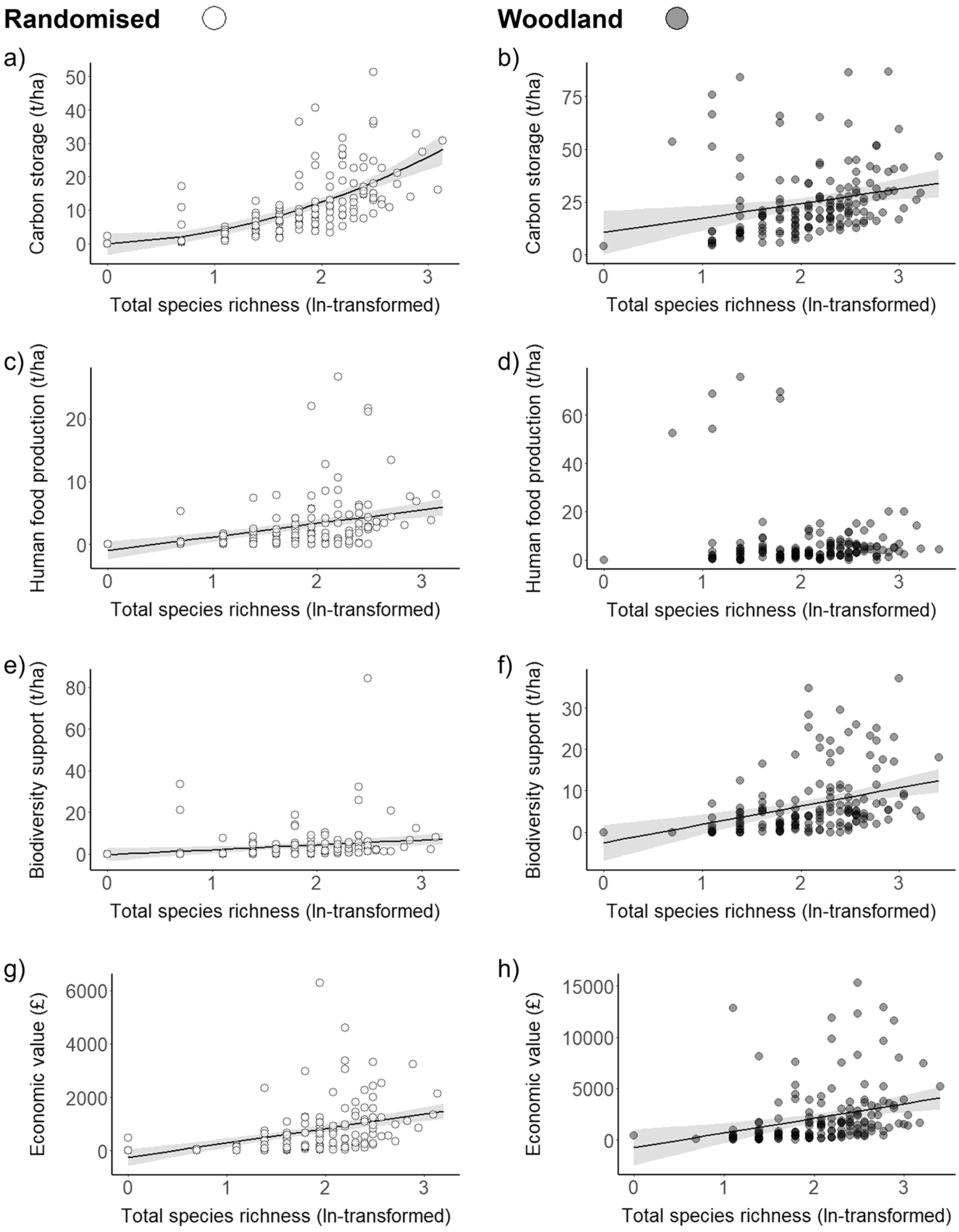

Fig. 4. Relationships between ecosystem service provision and total species richness (ln-transformed) at the randomised (white circles) and woodland points (grey circles). Fitted lines indicate predicted values and shading indicates 95% confidence intervals derived from the best fitting multiple regression models presented in Table 4. Human food production at the woodland points was not significantly associated with total species richness so no fitted line is exhibited.

(Table 5; Fig. 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 summed to £ 96,507 across randomised points (on average £643.4 ha), and £ 342,232 across woodland points (average £2281.5 ha). ECV increased linearly with ln-transformed total species richness at randomised (Fig. 4g; variance-function-based partial r^2 20.6%) and woodland points (Table 4; Fig. 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 5; Fig. 5h; variance-function-based partial r^2 9.9%).

4. Discussion

4.1. Study limitations

Tree biomass was estimated following the methodology typically used in tropical cities (e.g., Khadanga and Jayakumar, 2018; Ngo et al., 2013). This will accurately capture spatial variation in biomass due to the occurrence of substantial variation in tree numbers and size across survey sites. We do, however, advocate the development of urban specific allometric equations that are required for improving the accuracy of tree biomass calculations in tropical cities. Our analyses of biodiversity support focused on provision of food for frugivorous birds, the majority of such resources are insect pollinated, thus this metric also captures availability of floral resources for pollinators provided by trees. Research is, however, needed to assess how urbanisation influences the support that trees provide to other forms of biodiversity, such as herbivorous insects and fungi.

Table 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 (ln-transformed)				
								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

4.2. Impoverished urban tree communities and contributions of non-native species

Species richness is substantially lower than that in nearby natural forests - compare the 99 native and 162 total tree species found in our 230 ha cumulative survey area, with 204 species found in just a 30 ha study plot in Khao Yai National Park located c. 80 km from Bangkok (Brockelman et al., 2011). This contrasts with temperate studies that typically report much greater species richness in urban than natural forests (e.g., Gillespie et al., 2017). The extreme rarity of most tree species in our survey further emphasises that a small number of species contribute substantially to ecological functions and ecosystem service provision.

The numerical dominance of non-native trees confirms that tropical urban tree assemblages are typically dominated by non-native species (e.g., de Souza et al., 2020). It is thus unsurprising that non-native species contributed significantly more than natives to carbon storage and provisioning of human food. Approximately a quarter of the species in our study provide food for people, with the commonest species being non-native, such as mango (Table S1), also confirming that tree species composition in tropical cities is often driven by exotic fruit trees (e.g. Jaganmohan et al., 2012), with mango often being particularly dominant in supporting urban food security (e.g. Panyadee et al., 2016). 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 (Freitas et al., 2020; Threlfall et al., 2016).

4.3. 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

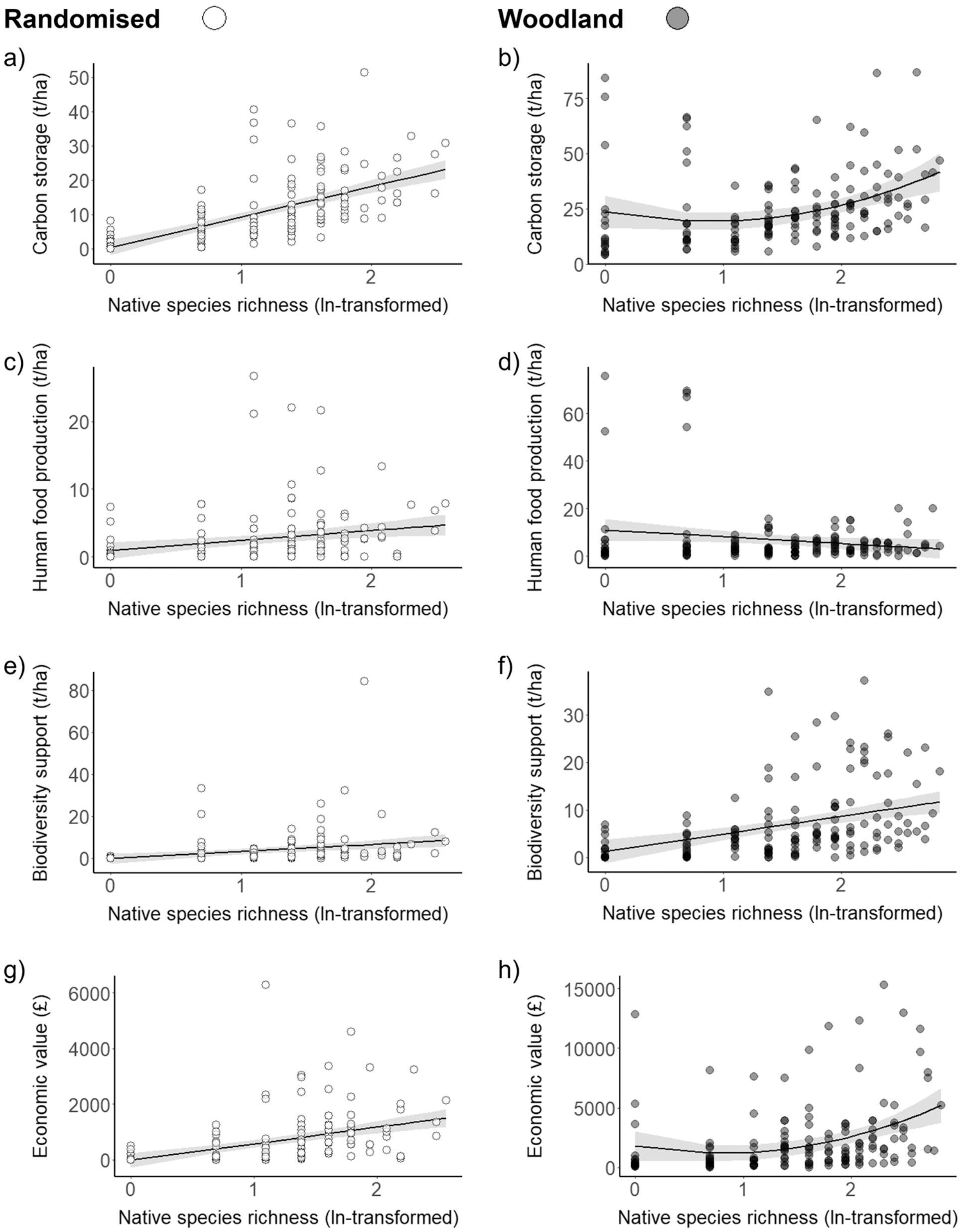

Fig. 5. Relationships between ecosystem service provision and native species richness (ln-transformed) at the randomised (white circles) and woodland points (grey circles). Fitted lines indicate predicted values and shading indicates 95% confidence intervals derived from the best fitting multiple regression models presented in Table 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.

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. 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. Notably, these patches also make substantial contributions to supporting avian biodiversity in Bangkok, including in highly urbanised locations (Thaweepworadej and Evans, In press). The tree species richness pattern probably partially arises because the largest woodland patches in the less urbanised locations consist primarily of commercial plantations, especially coconut, that contain very few tree species, whilst in urban locations the largest patches of trees comprise a wider range of forest types.

4.4. *Ecosystem services along the urbanisation gradient*

Provision of our focal ecosystem services (carbon storage (CS), human food provisioning (HFP), economic value (ECV) and biodiversity support (BDS)) 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). Our sampling protocols follow robust and standardised procedures and we do not believe these findings are driven by methodological artefacts although we encourage other researchers to assess if alternative measures of BDS follow similar

Table 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 (ln-transformed)				
								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**

patterns. CS 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 CS 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 CS in urban trees. The pattern that we document contrasts with observations from European temperate regions where CS peaks at intermediate urbanisation intensities (e.g., Larondelle and Haase, 2013) and temperate and subtropical Chinese cities where CS 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 CS 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, in domestic gardens can thus play 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 BDS, 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 BDS 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 the 148 species documented in nearby natural forests, i.e. Khao Yai (Kitamura et al., 2002) and in most locations only a few species (2.71 ± 0.12 se.) contributed to this service. 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.

ECV of urban trees (defined as collateral values for securing financial loans) was substantial, especially in wooded locations, but 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. It can be viewed as a form of an indirect payment for ecosystem service scheme although there is currently no clear link between the magnitude of payment (via increased access to loans) and the magnitude of service provision. As examples, all tree species detected in our survey will contribute to CS but only 43 of these can be used as collateral, similarly only seven species provide food for people and ten for frugivorous birds and can be used as collateral (Fig. S2a). There is thus a clear need to assess the effectiveness of the financial collateral scheme in determining landowners' 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 ECV.

4.5. Associations between tree species richness and ecosystem service provision

Associations between native species richness and provision of our focal ecosystem services, with the exception of CS at the woodland points, were not strongly positively correlated with each other. The lack of such relationships is not uncommon in either natural (van der Plas, 2019) or urban environments (Schwarz et al. 2017). Consequently, at the fine spatial scales relevant for urban planning, the 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 CS 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 (Winfree et al., 2015). That high level of ecosystem service provision is generated from a small number of tree species increased the vulnerability of future service provision to forthcoming 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).

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 through an indirect payment for ecosystems service scheme but the suite of eligible species needs adjusting 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.

CRediT authorship contribution statement

Phakhawat Thaweepworadej: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft preparation, Visualization. **Karl L. Evans**: Conceptualization, Methodology, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2022.127527.

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