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Squirrel and tree-shrew responses along an urbanisation gradient in a tropical mega-city – reduced biodiversity, increased hybridisation of *Callosciurus* squirrels, and effects of habitat quality

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Abstract

Urbanisation is rapidly transforming terrestrial environments, especially in the tropics. 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 rapidly urbanising tropical mega-city (Bangkok, Thailand) located within the Indo-Burma biodiversity hotspot. We used repeated point counts in 150 1 km cells, selected using random stratification across the urbanisation gradient. We quantified species responses to (i) urbanisation intensity (measured using impervious surface cover), (ii) environmental conditions (woodland quantity and quality, human disturbance and predation pressure from free-ranging cats and dogs) and (iii) urbanisation impacts on hybridisation between congeneric *Callosciurus* squirrels. Three of the six species from the regional species pool were extremely rare or absent within our study region (*Tamiops macclellandi*, *Callosciurus caniceps* and *Menetes berdmorei*). Of the three more widespread species (*Tupaia belangeri*, *Callosciurus finlaysonii* and *Callosciurus erythraeus*) only *C. finlaysonii* had a higher abundance in more urban locations. The increasing intensity of urbanisation has thus markedly reduced squirrel diversity and abundance, contrasting with the perception from temperate regions that squirrels typically tolerate urbanisation. Urbanisation is thus likely to have reduced important ecological functions provided by squirrels, such as seed dispersal. Models of species responses to environmental conditions suggest that improving habitat quality by increasing tree cover and diversity at local and landscape scales and reducing human disturbance and numbers of feral dogs would partially mitigating adverse impacts of urbanisation on tropical squirrels and tree-shrews. Urban infrastructure (bridge construction across the Chao-Praya River) appears to have increased the permeability of a geographic barrier that previously 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.

Introduction

The spatial extent of urban land is increasing across much of the globe, especially in tropical regions (Seto, Güneralp & Hutyra, 2012). The environmental change associated with this rapid urbanisation markedly alters the abiotic and biotic environment, creating strong selection pressures (Grimm et al., 2008; Parris, 2016). These environmental changes include urban heat island effects (Diamond et al., 2018), habitat fragmentation (Tian et al., 2011), altered predation pressure (such as from dogs *Canis lupus familiaris*; e.g.

Paker et al., 2014; Soultan et al., 2021, and cats *Felis canis*; e.g. Baker et al., 2008; Loss and Marra, 2017), and increased human disturbance (MacGregor-Fors and Schondube, 2011; Paker et al., 2014). Food availability also changes due to alterations in the composition and abundance of species at lower trophic levels (Rigacci et al., 2021; Schneiberg et al., 2020), and provision of supplementary food (Bonnington, Gaston & Evans, 2014; Galbraith et al., 2015).

The species composition of urban assemblages is thus very different from those occurring in nearby rural areas (McKinney, 2002; McKinney, 2008), although the magnitude

of divergence can depend on the amount of anthropogenic alteration of the focal rural habitat. 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).

Whilst a diverse range of mammals can occur in urban areas, certain taxa tend to dominate. Rodentia are, for example, amongst the top three mammalian orders represented in urban mammalian assemblages (Santini et al., 2019). One group of rodents – that is, squirrels – are present as native species in almost all urban locations across the globe, including North America (e.g. North American red squirrel *Tamiasciurus hudsonicus*; Mori, Zozzoli & Mazza, 2018), Europe (e.g. Eurasian red squirrel *Sciurus vulgaris;* Jokimäki et al., 2017), Africa (e.g. Cape ground squirrel *Xerus inauris*; Chapman, Rymer & Pillay, 2012), South America (e.g. Brazilian squirrel *Sciurus aestuans*; Fernandes et al., 2019), and Asia (*Callosciurus* spp.; Lekagul & McNeely, 1977). Squirrels play a major role in seed dispersal (Steele & Yi, 2020), and animal-mediated seed-dispersal is critical to the functioning of urban ecosystems (Gelmi-Candusso & Hämäläinen, 2019). The role of squirrels may be particularly important in urban areas due to the frequent rarity of other larger-bodied mammalian frugivores in highly urbanised areas (Tucker et al., 2021). In tropical settings tree-shrews (*Tupaia* spp.), whilst phylogenetically distinct, overlap with squirrels in their ecological functions (Langham, 1982; Lekagul & McNeely, 1977; Shanahan & Compton, 2000). Urban squirrels and tree-shrews both create significant urban management problems, many of which have economic costs, including gnawing electric wires (see Derbridge, Pepper & Koprowski, 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., 2021).

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 Eastern grey squirrels in urban environments in their native (e.g. Parker & Nilon, 2008; Koprowski, Munroe & Edelman, 2016) and non-native ranges (e.g. Bonnington, Gaston & Evans, 2014; La Morgia et al., 2017; Merrick, Evans & Bertolino, 2016). Far less attention has been paid to the urban ecology of tropical squirrel species, which is an important research gap, as these regions support large numbers of squirrel species and are currently experiencing the greatest urban expansion rates (Seto et al., 2012).

Our overall objective was to determine how the assemblages of squirrels and tree-shrews in the greater Bangkok region respond to urbanisation. We focused on Bangkok as it provides a useful case study of a rapidly urbanising tropical mega-city – that is, a city with over 10 million inhabitants (Estoque & Murayama 2015; Song et al., 2021) and is located in a biodiversity hotspot (Indo-Burma hotspot; Sodhi

et al., 2004). We started by assessing which of the species present in the wider region occur in urban locations and quantified for each of these species how their abundance varies along a gradient of urbanisation intensity. We then assessed 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 (Oshida et al., 2007; Timmins & Duckworth, 2008; Kuramoto et al., 2012; Balakirev & Rozhnov, 2019). There is increasing evidence that anthropogenic habitat alteration, which is most extreme under urbanisation, can break down ecological barriers that limit inter-specific gene flow thus promoting hybridisation (Lamont et al., 2003; Nolte et al., 2005; Grabenstein & Taylor, 2018). It is also plausible that urbanisation could reduce hybridisation rates by limiting the 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, Bettles & Roff, 2010), reptiles (Haines et al., 2016), and mammals (Frare et al., 2017).

Materials and methods

Study area and survey sites selection

Our survey design, field methods and analytical approach are based on Thaweepworadej & Evans (2022). Our focal study region consists of a 70 km × 80 km rectangle (5,600 km^2), centred on central Bangkok and covering parts of the surrounding provinces (Fig S1). In this study region, we constructed a grid of 1400 2 km × 2 km grid cells, and classified each cell's landcover using high-resolution Google Earth's imagery taken from 2017 to 2018 and a finer scale sampling grid comprising 100 uniformly distributed sampling point in each grid cell (based on Evans, Newson, and Gaston (2009)). Each sampling point was classified as (i) impervious surface cover, (ii) other non-vegetated land cover types (i.e. bare ground and construction sites), or (iii) trees and other vegetated land covers. 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., 2014), resulting in an urban study region of 2,658 km^2 (Fig. 1a).

In the urban study region, we used random stratification, achieved using 'sample_n' function (*dplyr* package; Wickham et al., 2021), 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. 1b). Survey points
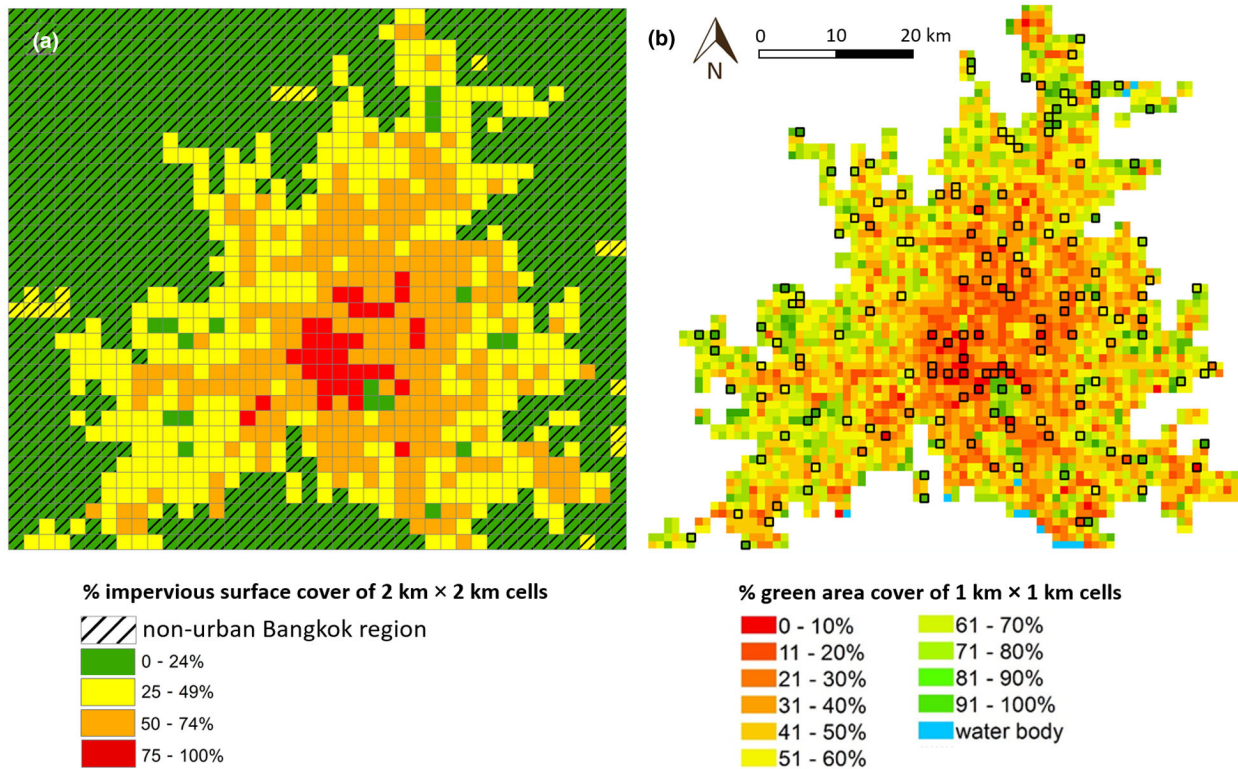
Figure 1 (a) land cover map of the Bangkok study region showing % impervious surface cover of 2 km × 2 km grid cells used to define the study region. Grid cells with ≥25% impervious surface cover that were isolated from the main urban region or had <25% impervious surface cover were considered to be part of other urban settlements and not classified as part of urban Bangkok, (b) the % cover of greenspace in 1 km × 1 km grid cells across the study region; grid cells outlined in black represent the 150 sampling cells selected using random stratification across each of the greenspace % cover categories (15 sampling grid cells for each of the ten categories). This Figure is modified from Thaweepworadej and Evans (2022).

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 (mean distance from the original point = 73.5 m ± 7.6 (SE), n = 109).

Squirrel and tree-shrew surveys

Our sampling methodology is based on Bonnington et al. (2014). Squirrel and tree-shrew surveys were conducted using 15-minute point counts with a 50 m survey radius. Each survey point was visited three times from March to July 2018 (first visit 12th March to 28th April; second visit 2 May to 11 June; third visit 12 June to 25 July). These survey dates avoid the most intense parts of the rainy season whilst overlapping with periods of high squirrel and tree-shrew activity (Langham 1982; Lurz et al. 2013). In each sampling period, we visited survey locations in an order that was unbiased with regard to their urbanisation intensity, and surveys were conducted on dry calm days from 6:30 am to noon. Typically, four sampling points were visited each day. These were in a similar part of the study region, or along travel routes to other survey sites visited that day. All the point count locations visited on a day were in different

urbanisation categories and were in different categories to those visited the previous day. The order in which each (daily) set of survey locations was visited was varied (between the three survey visits) to ensure that each survey site was surveyed once near the start, once near the middle and once towards the end of the daily survey period. We then estimated the abundance of each focal species as a maximum number of individuals across three survey visits. Consequently, across all our survey points there is negligible variation in the timing of surveys from which our response variables are calculated. To avoid the typical variation in number of people and human activities during weekday and weekend surveys, weekend surveys were avoided during the first and second survey periods but were conducted in 13 of our 150 grid cells during the third survey period due to disruption of weekday surveys by heavy rain. All the sites with weekend surveys were privately owned sites, such as farmland, where few people were counted during each of the three surveys.

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. During each survey we recorded the number of adult individuals of

each taxon present in the survey area – adults were distinguished from juveniles based on size as per criteria in Francis (2017) and Lekagul & McKneely (1977). When squirrels and tree-shrews were observed eating fruits, nuts or seeds, we also noted which species they were consuming (these data were subsequently used to revise information on which tree species provide food for our focal species).

All detected squirrels and tree-shrews were recorded and identified to species. Identification of northern tree-shrew *Tupaia belangeri* and Himalayan striped squirrel *Tamiops macclellandi* was straightforward and based on Francis (2017) and Lekagul & McKneely (1977). The taxonomy and identification of *Callosciurus* species is more complicated. We followed the criteria advocated by Lekagul & McKneely (1977), Boonkhaw *et al*. (2017), Francis (2017), and identified Finlayson's squirrel *C. finlaysonii*, Pallas's squirrel *C. erythraeus* and hybrids between these two species (hereafter called *C.* hybrid) depending on the precise colour patterns of the upperparts, tail, belly and face (primarily similar external features to *C. erythraeus* with a partial white ring around the eyes; see Table S1; Fig. S2 for more details).

Environmental conditions and urban selection pressures

We recorded the total number of people in each point count radius during each of the three 15-minute surveys. An index of human disturbance was calculated as the mean of these values.

Predators that are capable of predating squirrels within urban Bangkok are primarily free-ranging cats *Felis catus* and dogs *Canis lupus familiaris*. Other mammalian predators are largely absent and diurnal avian predators are rare and localised (see Thaweepworadej & Evans, 2022). Whilst some owl species are reported to be widespread, for example, Collared scops owl *Otus lettia* (Round & Gardner, 2008), these have a predominately invertebrate based diet (Wilman *et al*., 2014). Predatory snakes also occur but there is a paucity of data on their distributions and abundance. We generated an index of predation pressure by recording 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. Cats are partially active at night, but diurnal direct observation surveys and camera traps (which operate 24 hours per day) uncover similar spatial patterns in cat densities in urban areas and uncover similar relationships between cat densities and environmental variables (Bennett *et al*., 2021). We are thus confident that our data provided a useful index of cat abundance.

All trees in the point count radius with a diameter-at-breast-height (DBH) >25 cm were identified to species (based on Gardner, Sidisunthorn & Anusarnsunthorn (2000) and Veesommai & Kavduengtian (2004)) and their height recorded (to the nearest 0.5 m, using a clinometer) and DBH (to the nearest 1 cm, measured at 1.3 m). We defined tree species that produce food for squirrels as those a) in genera that produce seed, fruits or nuts recorded as being consumed by squirrels following 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 S2). The diet of *T. belangeri* overlaps with those of squirrels but *T. belangeri* 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 S2). We then calculated the number of tree species in 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, Cámara-Cabrales & Kelty, 2005; Ouedraogo *et al*., 2020) and we calculated the above-ground biomass of each tree in 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 the total biomass of fruit-producing trees to provide an estimate of potential food availability for squirrels and tree-shrews in 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 (Lekagul & McNeely, 1977; Bertolino *et al*., 2004). 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 in the focal 1 km × 1 km grid cell, and (when the survey location overlapped with woodland) the size of the woodland in which our survey locations were located. These data were calculated using imagery taken within 9 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 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 (R Core Team, 2021), with the name of the R package used in each analysis provided below in italics. 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 ± SE = 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 the 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). The abundance of the Himalayan striped squirrel is not modelled as it was only recorded at one survey location.

We modelled the maximum abundance of each species and *C.* hybrids using generalised linear models ('glm' function in the *stats* package version 4.1.2; R Core Team, 2021). 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 S4; assessed using the 'dispersiontest' function in the *AER* package version 1.2.9; Kleiber & Zeileis, 2008).

We first quantified how each species responds to urbanisation by modelling the 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 selected the quadratic model only when the quadratic term is significant ($P < 0.05$) and the quadratic model has an Akaike information criterion value corrected for small sample size (AICc) that is at least two points lower than the AICc value of the linear model.

We then followed Whittingham *et al.* (2006) and constructed full models of each species' maximum abundance as a function of our indicators of urban conditions and selection pressures ($n = 150$), that is, 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 1 for more details). Predictor variables were ln-transformed when their un-transformed distributions were skewed as, in these situations, outliers can have an undue influence on parameter estimation. We modelled the maximum abundance of *C.* hybrids with the same set of predictor variables 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 version 3.0.12; Fox & Weisberg, 2019) were consistently below the threshold at which model inference is adversely impacted by multi-collinearity (Dorman *et al.*, 2013; Table S5). Model and partial r^2 values are calculated as KL-divergence-based r^2 (Cameron & Windmeijer, 1997) using the *rsq* package (version 2.2; Zhang, 2021).

We used Moran I's tests (*ape* package version 5.5; Paradis & Schliep, 2019) 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 I's values were consistently low (maximum value 0.11; Table S6). In these cases, we also constructed alternative models that took spatial autocorrelation into account. These were implemented using generalised linear mixed models with exponential spatial correlation structure (nlme package version 3.1.153; Pinheiro et al., 2021) and the parameter estimates for these models were qualitatively similar to those in the original non-spatial models (Table S7). We thus only report results from non-spatial models in the main manuscript.

Results

We detected three species in the family Sciuridae. *Tamiops macclellandi* was extremely rare, being detected in just one

Table 1 Predictor variables used in multiple regression models of the maximum abundance of squirrels and tree-shrews. Tree species providing fruit for tree-shrews and squirrels were defined separately to take dietary differences into account

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 tree biomass	t/ha	11.4 ± 1.0	8.0	0–89.9	ln (x + 1)
Biomass of fruit trees for tree-shrews	t/ha	3.4 ± 0.7	0.7	0–86.1	ln (x + 1)
Biomass of fruit trees for squirrels	t/ha	4.8 ± 0.8	2.1	0–86.6	ln (x + 1)

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. 2), with *C. finlaysonii* predominantly occurring on the eastern bank 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). The one tree-shrew species (*T. belangeri*)

occurred in approximately one-quarter of grid cells (Table S8).

Response to urbanisation intensity

T. belangeri abundance declined linearly with increasing urbanisation intensity, and *T. belangeri* was not detected at any survey location in grid cells with over 80% impervious surface cover (Table 2; Fig. 3). *C. erythraeus* occurred across the entire urbanisation gradient and its abundance
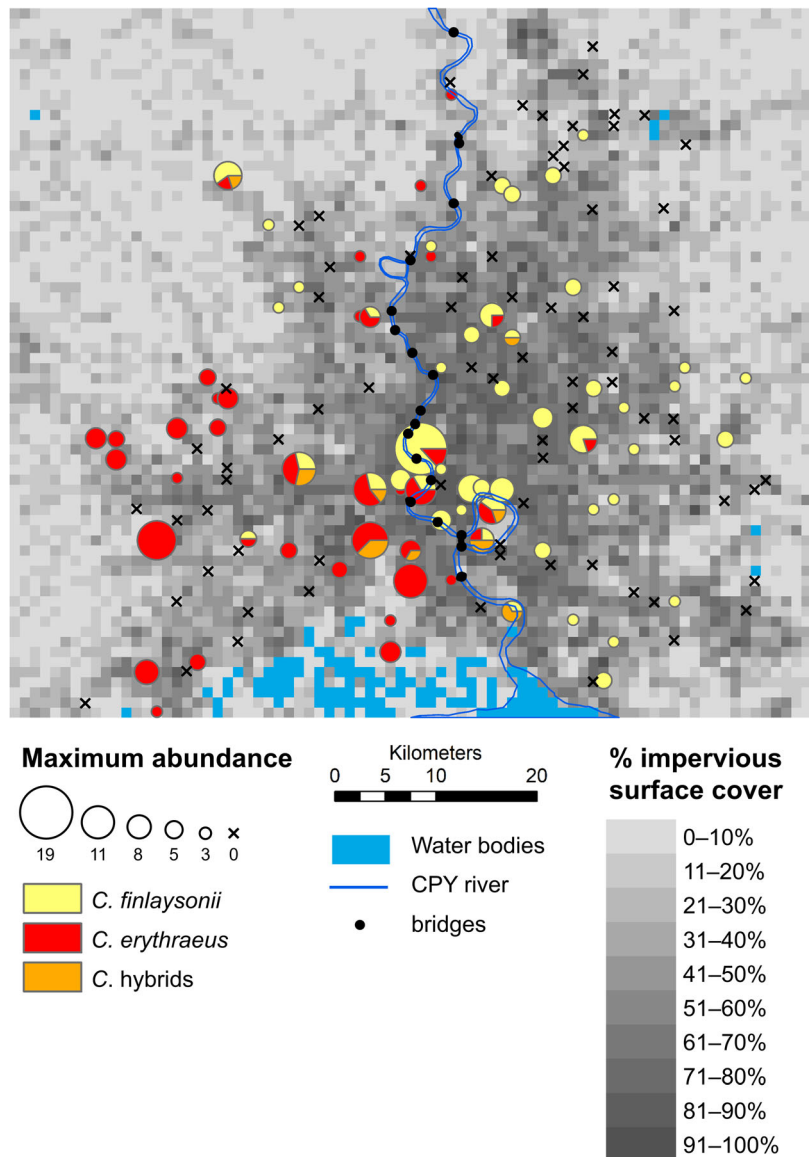
Figure 2 Maximum abundance and distribution of *C. finlaysonii* (yellow), *C. erythraeus* (red) and *C. hybrids* (orange) in 1 km × 1 km grid cells located along the urbanisation gradient. The size of the circles represents the maximum abundance of each species and × represents surveyed locations at which none of the focal taxa were detected. 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 in blue, with black circles indicating bridges crossing the river.

declined linearly with increasing urbanisation intensity (Table 2; Fig. 3). *C. finlaysonii* also occurred across the entire urbanisation gradient, but 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 2; Fig. 3).

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). Abundance increased significantly with increasing grid cell tree cover (ln-transformed) and tree species richness at the point count location (ln-transformed), and marginally significantly with the biomass of tree species that provided fruit consumed by tree-shrews (ln-transformed). There were marginally significant negative relationships between *T. belangeri* abundance and mean number of dogs (ln-transformed), distance to the largest woodland and woodland size (ln-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). Abundance was significantly positively associated with tree biomass within the point count (ln-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). 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 in which predictors only provide information on percentage impervious surface cover). There was a significant negative relationship between *C. erythraeus* abundance and mean number of people (ln-transformed), and a marginally significant negative relationship with mean number of dogs (ln-transformed). 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). *C.* hybrids abundance increased significantly with tree biomass in the point count area (ln-transformed), and marginally significantly with percentage tree cover in the grid cell (ln-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 2 Models of the maximum abundance of each taxon in response to urbanisation intensity using generalised linear models (*Tupaia belangeri* and *Callosciurus* hybrids abundance modelled with Poisson error structure; *Callosciurus finlaysonii* and *Callosciurus erythraeus* abundance modelled with a negative binomial error structure). Model r^2 was estimated as KL-divergence-based r^2 using *rsq* package which uses the methodology from Cameron and Windmeijer (1997). Parameter estimates and 95% confidence intervals are in bold for significant predictors (P < 0.05).

Response variable	Model	Model r^2	AICc	Intercept Coeff	Intercept 95% CIs	% impervious surface (Linear term) Coeff	% impervious surface (Linear term) 95% CIs	% impervious surface (Linear term) P	% impervious surface (Quadratic term) Coeff	% impervious surface (Quadratic term) 95% CIs	% impervious surface (Quadratic term) P
T. belangeri	Linear	12.38	196.15	−0.349	−0.842, −0.097	**−0.024**	**−0.037, −0.012**	**$1.3e^{-4}$**			
	Quadratic	14.63	195.17	−0.773	−1.547, −0.108	0.013	−0.030, 0.061	0.562	$-4.8e^{-4}$	−0.001, $5.4e^{-5}$	0.103
C. finlaysonii	Linear	6.17	315.31	−1.260	−1.929, −0.608	**0.015**	**0.004, 0.026**	**0.010**			
	Quadratic	6.61	316.91	−0.997	−1.987, −0.033	−0.001	−0.045, 0.044	0.971	$1.6e^{-4}$	$-2.7e^{-4}$, $5.9e^{-5}$	0.481
C. erythraeus	Linear	4.83	291.72	0.043	−0.606, 0.751	**−0.014**	**−0.028, −0.001**	**0.037**			
	Quadratic	5.21	293.47	0.247	−0.657, 1.284	−0.029	−0.080, 0.019	0.259	$1.6e^{-4}$	$-3.6e^{-4}$, $6.9e^{-4}$	0.550
C. hybrids	Linear	1.27	105.20	−1.953	−2.965, 1.123	−0.010	−0.030, 0.009	0.317			
	Quadratic	2.71	106.11	−2.514	−4.264, 1.224	0.030	−0.043, 0.115	0.448	$-4.5e^{-4}$	−0.001, $3.4e^{-4}$	0.303
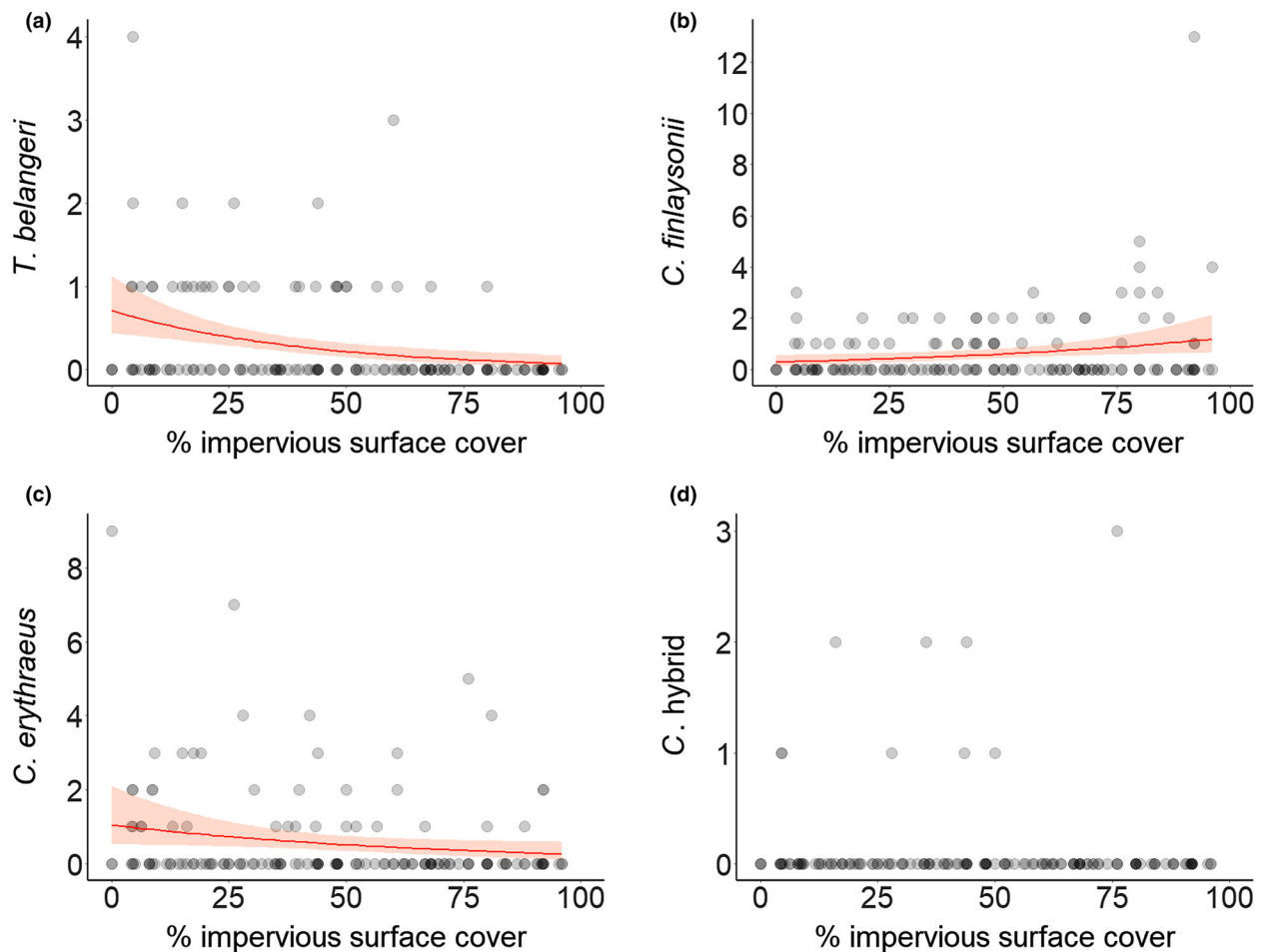
Figure 3 Relationships between the maximum abundance of *Tupaia belangeri*, *Callosciurus finlaysonii*, *Callosciurus erythraeus* and *Callosciurus* hybrids and percentage impervious surface cover. Fitted lines indicate predicted values, with shading indicating 95% confidence intervals, from generalised linear models reported in Table 2. The abundance of *C.* hybrids was not significantly associated with urbanisation intensity so no fitted line is provided.

Discussion

Study limitations

We use an established morphological classification scheme for hybrid identification that provides useful data on the distribution of hybrid *Callosciurus* squirrels. However, hybrids (especially back-crosses or non-F_1 hybrids) may not always exhibit a clear difference in morphological features compared to their parental species. Our study thus probably provides a minimum estimate of the magnitude of gene flow between hybridising *Callosciurus* squirrels, and future research would benefit from the development and application of genetic markers. Our assessment of the impacts of predators on the abundance and distribution of squirrels and tree-shrews focuses on free-ranging cats and dogs as these are typically the numerically dominant predator species in urban environments, their densities are elevated in towns and cities and there is much concern regarding their environmental impacts

(Marra & Santella, 2016; Soultan, Attum & Lahue, 2021). We follow other studies and take an observational approach as a first step in assessing the impacts of these predators in a tropical city, but recognise that experimental approaches or ones that consider potential meso-predator release following any reduction in predator abundance would be advantageous.

Urban filtering of the regional species pool

Only three of the six diurnal squirrel species that occur within the Chao-Praya lowlands were detected regularly within our study area (Duckworth, 2016a; Duckworth, 2016b; Walston, Duckworth & Molur, 2016). Himalayan striped squirrel *Tamiops macclellandi* was only detected at one sampling location and grey-bellied squirrel *Callosciurus caniceps* and Indochinese ground squirrel *Menetes berdmorei* were entirely absent. It is clear that urbanisation has driven a marked reduction in the number of squirrel species that occur regularly in the greater Bangkok region. This is perhaps surprising given that rodents, including

Table 3 Multiple regression models of the maximum abundance of *Tupaia belangeri*, *Callosciurus finlaysonii*, *Callosciurus erythraeus* and *Callosciurus* hybrid. Models are generalised linear models fitted with a Poisson error structure for *T. belangeri* and *C.* hybrids, and a negative binomial structure for *C. finlaysonii* and *C. erythraeus*. Parameter estimates and 95% confidence intervals are in bold for significant predictors ($P < 0.05$) and in italics for marginally significant predictors ($0.05 \leq P < 0.10$). 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.* hybrids (Model r^2 = 65.56)			
	Coeff	95% CIs	P	Partial r^2	Coeff	95% CIs	P	Partial r^2	Coeff	95% CIs	P	Partial r^2	Coeff	95% CIs	P	Partial r^2
% impervious surface	−0.007	−0.028, 0.012	0.469	0.86	*0.014*	*−0.002, 0.031*	*0.075*	*2.82*	**0.023**	**0.003, 0.044**	**0.019**	**5.46**	0.010	−0.039, 0.059	0.675	0.62
% tree cover*	**0.668**	**0.129, 1.320**	**0.029**	**9.21**	0.177	−0.267, 0.650	0.420	0.56	**1.379**	**0.667, 2.197**	**1.7e^{-4}**	**15.89**	*1.585*	*0.193, 3.886*	*0.091*	*16.73*
Woodland size*	*−0.403*	*−0.859, 0.009*	*0.067*	*5.66*	−0.202	−0.710, 0.255	0.433	0.69	−0.146	−0.744, 0.506	0.532	0.23	**−0.860**	**−1.801, −0.129**	**0.038**	**16.34**
Distance to largest woodland	*−0.003*	*−0.006, 1.0e^{-4}*	*0.063*	*5.57*	*−0.002*	*−0.004, 1.1e^{-4}*	*0.081*	*3.21*	−0.002	−0.005, 0.001	0.126	2.45	−0.005	−0.013, 0.001	0.167	7.52
Mean no. of people*	−0.220	−0.677, 0.208	0.328	1.59	0.207	−0.144, 0.563	0.226	1.26	**−0.601**	**−1.077, −0.154**	**0.006**	**7.28**	*−0.868*	*−2.017, 0.022*	*0.081*	*11.50*
Mean no. of cats*	−0.540	−2.012, 0.678	0.427	1.11	−0.348	−1.103, 0.395	0.368	0.80	0.134	−1.033, 1.276	0.803	0.06	0.738	−1.700, 2.853	0.496	1.51
Mean no. of dogs*	*−0.512*	*−1.079, 0.034*	*0.069*	*5.23*	0.024	−0.463, 0.505	0.918	0.01	*−0.528*	*−1.083, 0.002*	*0.055*	*4.07*	−1.042	−2.590, 0.298	0.144	7.59
Tree species richness*	**1.112**	**0.169, 2.106**	**0.024**	**8.08**	0.264	−0.846, 1.347	0.590	0.21	0.349	−0.733, 1.435	0.537	0.45	0.927	−1.302, 3.353	0.414	2.36
Fruit tree species richness*	−0.106	−1.224, 0.968	0.849	0.06	0.567	−0.546, 1.744	0.298	0.32	0.757	−0.384, 1.940	0.213	1.84	−0.084	−1.898, 1.713	0.925	0.03
Tree biomass*	0.501	−0.124, 1.104	0.109	3.91	**0.945**	**0.287, 1.655**	**0.002**	**7.16**	0.427	−0.274, 1.147	0.246	1.57	**3.234**	**1.545, 5.691**	**0.001**	**36.21**
Fruit tree biomass*	*0.478*	*−0.095, 1.048*	*0.099*	*4.21*	−0.043	−0.631, 0.524	0.874	0.02	−0.137	−0.781, 0.494	0.671	0.20	*−1.108*	*−2.408, −0.030*	*0.061*	*12.69*
Distance to the nearest bridge*													**−0.278**	**−0.541, −0.113**	**0.009**	**37.01**

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*., 2019). Urbanisation induced declines in the number of squirrel species are thus likely to occur in other large tropical urban areas.

Squirrels play a key role in animal-mediated seed-dispersal (Steele & Yi, 2020) which is considered critical for maintaining ecological processes in urban areas (Gelmi-Candusso & Hämäläinen, 2019). The reduced diversity of squirrel species, negative responses of two of the three remaining species to urbanisation, combined with the absence or extreme rarity of larger-bodied frugivorous arboreal mammals during our surveys (see Table S9) 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 these species provide.

Species responses to urbanisation and impacts on hybridisation

Northern tree-shrew *T. belangeri* and Pallas's squirrel *C. erythraeus* are widespread and occur in highly urbanised locations, but decline in abundance as urbanisation intensity increased. The marked urban expansion into rural areas and urban densification within our study area in recent decades (Estoque & Murayama, 2015; Song *et al*., 2021), has thus probably reduced the regional population size of these species. In contrast to *C. erythraeus*, *C. finlaysonii* abundance 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 as studies find strong phylogenetic signals in inter-specific variation in urbanisation tolerance (e.g. reptiles; Winchell *et al*., 2020, birds; Callaghan *et al*., 2019, mammals; Johnson & Munshi-South, 2017), and evidence that urbanisation influences polymorphisms of candidate genes for behavioural traits influenced by urban selection pressures (Müller *et al*., 2013). Moreover, these hybridising congeneric species exhibit divergent 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.

Our results confirm the suggestion that the Chao-Praya River acts as a geographic barrier that partially separates the distributions of *C. finlaysonii* and *C. erythraeus* (Boonkhaw *et al*. (2017). 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 is still primarily confined to either side of the river. In 2020, a vegetated pedestrian bridge was built across the Chao-Praya River, which is likely to facilitate wildlife dispersal across the river. Our data provide a suitable baseline for assessing the impacts of this potential corridor on species distributions and hybridisation rates.

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 given the arboreal nature of these species (Lekagul & McNeely, 1977; Bertolino *et al*., 2004). Our results thus strongly suggest that increasing urban tree cover can mitigate some of the adverse impacts of urbanisation intensity on our focal species. Urban planners may, however, need to balance conservation objectives with the potential economic damage imposed by some of our focal species (Derbridge, Pepper & Koprowski, 2016). We found no evidence that measures of the abundance or diversity of food resources (in the form of fruit, nuts etc.) influenced the abundance of any of 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*., 2014; Jokimäki *et al*., 2017). The diversity of tree species was, however, positively correlated with *T. belangeri* abundance. This is a generalist species, 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, Östberg & Bühler, 2012).

C. erythraeus and *C.* hybrids abundance declines with the number 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 & Crooks, 2006) and some bird species (Kang *et al.*, 2015) respond negatively to human activity in urban systems, but evidence for smaller mammal species is much rarer (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 & 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 & 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 the abundance of free-ranging dogs and the densities of *T. belangeri* and *C. erythraeus*. The ecological impacts of dog *Canis lupus familiaris* have received less attention than those of *Felis,* but the 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 in urban Bangkok, as reported in some other urban studies (e.g. Mella-Méndez et al., 2019; Soultan *et al.*, 2021). Experimental manipulations of dog populations would be required to confirm a causal link between dog and squirrel abundances and quantify the extent to which feral dog 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, Jitapunkul & Sitprija, 2011).

Conclusions and recommendations

Three of the six diurnal squirrel and tree-shrew species occurring within our focal region are absent or extremely rare in our urbanised survey region. Only one of the three widespread species *C. finlaysonii* is more abundant in more urbanised locations, with *C. erythraeus* and *T. belangeri* occurring at lower densities. These results highlight the sensitivity of tropical squirrel species to urbanisation, contrasting with the urban tolerance of squirrels often reported from temperate regions. Animal-mediated seed dispersal is critical for maintaining ecosystem function in urban areas and is likely to be adversely impacted by these changes in diversity and abundance as squirrels typically play a key role in seed dispersal. Modelling of relationships between abundance and

environmental conditions suggest that our focal mammal assemblage could benefit from urban management that increases tree cover and diversity, reduced disturbance from people and control of the free-ranging dog population. Rates of interspecific gene flow need to be confirmed with genetic approaches, but urbanisation appears to be increasing hybridisation between *C. finlaysonii* and *C. erythraeus*, partially through urban infrastructure increasing the permeability of geographic barriers.

Acknowledgements

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Identification of *Callosciurus* squirrel taxa based on morphological characteristics following Francis (2017) and Lekagul and McKneely (1977) – see Fig. S2 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).

Table S2. 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.

Table S3. 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.

Table S4. 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.

Table S5. 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).

Table S6. 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.

Table S7. Comparison of coefficients and standard errors in non-spatial and spatial models of response variables where there is evidence of significant spatial autocorrelation (Table S6): 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.

Table S8. Data on occupancy (defined as present in at least one of three survey) 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.

Table S9. Frugivorous terrestrial mammalian species from the regional species pool (i.e., Chao-Praya lowland) that were absent or extremely rare during this study. Asterisks indicate nocturnal species which our surveys are not well designed to detect this group of species.

Figure S1. 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 the grey border represents the 70 km × 80 km rectangle delimiting our study region, in which it was divided to 1,400 2 km × 2 km grid cells used in landcover classification and 5,600 1 km × 1 km sampling grid cells.

Figure S2: *Callosciurus* squirrels in Bangkok: *C. finlaysonii* (a–f), *C. erythraeus* (g–i), and *C.* hybrids (j–l). Photo taken by Budda Chotimanvijit (a–d, g), Phakhawat Thaweepworadej (e, f, h, i, l), Thanawat Jinjarak (j), and Nidchakan Chidcheaw (k).

Figure S3. Proportion of grid cells containing squirrels and maximum abundance of *Callosciurus* squirrels comparing between western (blue) and eastern (orange) side of the Chao-Praya river. Thick solid and dashed horizontal lines represent median and mean maximum abundance, respectively. Interquartile boxes represent middle 50% (25th to 75th percentile) of the data, whiskers represent 25% ranges for the bottom and top of the data values, and dots represent outliers.