

## **Highlights**

- Urban trees made up part of the viewscape from 97.7% of buildings
- The contribution of individual trees to indirect nature experiences is skewed
- Trees in private gardens were more important than those on public land
- Trees in low income high density housing provided nature experiences to more people
- Individual organisms contribute differently to human experiences of nature

# Skewed contributions of individual trees to indirect nature experiences

Daniel T. C. Cox<sup>1,2\*</sup>, Jonathan Bennie<sup>3</sup>, Stefano Casalegno<sup>1</sup>, Hannah L. Hudson<sup>1</sup>, Karen Anderson<sup>1</sup> and Kevin J. Gaston<sup>1</sup>

Daniel T. C. COX (dan.t.cox@googlemail.com) <sup>1,2\*</sup>

Jon BENNIE (j.j.bennie@exeter.ac.uk) <sup>3</sup>

Stefano CASALEGNO (stefano@casalegno.net) <sup>1</sup>

Hannah L. HUDSON (h.hudson@exeter.ac.uk) <sup>1</sup>

Karen ANDERSON (karen.anderson@exeter.ac.uk) <sup>1</sup>

Kevin J. GASTON<sup>1</sup> (k.j.gaston@exeter.ac.uk) <sup>1</sup>

<sup>1</sup> Environment & Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9FE, U.K.

<sup>2</sup> European Centre for Environment and Human Health, University of Exeter Medical School, Truro, Cornwall, TR1 3HD, U.K.

<sup>3</sup> Centre for Geography, Environment and Society, University of Exeter, Penryn, Cornwall TR10 9FE, U.K.

\* **Corresponding Author.** Environment & Sustainability Institute, University of Exeter, Penryn, Cornwall, TR10 9FE, U.K. E-mail: dan.t.cox@googlemail.com; +44 (0) 7800556070, Mobile: +44 (0) 7800556070.

## **Abstract**

Exposure to nature is associated with a broad range of benefits to human health. Whilst there has been exploration of how these experiences vary amongst people, the converse – how different individual organisms contribute to human nature experiences – has largely been overlooked. The most common way that people experience nature occurs indirectly, when they are in a room with a natural view. Here, we estimate variation in how individual trees provide indirect nature experiences in an urban human population. As a proxy for its contribution towards indirect nature experiences, within an extended urban area in southern England, UK (n = 612,920) we calculated the number of buildings with line of sight to each tree. We then modelled each tree's contribution towards these experiences against potential predictors, namely tree height, land ownership, social deprivation, while controlling for human population density. We demonstrate that a small number of trees contribute disproportionately towards indirect nature experiences, with individual trees in socio-economically deprived high density housing falling within the viewscape of significantly more buildings. Further, trees in private gardens were generally more important for providing indirect nature experiences than those in public green spaces. This novel study demonstrates the skewed contribution of different organisms to human population indirect nature experiences. This approach can be applied more broadly to understand how individual organisms provide indirect, incidental and intentional nature experiences. Understanding the ecology behind human nature experiences is an important step towards linking urban design and policy for maximising the health benefits from nature.

## 1 **Introduction**

2 Urbanisation is emerging as one of the most important human health issues of the 21<sup>st</sup> century  
3 (World Health Organisation, 2015), with cities becoming epicentres for chronic and non-  
4 communicable physical and mental health conditions (Dye, 2008). Nature in cities has the potential  
5 to mitigate many of these health issues, with demonstrable links between exposure to nature and  
6 health and well-being benefits (e.g. Keniger, Gaston, Irvine, & Fuller, 2013). These benefits span a  
7 remarkable range of health outcomes, including but not limited to, reduced all-cause mortality and  
8 mortality from cardiovascular disease (e.g. Donovan et al., 2008; Mitchell & Popham, 2008),  
9 reduced healing times (Raanaas, Patii, & Hartig, 2012; Ulrich, 1984,), reduced stress (e.g. van den  
10 Berg, & Custers, 2011), reduced respiratory illness and allergies (e.g. Hanski et al., 2012; Lovasi,  
11 Quinn, Neckerman, Perzanowski, & Rundle, 2008), improved self-reported wellbeing and reduced  
12 risk of poor mental health (e.g. Cox et al., 2017a; Dallimer et al., 2012; Fuller, Irvine, Devine-  
13 wright, Warren, & Gaston, 2007), and improved cognitive ability (e.g. Berman, Jonides, & Kaplan,  
14 2008).

15  
16 Within the urban environment exposure to nature is more complex and versatile than often  
17 portrayed; to a greater or lesser extent people are exposed to components of nature throughout their  
18 daily lives. Keniger, Gaston, Irvine, & Fuller (2013) identified three main types of nature  
19 experience. First, people experience nature indirectly while not actually being present in it (e.g.  
20 having a view of nature from home or work). Second, nature is experienced incidentally while  
21 carrying out another activity (e.g. walking to the shops). Third, people intentionally experience  
22 nature (e.g. visiting parks or gardens). With the rise in urban living, most people now spend much  
23 of their day indoors, therefore the green viewscape from home or from work often constitutes by far  
24 their most common nature experience (Cox, Hudson, Shanahan, Fuller, & Gaston, 2017b). Having a  
25 room with a view of nature does not necessarily mean that people are continuously experiencing  
26 that view. Instead, people spend a significant amount of time with their attention directed towards  
27 specific tasks, and the presence of a window with a natural scene allows micro-restorative  
28 experiences (Kaplan, 1993, 2001), with scenes that are more fascinating being likely to be more  
29 restorative (Kaplan & Kaplan, 1989). Indeed, there is robust evidence to suggest that indirect nature  
30 experiences provide a broad range of health and wellbeing benefits, including increased  
31 psychological wellbeing (Kaplan, 2001), improved cognitive function (e.g. Zijlema et al., 2017) and  
32 concentration (Bodin, Björk, Ardö, & Albin, 2015), reduced healing times (Ulrich, 1984) and  
33 reduced stress at work (Kaplan, 1993; Largo-Wright, Chen, Dodd, & Weiler, 2008; Leather,  
34 Pyrgas, Beale, & Lawrence, 1998). However, indirect nature experiences are not evenly

35 distributed across the population, with a relatively small proportion of people spending  
36 disproportionately more time indirectly experiencing nature (Cox et al., 2017a).

37

38 As well as there being variation in the degree to which people experience nature, there will also be  
39 variation in how individual organisms contribute towards providing those experiences (Gaston et  
40 al., 2018). Some will almost certainly be major contributors, others minor ones and some may not  
41 contribute at all. However, to date this issue has not been explored. Intuitively, those individuals  
42 that are present where people occur and are more visible within natural viewsapes will be seen by  
43 a greater number of people, and so will be relatively more important for providing indirect nature  
44 experiences. For example, trees are a highly visible component of many urban viewsapes (Nowak  
45 et al., 1996) and potentially provide a wide range of health and well-being benefits (Salmond et al.,  
46 2016). As such, their location in the landscape seems likely to be critical for determining how often  
47 and for how long people experience them (Kardan et al., 2015). Those trees that fall within the  
48 viewscape of more buildings are likely to be disproportionately more important for providing health  
49 benefits associated with indirect nature experiences.

50

51 Here, we explore how individual urban trees vary in their contribution to indirect nature  
52 experiences in a human population. Determining which individual trees contribute more  
53 experiences may not be straightforward, but one might predict that larger trees are more visible, as  
54 are those that occur in areas of denser human population and on public lands. Trees in wealthier  
55 areas seem likely also to provide more nature experiences, because less dense and more designed  
56 urban spaces tend to favour views from associated properties (Landry & Chakraborty, 2009). We  
57 test these predictions using a spatial dataset derived from aerial photography and colour infrared  
58 data with high resolution digital surface models, within which the location of every tree within an  
59 extended urban area in southern England, UK was mapped, and its height estimated. Using spatial  
60 analysis algorithms implemented within geographic information systems (GIS), we determined the  
61 number of buildings that had line of sight to each tree, which we used as a proxy for indirect nature  
62 experiences from home or from work. To understand the important predictors of a tree's  
63 contribution towards these experiences, and so inform urban design and planning towards green  
64 health interventions, we modelled the response against potential predictors, namely: tree height,  
65 because this may influence a tree's visibility; landownership, because broadly speaking this will  
66 determine the type of land and tree management; and social deprivation to account for socio-  
67 economic variation in human neighbourhoods which is known to influence both tree and human  
68 populations (e.g. Ferguson, Roberts, McEachan, & Dallimer, 2018). We expect that there will be a  
69 positive relationship between the number of buildings with line of sight to a tree and human

70 population density, therefore to tease out the effects of other predictors we controlled for the  
71 potentially confounding effects of spatially-variable human population density surrounding each  
72 tree.

73

## 74 **Methods**

### 75 *Study area*

76 This study focused on the urban area of the ‘Cranfield triangle’, a region in southern England, U.K.  
77 (52°07’N, 0°61’W). This comprises the three adjacent towns of Milton Keynes, Luton, and  
78 Bedford, which have a combined human population of c.546,000 (Office of National Statistics,  
79 2016), and occupy c.197 km<sup>2</sup>. Within this region there is great variation in human population  
80 density and urban form (including representatives of low- and high density living). The urban limits  
81 were defined as where continuous residential or commercial properties ended, and rural green space  
82 began (Gaston, Warren, Thompson, & Smith, 2005).

83

### 84 *Data sources*

85 A fine-spatial resolution digital surface model (DSM) for the study area was generated from  
86 airborne light detection and ranging (LiDAR) data captured by the Natural Environment Research  
87 Council Airborne Research and Survey Facility between June and September 2012. The DSM has a  
88 horizontal resolution of 1 m and widely known biases for vegetation height retrieval that result in a  
89 nominal vertical accuracy of  $\pm 0.5$  m. The position (centre point) and height of every tree  $>3$  m in  
90 height within a 100 m buffer surrounding the urban limits of the Cranfield triangle was obtained as  
91 a point vector point data from a commercial product called the “National Tree Map” (NTM; n =  
92 612,920; Bluesky International LTD; <http://www.blueskymapshop.com>). A vector polygon layer of  
93 the outlines of buildings and structures was obtained from the United Kingdom Ordnance Survey  
94 VectorMap (OS VectorMap; <http://digimap.edina.ac.uk/>; accessed 2016). All building polygons  
95 with an area between 36 m<sup>2</sup> and 360 m<sup>2</sup> were selected; this was a size range that was considered to  
96 represent buildings with windows that people are likely to use for home and work (i.e. removing  
97 smaller non-inhabited structures such as sheds and garages, and larger structures such as  
98 warehouses. All spatial data manipulations were performed in R software for statistical computing  
99 version 3.3.3 (R Development Core Team, 2016) and QGIS v2.14 (Quantum GIS Development  
100 Team, 2016). The registration correspondence between the NTM and the LiDAR DSM was visually  
101 good, but we were unable to arrive at a spatially-distributed registration error estimate for two  
102 reasons. First the NTM was a commercial product, for which quantitative error information were  
103 unavailable beyond a generic statement from Bluesky that states “*overall canopy coverage*  
104 *represented in NTM is accurate to over 90% and over 95% accurate within 50m of buildings*”.

105 Second, the LiDAR data had an associated measurement uncertainty that was spatially variable but  
106 unknown for this site – the technical specifications of the Leica ALS500-II sensor state that it has a  
107 “lateral placement accuracy of 7 - 64 cm and vertical placement accuracy of 8 - 24 cm (one  
108 standard deviation) from full-field-filling targets” (www.nts-info.com/inventory/images/ALS50-  
109 II.Ref.703.pdf).

110

### 111 *Identifying lines of sight between buildings and trees*

112 As a measure of the contribution of individual trees to indirect nature experiences, we calculated  
113 the number of buildings that had the potential for an unobscured view of each tree from an upstairs  
114 window, allowing for the effects of topography, other buildings and structures and vegetation in  
115 obscuring this line of sight. A tree will be perceived to be smaller if it is further away, and as a  
116 consequence the ability of a viewer to distinguish ecological detail will lessen, which is likely to  
117 influence the type of nature experience. For example, it is possible to recognise a small songbird  
118 such as a robin *Erithacus rubecula* as a perching bird, by eye at 350 feet (c.100 m) but not to  
119 determine the species (Wood, 1937). At a distance of 100 m the perceived height of an averagely  
120 sized urban tree (8.36 m, min 1.0 m; max 49.7 m) will be 0.0836 m (true height / distance  
121 = perceived height / distance to perceived height, or in this case;  $(8.36 / 100) \times 1$ ). We considered  
122 that at sizes much smaller than this features of the tree will be difficult to distinguish and so the  
123 type of nature experience is likely to be different. Therefore, to capture the likely near nature  
124 experience we considered a tree to be potentially “visible” from a building if (a) it was within 100  
125 m of at least one edge of the building (although we recognise that trees further than 100 m away  
126 may also be visible from buildings), and (b) there was a clear line of sight from the central point of  
127 the tree (at mid-height) to the edge of the building (at one metre below the height of the building at  
128 that edge, to allow for the view from a top floor window slightly below the roof-line). The DSM,  
129 which includes terrain, vegetation canopy, buildings, and structures such as walls, was used to  
130 determine where lines of site were obscured. We calculated the number of buildings that had line of  
131 sight to each tree, as a proxy for a tree’s contribution towards indirect nature experiences. This was  
132 done using an algorithm written in R (R Development Core Team, 2016) using the raster package  
133 (Hijmans, 2016) and rgdal package (Bivand, Keitt & Rowlingson, 2016). The algorithm first loops  
134 through each tree in the vector file, and selects all buildings within a 100 m radius. Each building is  
135 then selected in turn, and all DSM pixels falling on the edge of the building (i.e. intersecting the  
136 building outline) are selected. The DSM is then checked for a direct line of sight between the  
137 central point of the tree and the building edge, using the method described in Bennie, Davies, Inger,  
138 & Gaston (2014). To prevent the line of sight to the centre of a tree being apparently blocked by the  
139 outer branches of the tree itself, or by mismatches between the polygon edge of the building and the

140 height of the DSM, obstructions within three metres of the centre of the tree or edge of the building  
141 were ignored. For each building within 100 m that had an unobstructed line of sight to a tree, a tally  
142 was added to a column in the attribute table of the tree point data. In this way, the number of  
143 buildings from which each tree was “visible” could be counted.

144

#### 145 *Land ownership, social deprivation and human population density*

146 We determined land ownership for each tree by again using the OS VectorMap. We created a three-  
147 level factor, of non-neighbourhood trees, neighbourhood trees on private land, and neighbourhood  
148 trees on public land (termed land ownership). Non-neighbourhood trees were those without line of  
149 sight to a building (n = 231,783). We then developed a spatial layer to categorise remaining trees as  
150 being located within a residential garden polygon (n = 177,842), or being located on publicly  
151 owned land (n = 202,294).

152

153 To arrive at a generalised measure of deprivation in the neighbourhood surrounding each tree, we  
154 used weekly household wages. These were derived from model-based estimates for households  
155 (Office of National Statistics; <http://www.neighbourhood.statistics.gov.uk>). This index estimates  
156 income per household per week in pounds sterling, from data identified during the period April  
157 2007 to April 2008. The household data are averaged across the Middle layer Super Output Area  
158 (MSOA), a geographical hierarchy consisting of 2,000-6,000 households and were the most recent  
159 data currently available. To each tree, we assigned the weekly household income from the MSOA  
160 that the tree was located within.

161

162 Based on the UK gridded population map (Reis et al., 2016), we estimated human population  
163 density as the number of people within a 500 m radius surrounding each tree. Estimating human  
164 population density at this scale provides an estimate of high to low density housing surrounding a  
165 tree, without being skewed by localised clustering of buildings. This dataset consists of gridded  
166 population data with a spatial resolution of 1 km<sup>2</sup>, assigned to the UK National Grid. We scaled the  
167 human population density for each tree, and where the 500 m radius covered multiple grid cells we  
168 weighted this population density by the percentage of the radius in each cell. The human population  
169 density in the vicinity of each tree was only weakly correlated to the response (i.e. the number of  
170 buildings that had line of sight to each tree; Pearson’s correlation coefficient = 0.43).

171

#### 172 *Statistical analysis*

173 We log-transformed the response variable (i.e. the number of buildings that had line of sight to each  
174 tree), so that it was approximately normally distributed. We used the *dnearneigh* function in the



175 *spdep* package (Bivand & Piras, 2015) to create spatial weights for neighbours list of the trees that  
176 fell within 100 m of each tree (mean = 114; range = 1-578). Trees with no neighbouring trees  
177 within 100 m were excluded (n = 5). We then built a spatially lagged dependent variable model  
178 (also known as an SLX model) using the *lmSLX* command in the ‘*spdep*’ R package. Spatially  
179 lagged models such as SLX provide coefficients for the effect of independent variables on the  
180 response (‘direct’ effect), and coefficients for the mean effect of the values of the independent  
181 variables at the sites of neighbouring trees (‘indirect’ effects). For example, in this case, along with  
182 modelling the direct influence of tree height on the response, the SLX model also accounts for an  
183 indirect effect of mean height of neighbouring trees. We used the *impacts* command in the ‘*spdep*’  
184 package to give the overall effect of both the direct and indirect effects (i.e. total coefficients). The  
185 model took the following form:

$$186 \quad \gamma = \chi\beta + \omega\chi\theta + \varepsilon$$

187 Where  $\gamma$  is the number of buildings with line of sight to that tree.  $\chi\beta$  represents the independent  
188 variables and coefficients, namely: tree height (predictor), neighbourhood income (predictor), land  
189 ownership (predictor) and human population density (confounding). The spatial weights matrix is  
190  $\omega\chi\theta$ , which is the average value of independent variables of trees within 100 m of the response.

191

## 192 **Results**

193 Within the urbanised study area (196.7 km<sup>2</sup>) there were 612,920 trees (Milton Keynes, 308,501 in  
194 104.8 km<sup>2</sup>; Luton, 196,365 in 58.3 km<sup>2</sup>; Bedford, 108,054 in 33.6 km<sup>2</sup>). This is equivalent to 1.12  
195 trees per person, with an average human population density of 87 ( $\pm 63$ ) people within 100 m of  
196 each tree. The contribution of each tree to indirect nature experiences (i.e. the number of buildings  
197 that had line of sight to that tree) varied across the three towns (Fig. 1), and was highly skewed,  
198 with 75% of all indirect experiences being provided by c.25% of trees (Fig. 2a). Trees had an  
199 average height of  $8.5 \pm 4.8$  m, with non-neighbourhood trees being  $10.2 \pm 5.5$  m tall (i.e. those with  
200 line of sight to no buildings), and neighbourhood trees on public land ( $8.4 \pm 4.3$  m) tending to be  
201 taller than those on private land ( $6.5 \pm 3.4$  m). 380,137 (62%) trees fell within the viewscape of at  
202 least one building; of these 202,294 (53%) were located on public land and could be seen by  $11 \pm$   
203 13 buildings, while 177,843 (47%) trees were located in private gardens and could be seen by  $24 \pm$   
204 17 buildings.

205

206 The direct and indirect predictors in the SLX model explained a high proportion of the variance,  
207 with a  $pR^2$  of 0.81 (Table 1). When direct and indirect effects are considered together, the height of  
208 a tree was significantly, but weakly negatively associated with the number of buildings that could  
209 see it ( $-0.02 (\pm 3.8e-4)$ \*\*\*; Table 1). When considering direct effects alone, there was a significant,

210 weak positive relationship between the response and the height of a tree ( $0.013 (\pm 2.4e-4)^{***}$ ; Table  
211 1), whilst for indirect effects, there was a significant weak negative relationship with the mean  
212 height of neighbouring trees ( $-0.033 (\pm 0.001)^{***}$ ; Table 1).

213  
214 Direct and indirect effects considered both separately and together showed that, of neighbourhood  
215 trees those located in private gardens were more important for indirect nature experiences than  
216 those located on public land (Table 1; Fig. 2b). Further, trees in more socio-economically deprived  
217 areas contributed more to indirect nature experiences than those in wealthier neighbourhoods  
218 (Table 1). As expected, when direct and indirect effects were considered together, there was a  
219 positive relationship between the contribution of individual trees to indirect nature experiences and  
220 human population density ( $65.6 (\pm 0.6)^{***}$ ; Table 1; Fig. 2c). However, on the basis of direct effects  
221 alone, there was a weak negative relationship between the response and human population density  
222 ( $-82.0 (\pm 7.3)^{***}$ ; Table 1), but a strong positive relationship with the mean population density of the  
223 tree's neighbours ( $147.6 (\pm 7.4)^{***}$ ; Table 1).

224

## 225 **Discussion**

226 This novel study demonstrates for the first time the importance of considering the spatial and  
227 volumetric role of specific nature components for providing indirect nature experiences to people.  
228 We show that the contribution of individual trees to indirect nature experiences is highly skewed.  
229 Quantifying the relative importance of individual trees to people, and understanding how trees are  
230 indirectly experienced is an important step towards linking urban design and policy for maximising  
231 the health benefits from urban nature.

232

233 Trees located in private gardens are generally visible from more buildings than those  
234 neighbourhood trees on public land. When considering direct and indirect neighbourhood effects  
235 together, there was a weak negative relationship between a tree's height and its importance for  
236 providing indirect nature experiences. In retrospect this is unsurprising considering that trees that  
237 were visible from at least one building were on average 2.9 m shorter than trees with no line of  
238 sight to a building. Further, direct effects show that if a tree is tall, while its neighbours are short, it  
239 can also be seen by more buildings. This suggests that although in the main, it is a tree's location  
240 that is the most important determinant of their provision of indirect nature experiences, individual  
241 characteristics of the tree such as height can further influence this provision. The management of  
242 garden trees by individual households has the potential to influence the nature experiences of many  
243 more households in the neighbourhood. Unfortunately, largely due to conflict with urban  
244 intensification these trees may also be at the greatest risk of removal (Wyse, Beggs, Burns, &

245 Stanley, 2015). Therefore conservation schemes need to raise awareness of the importance of  
246 garden trees not only for the health and well-being of the household whose land the tree is on, but  
247 also of their neighbours who benefit from it through indirect nature experiences. As expected when  
248 considering direct and indirect neighbourhood effects together, there was a positive relationship  
249 between human population density and the provision of nature experiences, however individually  
250 trees with more space around them (i.e. lower human population density) had line of sight to more  
251 buildings (see Human population density, Table 1). Those trees located in low income, high density  
252 housing tended to fall within the viewscape of significantly more buildings, and thus have the  
253 potential to provide indirect nature experiences to more people. These trees are often located in  
254 areas with low levels of green space where people already have a reduced daily exposure to nature  
255 (Shanahan, Lin, Gaston, Bush, & Fuller, 2014), therefore the importance of these trees may  
256 increase further as they contribute a greater proportion of a person's daily nature experience and so  
257 associated health and well-being benefits.

258

259 Undoubtedly urban form is critical for determining how often and for how long individual  
260 organisms are experienced by people in towns and cities. Although Milton Keynes, a planned green  
261 town, had more trees, individually those trees contributed less to indirect nature experiences than  
262 did trees in Luton and Bedford (Fig. 1). At face value this suggests that individual trees in Milton  
263 Keynes are less important, however, experiences of nature are of course more complex and diverse  
264 than providing only indirect nature experiences between individual trees and people. People who  
265 experience multiple trees simultaneously may have an enhanced experience, further trees also  
266 provide nature experiences incidentally, such as while people are travelling to work or the shops, or  
267 intentionally such as when people experience trees by going to public parks (Keniger et al., 2013).  
268 Trees also provide vital ecosystem services such as pollution filtration, storm water processing and  
269 thermoregulation, the effectiveness of which will often also be dependent on their abundance and  
270 the structure of the landscape (e.g. Endreny et al., 2017). Here we explored the contribution of  
271 individual trees to indirect experiences in English towns that contain a broad range of urban forms,  
272 with examples ranging from highly industrialised to planned green town suburbs. It is likely that the  
273 general patterns in the distribution of nature experience provision shown here will be applicable  
274 more broadly across different urban designs. For example, suburban trees in Tokyo (typified by  
275 highly compact urban design) are likely to be experienced by a greater number of people than  
276 suburban trees in Brisbane (typified by sprawling green urban design).

277

278 Understanding how trees are experienced, both individually and collectively, is critical so that  
279 urban areas can be designed to maximise both positive nature experiences and ecosystem service

280 provision, to mitigate many of the health issues associated with urban living while also maintaining  
281 the health benefits from living in these areas. Encouragingly, only 2.3% of buildings in the study  
282 area had no line of sight to a tree (within 100 m of the building). These buildings were generally  
283 sporadically distributed, although there was an example of a development with few indirect nature  
284 experiences of this kind (Fig. 3a). We show how the strategic positioning of a small number of trees  
285 in existing green spaces has the potential to provide indirect nature experiences to a  
286 disproportionate number of buildings (Fig. 3b). We recognise that some urban trees may deliver  
287 more nuanced ecosystem services – e.g. some species will blossom more prolifically than others,  
288 some will provide enhanced branching structures within which birds can nest, and others will  
289 deliver fruit or food sources for both humans and wildlife. Accounting for these spatially variable  
290 attributes and placing different values on trees accordingly could provide a further interesting  
291 avenue of future research. Thus, we posit that trees are a significant component of green  
292 infrastructure, and their position in the landscape has the potential not only to provide indirect  
293 nature experiences, but also incidental experiences and to promote people seeking intentional nature  
294 experiences (Beery et al., 2017; Church, 2018). Indeed, there is a positive association between  
295 neighbourhood tree cover and a person’s orientation towards nature (Shanahan et al., 2017), with  
296 evidence that a person’s nature orientation is linked not only to their desire to seek health benefits  
297 but also their ability to receive these benefits (Capaldi, Dopko, & Zelenski, 2014).

298  
299 In sum, the biological world is hugely complex, and logically there will be significant variation not  
300 only in how people indirectly experience individual organisms, but also in how they are  
301 experienced incidentally and intentionally (Gaston et al., 2018). An organism’s contribution to  
302 these experiences of nature will be dependent on its position in space and time relative to people,  
303 and in urban areas this will often be driven by urban form. For stationary organisms, urban forms  
304 with increased connectivity for people will increase the number of people that encounter them,  
305 while greater green space connectivity will increase the ability of mobile organisms such as birds to  
306 move within and between green spaces and so encounter people (Cox, Inger, Hancock, Anderson,  
307 & Gaston, 2016). Finally, a species’ ecology will influence how conspicuous it is to human senses,  
308 with those species that are more visible or vocal, larger or have a stronger scent being more likely  
309 to be experienced by people. Future studies need to move beyond considering urban environments  
310 as binary combinations of green space and non-green space, and towards understanding the roles  
311 that individual organisms play in providing nature experiences. As urban intensification continues,  
312 while increased knowledge of the importance of greenspace is encouraging retrofitting of green  
313 infrastructure, relevant stakeholders need to invest often limited resources and space towards those  
314 species and groups of species that are experienced by the greatest numbers of people.

315

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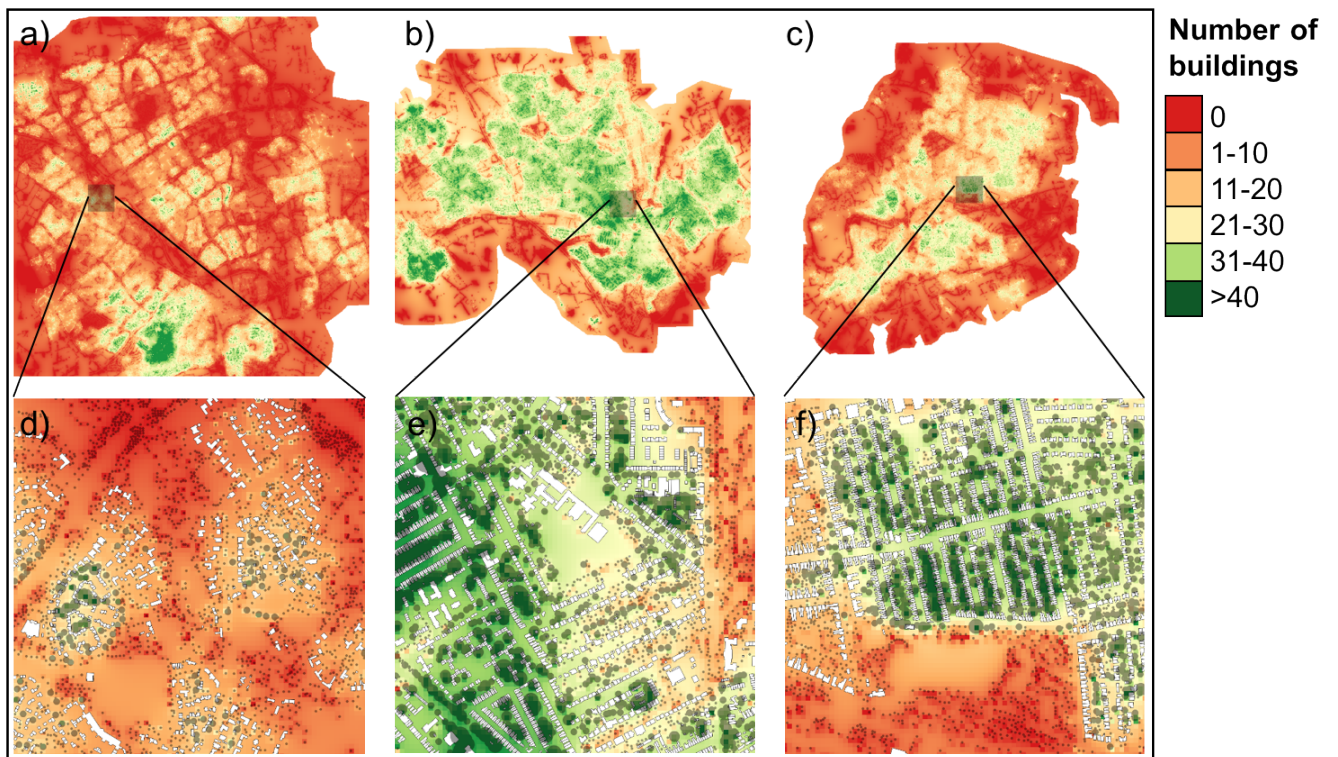
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**Table 1.** Predictors of the contribution of individual urban trees to indirect nature experiences in an urban human population. We show the direct (effect of independent variables on the response), indirect (mean effect of independent variables on neighbouring trees) and total (direct and indirect combined) unstandardized coefficients. Land ownership is against a base factor level of non-neighbourhood trees, and statistical significance is shown (\* $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; see supplementary material for the standardised coefficients (Table S1) and bivariate coefficients (Table S2)). The pseudo  $r$  squared is McFadden's.

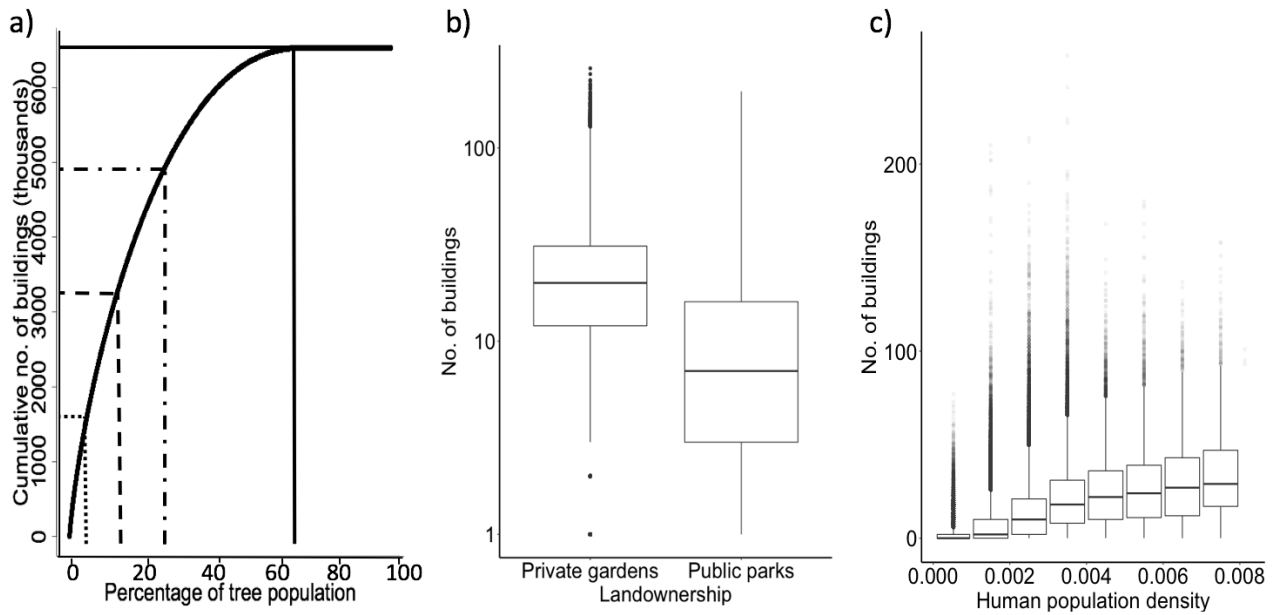
Variable	Direct coefficients	Indirect coefficients	Total coefficients
Tree height (m)	0.013 ( $\pm 2.4e-4$ )***	-0.033 ( $\pm 0.001$ )***	-0.02 ( $\pm 3.8e-4$ )***
Human population density <sup>#</sup>	-82.0 ( $\pm 7.3$ )***	147.6 ( $\pm 7.4$ )***	65.6 ( $\pm 0.6$ )***
Income <sup>##</sup>	-1.4e-4 ( $\pm 2.3e-5$ )***	-5.8e-4 ( $\pm 3.0e-5$ )***	-7.2e-4 ( $\pm 6.0e-6$ )***
<i>Land ownership</i>			
Private garden	2.0 ( $\pm 3.8e-3$ )***	1.3 ( $\pm 5.5e-3$ )***	3.3 ( $\pm 3.8e-3$ )***
Public land	1.7 ( $\pm 3.2e-3$ )***	0.2 ( $\pm 5.1e-3$ )***	1.9 ( $\pm 3.9e-3$ )***
pR <sup>2</sup>	0.81		

<sup>#</sup> Number of people per 500 m radius of each tree

<sup>##</sup> Average weekly household income



**Fig. 1.** Spatial variation in the contribution of individual trees to indirect nature experiences in three towns in Southern England: a) Milton Keynes, b) Luton, and c) Bedford. Heat maps have been graded from red (areas containing trees with line of sight to no buildings) to dark green (areas containing trees with line of sight to >40 buildings). d-f) magnified area within each town, illustrating typical urban forms. Green circles show trees, with the size of each circle being weighted by the number of buildings with line of sight to that tree. Upper panels have a width of 12,000 m, and lower panels 750 m.



**Fig. 2.** a) The cumulative number of buildings that have line of sight to each tree ( $n = 612,920$ ). We show the percentage of the tree population that accounts for 25% (dotted line), 50% (dashed line), 75% (dash/dot line) and 100% (solid line) of total indirect experiences (individual buildings may have line of sight to multiple trees, therefore the number of buildings shown here is an over representation of the true number at the study site). Relationships between the contribution of individual trees to indirect nature experiences, and b) land ownership (note: we do not show non-neighbourhood trees because these were selected as having line of sight to no buildings), and c) human population density.

**Fig. 3. a)** An example of an urban form where few buildings have line of sight to trees. Black polygons show buildings with line of sight to no trees, white polygons show buildings with line of sight to at least one tree. Green circles show trees, with the size of the circle being weighted by the number of buildings with line of sight to that tree (0 (smallest); 1-2; 2-11; >11 (largest)). Light grey polygons show existing public green spaces. **b)** Example of how the strategic placement of three trees (red circles) in existing public green spaces can provide indirect nature experiences to occupants of 126 buildings (red polygons).



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**Conflicts of interests**

We have no competing interests to declare.

**Ethical clearance**

Not applicable.

**Supplementary material:** Skewed contributions of individual trees to indirect nature experiences.

**List of appendices**

**Table S1.** Standardised coefficients for spatially lagged X model.

**Table S2.** Bivariate coefficients for spatially lagged X model.



**Table S1. Standardised coefficients for spatially lagged X model.** Predictors of the contribution of individual urban trees to indirect nature experiences in an urban human population. We show the direct (effect of independent variables on the response), indirect (mean effect of independent variables on neighbouring trees) and total (direct and indirect combined) standardized coefficients. Land ownership is against a base factor level of non-neighbourhood trees, and statistical significance is shown (\* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ). The pseudo r squared is McFadden's.

Variable	Direct coefficients	Indirect coefficients	Total coefficients
Tree height (m)	0.06 ( $\pm 0.001$ )***	-0.15 ( $\pm 0.002$ )***	-0.09 ( $\pm 0.002$ )***
Human population density <sup>#</sup>	-0.15 ( $\pm 0.01$ )***	0.27 ( $\pm 0.01$ )***	0.12 ( $\pm 0.001$ )***
Income <sup>##</sup>	-0.02 ( $\pm 0.005$ )***	-0.09 ( $\pm 0.005$ )***	-0.11 ( $\pm 0.001$ )***
<i>Land ownership</i>			
Private garden	2.0 ( $\pm 0.004$ )***	1.3 ( $\pm 0.006$ )***	3.2 ( $\pm 0.004$ )***
Public land	1.7 ( $\pm 0.003$ )***	0.2 ( $\pm 0.005$ )***	1.9 ( $\pm 0.004$ )***
pR <sup>2</sup>	0.81		

<sup>#</sup> Number of people per 500 m radius of each tree

<sup>##</sup> Average weekly household income

**Table S2. Bivariate coefficients for spatially lagged X model.** We show the direct (effect of independent variables on the response), indirect (mean effect of independent variables on neighbouring trees) and total (direct and indirect combined) unstandardized coefficients. Land ownership is against a base factor level of non-neighbourhood trees, statistical significance is shown (\* $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ), and the pseudo r squared is McFadden's.

Variable	Direct coefficients	Indirect coefficients	Total coefficients	$pR^2$
Tree height (m)	1.3-4 ( $\pm 4.9e-4$ )***	-0.23 ( $\pm 8.2e-4$ )***	-0.23 ( $\pm 6.4e-4$ )***	0.21
Human population density <sup>#</sup>	-374 ( $\pm 14.6$ )***	737 ( $\pm 14.8$ )***	363 ( $\pm 1.0$ )***	0.22
Income <sup>##</sup>	-6.3e-4 ( $\pm 6.6e-4$ )***	-0.002 ( $\pm 6.8e-4$ )***	-0.02 ( $\pm 1.2e-4$ )***	0.03
<i>Land ownership</i>				0.79
Private garden	2.0 ( $\pm 0.004$ )***	1.6 ( $\pm 0.005$ )***	3.6 ( $\pm 0.003$ )***	
Public land	1.7 ( $\pm 0.003$ )***	0.4 ( $\pm 0.005$ )***	2.1 ( $\pm 0.004$ )***	

<sup>#</sup> Number of people per 500 m radius of each tree

<sup>##</sup> Average weekly household income