Urban development, land sharing and land sparing: the importance of considering restoration

Lydia Collas[1], Rhys E. Green[1,2], Alexander Ross[1], Josie H. Wastell[1], and Andrew Balmford[1]

[1] Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

[2] RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy SG19 2DL, UK

Corresponding author:

Lydia Collas

Les Naftiaux Villa, Rue des Bailleuls, St Andrews, Guernsey, GY68XA

01481 237880

lydiacollas@gmail.com

Running title: Urban sharing vs sparing and habitat restoration

Summary

1. At present, there is limited knowledge of how best to reconcile urban development with biodiversity conservation, and in particular whether populations of wild species would be greater under low-density housing (with larger gardens), or high-density housing (allowing more area to be left as undeveloped green spaces). The land sharing/sparing framework – originally developed in the context of farming – can be applied to address this question.
2. We sampled the abundance of trees in the city of Cambridge, UK, along a gradient of human density. We designed different scenarios of urban growth to accommodate the human population predicted in 2031. For each scenario, we projected the future city-wide tree population size and quantified its carbon sequestration potential. We also considered, for the first time in an urban sharing-sparing context, the implications of habitat restoration on degraded urban green space.
3. We found that the density of most native and non-native tree species is presently highest in areas of low human density, compared to both higher-density areas and green space (which is largely maintained with few trees). However, restoring woodland in green spaces would lead to far greater densities of native trees than on any existing land use. Hence provided >2% of green space is restored, native tree population sizes would be larger if urban growth followed a land-sparing approach. Likewise, carbon sequestration would be maximised under land sparing coupled with restoration, but even so only a maximum of 2.5% of the city's annual greenhouse gas emissions could be offset.
4. Whilst both tree populations and carbon storage thus appear to benefit from land-sparing development, the risk that this might widen the existing disconnect between people and nature must also be addressed – perhaps through a combination of adding housing in low density areas while ensuring these are in close proximity to high-quality green space.
5. *Synthesis and applications*. In regions which have already been cleared of intact habitat, a combination of land-sparing urban development with the restoration of green space could

accommodate urban population growth whilst dramatically improving the existing status of local tree populations. Where cities are expanding into intact habitat, the merits of urban development by land sparing may be even more pronounced. Studies in such regions are urgently needed.

Key-words: City growth, human population, land sparing, land-use intensity, restoration, sustainable cities, urban nature, urban planning, urbanisation.

Introduction

The expansion of urban cover- the fastest growing land use (Seto *et al.* 2011)- is a major threat to biodiversity (Sala *et al.* 2000). The landscape changes vastly under urbanisation, with impacts extending to hydrological systems, climate, land-cover and biodiversity (Grimm *et al.* 2008). Furthermore, the human lifestyle changes that accompany a shift to urban living, particularly relating to diet, may place additional pressure on the environment elsewhere (Tilman & Clark 2014). Whilst cities thus present problems for biodiversity, they may also form part of the solution, given the increased efficiencies that can be achieved by people living close together (Dodman 2009; Gómez-Ibánez & Humphrey 2010). With 66% of the world's population predicted to live in cities by 2050 (UN 2014), the challenge of reconciling urban growth with biodiversity conservation demands attention.

Although the environment is altered by urbanisation, there is potential for cities to support a great deal of biodiversity. The assemblages found in cities tend to be unique and can be of global conservation value (Fuller, Tratalos & Gaston 2009; though see Shwartz *et al.* (2014)). Moreover, people benefit from urban biodiversity through the enhanced delivery of ecosystem services, including air filtration, local climate regulation, water infiltration, and human health and wellbeing (Bolund & Hunhammar 1999; Fuller *et al.* 2007). However, further study is needed to determine whether different ecosystem services can be maximised simultaneously (Bennett, Peterson &

Gordon 2009) and if ecosystem service delivery correlates positively to biodiversity (Anderson *et al.* 2009). Finally, the exposure of city residents to nature is thought to be important for maintaining a connection between people and the environment, potentially boosting interest in conservation (Miller 2005). This may be important for protecting biodiversity globally, given that the majority of people live in towns and cities, and that their actions also have impacts on the environment outside city boundaries.

Clearly there is much to be gained from maintaining nature in cities, which begs the question of how best to achieve it. The land sharing/sparing framework was initially developed in an agricultural context to determine how to meet increasing food demand at least cost to the environment (Green *et al.* 2005; Phalan *et al.* 2011). The relevance of the framework to an urban context has since been highlighted (Lin & Fuller 2013). Under land sharing, residents are housed in low-density housing with large, potentially wildlife-friendly gardens; these, however, increase the overall spatial footprint of the city. In contrast, in land-sparing cities residents are housed more densely, thereby requiring less land, potentially leaving space for large areas of green space in the same total area. To establish which of these extreme alternatives (or some intermediate approach) is best for biodiversity, the population densities of species of interest must be sampled along a gradient of human density, including in areas of open green space within the city. Evidence in favour of either strategy is so far limited, but preliminary studies largely favour a land-sparing approach (Sushinsky *et al.* 2012; Gagné & Fahrig 2010; Caryl *et al.* 2015), though this may not extend to all taxa and may depend on the degree of population growth to be accommodated (Soga *et al.* 2014).

Trees are an important group to consider in studies of urban sharing vs sparing. They provide important ecosystem services in urban areas including air filtration, microclimate regulation, noise reduction, rainwater drainage and recreational and cultural values (Bolund & Hunhammar 1999). Additionally, tree density has been found to positively correlate with the diversity of other taxa in urban areas (Smith *et al*. 2005; Fernandez-Juricic & Jokimäki 2001;

Murgui 2007), and urban tree species richness to increase with that of other species (Shwartz, Shirley & Kark 2008; but see Smith *et al.* 2005).

This paper explores variation in the distribution of trees across the city of Cambridge, UK, to investigate alternative approaches to limiting the environmental impact of urban growth. The human population of Cambridge is expected to increase by 22% between 2011 and 2031 (Cambridgeshire City Council 2013). By establishing relationships between tree density and human density in the city, we explore, for the first time, under what mode of urban growth trees will be more abundant. Importantly we also investigate alternatives to current green space by examining the implications of woodland restoration on open land. Finally, we investigate how to maximise an ecosystem service alongside urban growth, by quantifying the carbon sequestration potential of vegetation within the city.

Materials and methods

Study region

This study was conducted in Cambridge, UK. The study region was defined by the city boundary, giving an area of 40.7 km^2. We also conducted sampling in an area beyond the northwest city boundary which is earmarked for development (Cambridge City Council 2009), but excluded this area from scenario projections. In 2031, the population of Cambridge is expected to have grown by 27,000 people, from a population of 123,900 people in 2011 (Cambridgeshire City Council 2013). We used stratified random sampling to select 52 one-hectare plots. To ensure the full spectrum of human densities within the city were sampled, we viewed every hectare square on Digimap (EDINA Digimap Service) and assigned it to one of five strata based on the percentage of the plot that was covered by housing: Low (1-14% housing cover), Mid (15-40%), High (>40%), Green Space (<1%) and Concrete (plots developed for non-residential purposes which were not considered for sampling). From the remaining four strata, we randomly selected 12 hectare plots. To ensure these plots were spaced across the city, the study region was divided into four quadrants around its

N-S and E-W mid-points, and took three plots in each stratum from each quadrant. After preliminary data collection, we created an additional stratum for squares which appeared to have a very high density of housing (>70% housing cover), and randomly selected four plots within this category for sampling (one from each quarter) to ensure the higher end of the spectrum was adequately represented. We therefore sampled a total area of 52 hectares.

Study species

We used tree abundance as a measure of biodiversity. Each plot was visited in person to count the trees present and determine their identity to species level. Trees were counted provided their diameter at a height of 1.3m exceeded 20cm. A total of 106 species were counted at least once. We were unable to identify 38 trees, all thought to be non-native species. We then fitted curves (see below) to all species (12 natives, 9 non-natives - The Woodland Trust 2016) for which we recorded 20 or more individuals. Together these accounted for 76% of the trees counted (see Table S1 in Supporting Information).

The relationship between tree density and human density

We measured human density from census data. The most recent data was from 2011 at a spatial scale of “Lower Super-Output Areas” (Office for National Statistics 2015). Often these census units were larger than one hectare and so encompassed the entirety of our hectare plots. Where a plot intersected within more than one census unit, we estimated human density based on the proportional area covered by each unit. We then correlated this to the tree density in each sampled hectare plot.

Given the response of trees to urbanisation is thought to be species-specific (McKinney 2008), we fitted regression models relating the population density of each tree species to human density. For each of the 21 most common species, we plotted tree density against human density. We fitted curves to these graphs using maximum-likelihood univariate Poisson regression models (as in Phalan *et al.* 2011). We fitted two models initially:

$$y = \exp\left(b_0 + b_1 \left(x^{\alpha} \right)\right)$$

and

$$y = \exp\left(b_0 + b_1 \left(x^{\alpha} \right) + b2 \left(x^{2\alpha}\right)\right)$$

where y is tree density, x is human density and b_0, b_1 and α are constants. Model B has an additional parameter characterising the relationship, so we selected Model B if its residual deviance was more than 3.84 (X^2 with one degree of freedom for $P = 0.05$) less than that of Model A. Otherwise, we selected Model A for reasons of parsimony. As a measure of model fit, for each species we calculated the Pearson correlation coefficient (*r*) between observed and modelled densities across our sites (as in Phalan et al. (2011); see Table S1).

Comparing tree abundance under land-sharing and land-sparing approaches

We estimated the impact of urban growth on the abundance of tree species across a range of land-sharing and land-sparing approaches. We designed six scenarios that each accommodate the population growth of 27,000 people expected in Cambridge by 2031:

1. Build low-density housing on green space.
2. Build mid-density housing on green space.
3. Build high-density housing on green space.
4. Replace low-density housing with mid-density housing.
5. Replace low-density housing with high-density housing.
6. Replace mid-density housing with high-density housing.

Scenarios 1-3 reflect land-sharing urban growth because housing is built on currently undeveloped land. In contrast scenarios 4-6 are relatively land-sparing because they increase human density in existing residential areas (infilling).

We created four categories of land-use (Low-, Mid-, and High-human density and Green Space). We set arbitrary thresholds to define these categories and calculated the area of our study region currently falling into each based on census data (Office for National Statistics 2011; see Table S2). Since the spatial scale of the census data was larger than one hectare, the area classified as green space has a human density of <14.1 people per hectare. We set this upper bound so that the area of green space matched that estimated in our earlier Digimap assessment. We calculated the mean human density of the land in each of the four categories based on the census data, and used this as the density at which housing was built during the scenario projections.

We used tree count data to estimate the total densities of all native tree species and all non-native tree species combined for each category. We then used these densities and the total area of each category to calculate total tree population sizes under each scenario. We assessed the uncertainty in our projections of tree populations by bootstrap resampling. For each of the four categories, we drew bootstrap samples at random and with replacement for our tree count data equal in number to the number of samples we surveyed in that category. From this bootstrap sample, we then calculated the mean density of all native tree species combined and all non-native tree species combined. We made 10,000 sets of bootstrap estimates of this kind and took the bounds of the central 9,500 of them to define the 95% confidence limits for total tree density. We also used these bootstrap values in the calculation of total tree populations under the different land use scenarios.

The implications of restoring green space to woodland

Alongside our basic assessment of sharing vs sparing strategies, we investigated the implications of altering green space from its present form into woodland. We sampled tree densities in three nearby secondary woodlands on land not at risk of flooding (Environment Agency 2016): Coton

(52.209°N, 0.076°E, decimal degrees), Fulbourn (52.180°N, 0.233°E), Wandlebury (52.159°N, 0.183°E). We also sampled one woodland at risk of flooding: Cow Hollow's Wood (52.260°N, 0.198°E). At Coton, Fulbourn and Wandlebury we counted and identified the trees present in eight randomly selected 20 x 20m plots, which were then combined to give an estimate of overall composition. At Cow Hollow's Wood we sampled the entirety of a one hectare plot.

We refined our restoration scenarios by estimating the area of green space at risk of flooding in the study region (from Environment Agency 2016). On this land we simulated planting woodland akin to that of Cow Hollow's Wood. We deemed this land to be unsuitable for development and so its area remained constant in all scenarios. The remaining green space was planted at the mean tree density recorded in the three other woodlands.

We wished to allow for uncertainty in our estimates of mean densities of native and non-native trees. However, our sample sizes for dry woods (n = 3) and wet woods (n = 1) were too small to adopt the non-parametric bootstrap approach that we used to assess uncertainty for urban and green space tree densities. We therefore used a parametric bootstrap procedure. We calculated the mean and standard error of the mean densities of all native tree species combined and all non-native tree species combined for the three dry woods. We used these values and normal random deviates to generate 10,000 parametric bootstrap values for mean tree densities in dry woodlands. For wet woodland, we assumed that the standard error of our estimate of tree density in wet woodland was the same, as a proportion of the mean, as that for dry woodland. These proportions were 0.177 for native tree species and 0.266 for non-native species. We then generated 10,000 parametric bootstrap values for mean tree densities in wet woodlands using the same procedure as for dry woodlands.

We used these sets of bootstrap estimates of mean tree density in woodlands, along with the non-parametric bootstrap estimates of mean tree density in urban areas and green space, described above, together with assumed areas of different land types in our scenarios, to calculate expected tree populations for each of the 10,000 sets of bootstrap values. We took the bounds of the central

9,500 of these tree population estimates to define the 95% confidence limits of tree population for each scenario. We also used these bootstrap values in the calculation of ratios of tree populations for one scenario relative to another. To do this, we calculated each ratio from each bootstrap replicate and took the bounds of the central 9,500 of the ratios to define the 95% confidence limits.

We supplemented these analyses with an investigation into the consequences of restoring only a proportion of green space to woodland. To do this, for each scenario we estimated the tree population size if 0-100% of green space (in 10% increments) is restored to woodland.

Maximising carbon sequestration

We estimated the mass of carbon that would be sequestered by the trees growing in each scenario. We wished to quantify sequestration on a species-specific basis since sequestration rates differ between species (as in Rogers *et al.* 2015). We did not use the above method for estimating tree populations in each scenario given the difficulty of calculating confidence limits for each species separately and due to the lack of uncertainty estimates in the sequestration rates. Instead, we used the density-density plots (Fig. 1) to calculate the density of trees of each species associated with each land-use category (see Table S2). And, based on the amount of land in each category in each scenario, we calculated the associated tree population sizes.

We quantified sequestration by urban trees (for both native and non-native species) based on species-specific data published in a report by i-TREE in London, UK (Rogers *et al.* 2015). This report detailed the number of trees of each species in London, and estimates their annual sequestration (based on allometric relationships). We used this to estimate carbon sequestration per tree, for each species, and hence for all urban trees in each scenario. This method assumed that the size and age distribution of urban trees in our study region was similar to that in London, and that factors affecting growth rate were equal. The i-TREE report adjusted sequestration rate based on whether a tree is growing in a stand or in isolation (trees not in stands are considered to gain biomass more slowly and so their sequestration rate was multiplied by 0.8 (Nowak *et al.* 1994)). We used the same adjustment, assuming that a similar proportion of urban trees in our study region were growing in stands.

For the restoration scenarios, we estimated the carbon sequestration potential of trees in planted woodland using a different method, based on data on observed sequestration rates per hectare of re-established woodland (Forestry Commission 2013). We used the figures for a sycamore-ash-birch woodland (which we considered representative of what would grow in our study region) and a yield class of 4 (which is thought to give a conservative estimate of growth rate). We determined the annual sequestration by each hectare of woodland in the restoration scenarios as a mean of that over the first 40 years following planting (as in Lamb *et al.* 2016).

To provide context, we compared sequestration under our scenarios with the estimated greenhouse gas footprint of the city of Cambridge in 2013 (Department of Energy & Climate Change 2015). This estimate included emissions arising from the production and processing of fuels, including electricity consumption, which were geographically allocated based on the end user. Emissions arising from land use and land-use change were also included. However, methane emissions arising from the drainage of land, all greenhouse gas emissions from the rewetting of land, and methane emissions from agriculture were not included (Webb *et al*. 2014). We then estimated the proportion of the city’s current emissions that could be offset by sequestration under each scenario of urban growth.

Results

Regression models fitted to characterise the relationship between tree density and human density revealed the majority of native and non-native species were more abundant in areas of low human density than in either green space or areas supporting more people (Figure 1a; 9 out of 12 natives, 7 out of 9 non-natives). Four species occurred at similar density on green space and in areas of low human density, only declining at higher human densities (Figure 1b; 3 out of 9 natives, 1 out of 9 non-natives). One non-native species increased in abundance with progressively higher human densities (Figure 1c).

The majority of native species studied were present in the sampled secondary woodlands, typically at much greater densities than in residential areas (Figure 1a-b; 9 out of 12 native species). Only one non-native species, *Acer pseudoplatanus*, occurred in the sampled woodlands, whilst the remaining three native species and eight non-native species were not found (Figure 1c).

In the absence of restoration, native and non-native tree population sizes were, on average, projected to be maximised under land-sharing development (Figure 2a), but confidence intervals for total tree population projections overlapped 1 (no difference) for many pairwise comparisons between scenarios (see Table S3). Given that current green space supports relatively few trees, increasing human settlement density on green space (Scenario 1) resulted in native tree populations approximately 15% larger than at present. Land-sparing approaches (Scenarios 4-6) resulted in small declines in both native and non-native tree population sizes of <5%, compared with present.

In contrast, when remaining green space was restored to woodland, projected native tree population sizes were maximised by a land-sparing approach and increased substantially under land sparing because secondary woodland supports much higher tree densities than any of our developed areas (Figure 2b, Scenarios 4-6). In contrast to the case with no restoration (see above), confidence intervals for total tree population projections for native species overlapped 1 (no difference) only for many pairwise comparisons among scenarios 4, 5 and 6 (see Table S4). Under infilling development, native tree populations were projected to be >12 times greater than their present day size. The exact mode of infilling had little effect (with results being similar across Scenarios 4-6). On average, projected non-native tree populations increased under restoration. More land-sparing approaches resulted in the number of non-native trees increasing >50%, owing to the presence of

Acer pseudoplatanus in our sampled woodlands, but confidence intervals for total non-native tree population projections overlapped 1 (no difference) for all pairwise comparisons between scenarios (see Table S4).

Our analysis of partial (rather than complete) restoration showed that the proportion of green space undergoing restoration that is needed for native tree populations to be larger under land sparing compared to land sharing was strikingly low (Figure 3). Provided ≥2% of green space (i.e. ≥30 ha) was restored to woodland (in addition to current coverage), the infilling scenarios (Scenarios 4-6) gave rise to greater native tree population sizes than the most extreme land-sharing scenario (Scenario 1), which performed best in absence of restoration.

The amount of carbon that could be captured was broadly similar in all scenarios when green space retained its current form. The combined annual sequestration of all trees in the city, across the most common 21 native and non-native species combined, was equivalent to the capture of 0.4-0.5% of the city's annual GHG emissions (Figure 4a). A far greater mass of carbon was sequestered under all scenarios when green space was restored to woodland, and capture was maximised under more land-sparing approaches (Figure 4b, Scenarios 4-6). However, even with 100% restoration the best-performing scenario captured only ~2.5% of the city's current annual emissions.

Discussion

We found the relationship between tree density and human density to be contingent on the status of green space. With green space in its current form, the majority of native and non-native species occur most frequently in areas of low human density. Consequently, urban growth by land sharing would result in minor increases to current tree population sizes, for both native and non-native species. However, in areas of secondary woodland, native species are found at densities far greater than in areas of either low settlement density or green space in its current form. Therefore, by combining land-sparing urban growth with the restoration of green space to woodland, the existing population of native trees could increase by an order of magnitude. Non-native populations would increase >50%, largely due to the occurrence of *Acer pseudoplatanus* in local woodlands. Land-sparing development gives rise to native tree populations that are larger in size than those under land sharing even if as little as 2% of available green space is restored to woodland.

In our projections, it must be noted that land-sparing restoration was not unanimously beneficial for all native species. Three species were found more frequently at low human settlement densities than in woodland. One species, *Malus sylvestris*, occurred frequently in gardens but is seemingly rarer in woodland. However, the other two species, *Ilex aquifolium* and *Sambucus nigra*, are not frequently planted during restoration, but nevertheless establish on land taken out of cultivation and left to return naturally to woodland (Jenkinson 1971). Hence even some of these species may increase in frequency under restoration, despite our projections.

The emissions footprint of the city's residents is considerably greater than we have considered here. Whilst the calculation of GHG emissions includes those arising from travel, construction and some forms of land-use change within the city, it excludes emissions relating to other forms of land-use change (such as rewetting and draining land), all agriculture-related methane emissions, and emissions caused by the activities of city residents which occur elsewhere (such as air travel; Department of Energy & Climate Change 2015; Webb et al. 2014). However, we have only estimated sequestration by urban trees for the 21 most frequently counted species, though this is unlikely to outweigh the extent to which the city's GHG footprint is underestimated given that our estimate includes the majority of urban trees (and all woodland trees) yet projects offset of 2.5% of the city's emissions at best. Therefore, we have likely overestimated sequestration capacity.

Policy regarding urban development will play a role in whether a land-sparing strategy is adopted. The Cambridge Local Plan (2006) dictates that >65% of new homes built between 1999-

2016 should be on previously developed land. Additionally, it promotes building housing at high densities, particularly in the city centre and around key transport interchanges. This is in line with UK-wide policy, in place since 2000, which has already led to increased housing density in built-up areas (Bibby 2009). However, high demand for housing in Cambridge may lead to development encroaching on green space as opportunities for infilling are exhausted. Indeed, land has already been taken out of the green belt for the purpose of urban development (Cambridge Local Plan 2006). With respect to policy on woodland restoration, there are plans to increase the city's tree cover by at least 2% above its present level of 17% (ADAS 2013) by the 2030s, through planting a diverse array of species (Cambridge City Council 2016).

Housing density is only one of many factors that influence tree density in urban areas. In private residential areas, housing age, terrain slope, level of education and household income are also correlated with variation in tree cover, though housing density is thought to be most important (Daniel, Morrison & Phinn 2016). Species composition is affected by biophysical factors, as well as people's preferences (Nitoslawski, Duinker & Bush 2016). New developments are typically associated with less vegetation (Lin *et al*. 2017; Daniel, Morrison & Phinn 2016), so unless this is addressed it is possible that future development will give rise to lower tree densities than projected here.

There is reason to believe our findings will extend to other taxa. Tree density in urban areas has been found to be correlated to that of insects (Smith *et al*. 2005) and birds (Fernandez-Juricic & Jokimäki 2001; Murgui 2007). However, it must be noted that plant taxa may fare better in towns than other taxonomic groups (McKinney 2008) and other taxa will likely respond differently to the restoration of woodland on green space. Where areas of green space are small and poorly connected some taxa will be unlikely to establish (Gaston *et al*. 1998; Bailey 2007), or will take time-particularly species that require mature woodland (Biaduń & Zmihorski 2011). That said, previous studies have also reported that, provided green space is of adequate quality, land-sparing urban development would be better than land sharing- for birds (Sushinsky *et al*. 2012; Gagné & Fahrig 2010), fruit bats (Caryl *et al.* 2015), and ground beetles (Soga *et al.* 2014). However, results are not unanimously in favour of sparing: Soga *et al.* (2014) find butterflies do better under land-sharing development, though only when human population growth is low.

Many ecosystem service benefits are thought to arise from increasing tree cover in cities including air filtration, microclimate regulation, noise reduction, rainwater drainage and recreational and cultural values (Bolund & Hunhammar 1999). Therefore, ecosystem services may be maximised under a land-sparing approach to development (Stott *et al.* 2015), which we have also shown to maximise carbon sequestration, provided it is coupled with the restoration of woodland on open green space. However, it must be noted that trees can generate disservices, through the risk of damage to physical structures posed by falling debris or tree roots (Lyytimäki & Sipilä 2009), an increased fear of crime (Nasar, Fisher & Grannis 1993) and elevated management costs (Escobedo, Kroeger & Wagner 2011). Therefore, increasing tree cover is unlikely to be desirable everywhere.

Further knowledge of the implications of land-sparing development on human health and wellbeing is required. Preliminarily evidence suggests it may be negatively affected under land-sparing development (Stott *et al.* 2015). However, the proximity of housing to green space is thought to be the crucial factor (Soga *et al.* 2015) and so strategic design to maintain this in a land-sparing city could offer a solution. Perhaps the greatest cost of a land-sparing city design is the risk that residents could become further disconnected from nature due to the separation of housing and green space. This has led some to question whether cities should serve to reverse this disconnect, even at the expense of local biodiversity, provided the global effect is positive (Shwartz *et al.* 2014). However further study is required to ascertain what measures are effective for reversing this disconnect, and to determine whether they indeed do need to come at the expense of local biodiversity. Large-scale restoration to return areas of green space within cities closer to a state of wilderness may prove most fruitful in restoring an interest in nature amongst people (Miller 2005).

Conclusion

Our study has demonstrated the importance of considering the status and restoration potential of open green space when investigating how to limit the negative environmental impacts of urban growth. For other cities in the UK and across Europe, which have generally long been cleared of natural habitat (Kaplan, Krumhardt & Zimmermann 2009), restoration in parallel with the expansion of higher-density housing would appear to offer greatest scope for accommodating population growth at least cost to nature. This would require policy and economic incentives to directly link high-intensity human land-use to large-scale restoration, as has recently been argued in the context of farming (Phalan *et al.* 2016). There remains an urgent need for studies in cities which are expanding into previously undeveloped land; these include some of the world's fastest-growing urban centres (Cincotta, Wisnewski & Engelman 2000). In these areas, where species sensitive to anthropogenic disturbance may have not yet been lost, the merits of land-sparing development could be even more pronounced.

Authors' contributions

AB and REG conceived the initial idea; all authors contributed to designing methodology; LC, AR and JHW collected the data; LC, AR, JHW and REG analysed the data and LC led the writing of the manuscript; AB and REG contributed critically to the drafts and all authors gave final approval for publication.

Data Accessibility

Data available from Dryad Digital Repository doi:10.5061/dryad.b19pd (Collas et al. 2017).

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Models of density of all tree species combined and calculation of uncertainty estimates in tree population projections,

Table S1. Summary of models fitted to count data.

Table S2. Land-use categories and associated human densities.

Table S3. Bootstrap 95% confidence limits for tree population sizes for scenarios without restoration.

Table S4. Bootstrap 95% confidence limits for tree population sizes for scenarios with restoration.

Figure S1. Density-density plots showing fitted regression models for 12 native and 9 non-native species.

Figure S2. Density-density plots showing fitted regression models for native and non-native species.

Figure S3. Projected population sizes for all native tree species for each scenario relative to Scenario 1 with 95% bootstrap confidence limits.

Figure legends for main text figures

Figure 1. Density-density plots showing fitted regression models based on data points collected in the sample region. Shading shows associated land use categories (with increasingly dark shades depicting green space and low-, mid- and high-population density areas). ~~Green~~ Triangular points represent tree densities at the four sampled secondary woodlands, but were not used in curve-fitting. *Betula pendula* and *Acer campestre* are native and both were recorded in woodland, unlike non-native *Platanus hispanica.*

Figure 2. Projected tree population sizes in each scenario relative to present. In (a) green space is maintained in its current form. In (b) green space is restored to woodland.

Figure 3. Projected native tree population sizes under different scenarios of urban growth, shown relative to that of Scenario 1 (the most land-sharing scenario), in relation to the proportion of remaining green space restored to woodland. The solid curve represents the ratio for Scenario 2 relative to Scenario 1, the dashed curve is for Scenario 3 and the dotted curve is for Scenarios 4, 5 and 6, which overlay one another. Uncertainties in these ratios are given in Figure S3.

Figure 4. The percentage of Cambridge's annual greenhouse gas emissions that could be offset by sequestration under different scenarios. In (a) green space retains its current form whilst in (b) it is restored to woodland.

References

ADAS (2013) Analysis and Interpretation of Tree Audit Data For Cambridge City Council. Ref: CEN5002.

Anderson, B., Armsworth, P., Eigenbrod, F., Thomas, C., Gillings, S., Heinemeyer, A., Roy, D. & Gaston, K. (2009) Spatial covariance between biodiversity and other ecosystem service priorities. Journal of Applied Ecology, 46, 888-896.

Bailey, S. (2007) Increasing connectivity in fragmented landscapes: An investigation of evidence for biodiversity gain in woodlands. Forest Ecology and Management, 238, 7-23.

Bennett, E., Peterson, G. & Gordon, L. (2009) Understanding relationships among multiple ecosystem services. Ecology Letters, 12, 1394-1404.

Biaduń, W. & Zmihorski, M. (2011) Factors shaping a breeding bird community along an urbanization gradient: 26-year study in medium size city (Lublin, se Poland). Polish Journal of Ecology, 59:381–389

Bibby, P. (2009) Land use change in Britain. Land Use Policy, 26, S2-S13.

Bolund, P. & Hunhammar, S. (1999) Ecosystem services in urban areas. Ecological Economics, 29, 293-301.

Cambridge City Council: North West Cambridge Area Action Plan. (2009). https://www.cambridge.gov.uk/content/north-west-cambridge-area-action-plan-0 (accessed October 2015).

Cambridge City Council (2006). Cambridge Local Plan. https://www.cambridge.gov.uk/content/local-plan-2006 (accessed 6/12/16).

Cambridge City Council (2016) City Wide Tree Strategy 2016 – 2026. Part One. https://www.cambridge.gov.uk/tree-strategy (accessed 6/12/16).

Cambridgeshire City Council: Population, Housing and Employment Forecasts Technical Report (2013). http://www.cambridgeshireinsight.org.uk/housing/current-version/PopHseEmp_TechReport2013 (accessed January 2016).

Caryl, F., Lumsden, L., van der Ree, R. & Wintle, B. (2015) Functional responses of insectivorous bats to increasing housing density support 'land-sparing' rather than 'land-sharing' urban growth strategies. Journal of Applied Ecology, 53, 191-201.

Cincotta, R., J. Wisnewski, & Engelman, R. (2000) Human population in the biodiversity hotspots. Nature, 404, 990-992.

Collas, L., Green, R.E., Ross, A., Wastell, J.H. & Balmford, A. (2017) Data from: Urban development, land sharing and land sparing: the importance of considering restoration. Dryad Digital Repository. http://doi:10.5061/dryad.b19pd

Department of Energy & Climate Change. (2015) 2005 to 2013 UK local and regional CO2 emissions: statistical release. https://www.gov.uk/government/statistics/uk-local-authority-and-regional-carbon-dioxide-emissions-national-statistics-2005-2013 (accessed March 2016).

Dodman, D. (2009) Blaming cities for climate change? An analysis of urban greenhouse gas emissions inventories. Environment and Urbanization, 21, 185-201.

EDINA Digimap Ordnance Survey Service. http://digimap.edina.ac.uk/ (accessed October 2015).

Environment Agency. (2016) Interactive Map: Flood Map for Planning (Rivers and Sea) http://maps.environment-agency.gov.uk/wiyby/wiybyController?lang=_e&topic=floodmap&layer=default&ep=map&layerGroups=default&scale=10&x=549811&y=264864#x=549749&y=265182&lg=1,2,10,&scale=4 (accessed July 2016).

Escobedo, F., Kroeger, T. & Wagner, J. (2011) Urban forests and pollution mitigation: Analyzing ecosystem services and disservices. *Environmental Pollution*, 159, 2078-2087.

Fernandez-Juricic, E., & Jokimäki, J. (2001) A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity & Conservation*, *10*(12), 2023-2043.

Forestry Commission. Carbon Lookup Tables V1.5 (worksheet 'Carbon Lookup Table'). (2013). http://www.forestry.gov.uk/forestry/INFD-8JUE9T (accessed July 2016).

Fuller, R., Irvine, K., Devine-Wright, P., Warren, P. & Gaston, K. (2007) Psychological benefits of green space increase with biodiversity. Biology Letters, 3, 390-394.

Fuller, R., Tratalos, J. & Gaston, K. (2009) How many birds are there in a city of half a million people? Diversity and Distributions, 15, 328-337.

Gagné, S. & Fahrig, L. (2010) The trade-off between housing density and sprawl area: Minimising impacts to forest breeding birds. Basic and Applied Ecology, 11, 723-733.

Gómez-Ibánez, J.A., & Humphrey, N. (2010) Driving and the built environment: the effects of compact development on motorized travel, energy use and CO2 emissions. Transportation Research Board: Special Report, 268, pp. 24–28.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. (2005) Farming and the fate of wild nature. Science, 307, 550-555.

Grimm, N., Faeth, S., Golubiewski, N., Redman, C., Wu, J., Bai, X. & Briggs, J. (2008) Global Change and the Ecology of Cities. Science, 319, 756-760.

Isbell, F., Tilman, D., Polasky, S. & Loreau, M. (2014) The biodiversity-dependent ecosystem service debt. Ecology Letters, 18, 119-134.

Jenkinson, D. S. (1971) The accumulation of organic matter in soil left uncultivated. Rothamsted Experimental Station Report for 1970, Part 2, 113-137.

Kaplan, J., Krumhardt, K. & Zimmermann, N. (2009) The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews, 28, 3016-3034.

Lamb, A., Green, R., Bateman, I., Broadmeadow, M., Bruce, T., Burney, J. et al. (2016) The potential for land sparing to offset greenhouse gas emissions from agriculture. Nature Climate Change, 6, 488–492

Lin, B., and R. Fuller. 2013. Sharing or sparing? How should we grow the world's cities? Journal of Applied Ecology 50: 1161–1168.

Lin, B., Gaston, K., Fuller, R., Wu, D., Bush, R. & Shanahan, D. (2016) How green is your garden?: Urban form and socio-demographic factors influence yard vegetation, visitation, and ecosystem service benefits. *Landscape and Urban Planning*, 157, 239-246.

Lyytimäki, J. & Sipilä, M. (2009) Hopping on one leg – The challenge of ecosystem disservices for urban green management. *Urban Forestry & Urban Greening*, 8, 309-315.

Miller, J. (2005) Biodiversity conservation and the extinction of experience. Trends in Ecology & Evolution, 20, 430-434.

McKinney, M. (2008) Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, 11, 161-176.

Murgui, E. (2007) Factors influencing the bird community of urban wooded streets along an annual cycle. *Ornis Fennica* 8, 66–77.

Nasar, J., Fisher, B. & Grannis, M. (1993) Proximate physical cues to fear of crime. *Landscape and Urban Planning*, 26, 161-178.

Nitoslawski, S., Duinker, P. & Bush, P. (2016) A review of drivers of tree diversity in suburban areas: Research needs for North American cities. *Environmental Reviews*, 24, 471-483.

Nowak, D. (1994) Atmospheric carbon dioxide reduction by Chicago’s urban forest, in McPherson, E., Nowak, D., Rowntree, R., (Eds). Chicago’s urban forest ecosystem: Results of the Chicago Urban Forest Climate Project. USDA Forest Service, Radnor, PA.

Office of National Statistics (2015) Mid-2014 Population Estimates for Census Output Areas in the East region of England. http://www.ons.gov.uk/peoplepopulationandcommunity/populationandmigration/populationestimates/datasets/censusoutputareaestimatesintheeastregionofengland (accessed December 2015).

Phalan, B., Green, R., Dicks, L., Dotta, G., Feniuk, C., Lamb, A., Strassburg, B., Williams, D., zu Ermgassen, E. & Balmford, A. (2016) How can higher-yield farming help to spare nature? Science, 351, 450-451.

Phalan, B., Onial, M., Balmford, A. & Green, R. (2011) Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. Science, 333, 1289-1291.

Rogers, K., Sacre, K., Goodenough, J., Doick, K. (2015) Valuing London's Urban Forest: Results of the London i-TREE Eco Project Treeconomics London.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. et al. (2000) Global biodiversity scenarios for the year 2100. Science, 287, 1770–1774.

Seto, K., Fragkias, M., Güneralp, B. & Reilly, M. (2011) A Meta-Analysis of Global Urban Land Expansion. PLoS ONE, 6, e23777.

Shwartz, A., Shirley, S. & Kark, S. (2008) How do habitat variability and management regime shape the spatial heterogeneity of birds within a large Mediterranean urban park?. *Landscape and Urban Planning*, 84, 219-229.

Shwartz, A., Turbé, A., Julliard, R., Simon, L. & Prévot, A. (2014) Outstanding challenges for urban conservation research and action. Global Environmental Change, 28, 39-49.

Smith, R., Warren, P., Thompson, K. & Gaston, K. (2005) Urban domestic gardens (VI): environmental correlates of invertebrate species richness. *Biodiversity and Conservation*, 15, 2415-2438.

Soga, M., Yamaura, Y., Aikoh, T., Shoji, Y., Kubo, T. & Gaston, K. (2015) Reducing the extinction of experience: Association between urban form and recreational use of public greenspace. Landscape and Urban Planning, 143, 69-75.

Soga, M., Yamaura, Y., Koike, S. & Gaston, K. (2014) Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation? Journal of Applied Ecology, 51, 1378-1386.

Stott, I., Soga, M., Inger, R. & Gaston, K. (2015) Land sparing is crucial for urban ecosystem services. Frontiers in Ecology and the Environment, 13, 387-393.

Sushinsky, J., Rhodes, J., Possingham, H., Gill, T. & Fuller, R. (2012) How should we grow cities to minimize their biodiversity impacts? Global Change Biology, 19, 401-410.

The Woodland Trust. http://www.woodlandtrust.org.uk/visiting-woods/trees-woods-and-wildlife/british-trees/ (accessed February 2016).

Tilman, D. & Clark, M. (2014) Global diets link environmental sustainability and human health. Nature, 515, 518-522.

United Nations Department of Economic and Social Affairs, Population Division. (2014) World Urbanization Prospects: The 2014 Revision, Highlights (ST/ESA/SER.A/352).

Vilà, M., Vayreda, J., Comas, L., Ibáñez, J., Mata, T. & Obón, B. (2007) Species richness and wood production: a positive association in Mediterranean forests. Ecology Letters, 10, 241-250.

Webb N, Broomfield M, Cardenas L, MacCarthy J, Murrells T, Pang Y, Passant N, Thistlethwaite G, Thomson A, UK Greenhouse Gas Inventory, 1990 to 2013: Annual Report for submission under the Framework Convention on Climate Change. http://naei.defra.gov.uk/reports/reports?report_id=747 (accessed 4/12/16).