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Quantifying nectar production by flowering plants in urban and rural landscapes

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Abstract

1. Floral resources (nectar and pollen) provide food for insect pollinators but have declined in the countryside due to land use change. Given widespread pollinator loss, it is important that we quantify their food supply to help develop conservation actions. While nectar resources have been measured in rural landscapes, equivalent data are lacking for urban areas, an important knowledge gap as towns and cities often host diverse pollinator populations.

2. We quantified the nectar supply of urban areas, farmland and nature reserves in the UK by combining floral abundance and nectar sugar production data for 536 flowering plant taxa, allowing us to compare landscape types and assess the spatial distribution of nectar sugar among land uses within cities.

3. The magnitude of nectar sugar production did not differ significantly among the three landscapes. In urban areas the nectar supply was more diverse in origin and predominantly delivered by non-native flowering plants. Within cities, urban land uses varied greatly in nectar sugar production. Gardens provided the most nectar sugar per unit area and 85% of all nectar at a city scale, while gardens and allotments produced the most diverse supplies of nectar sugar. Floral abundance, commonly used as a proxy for pollinators' food supply, correlated strongly with nectar resources, but left a substantial proportion of the variation in nectar supply unexplained.

4. *Synthesis*. We show that urban areas are hotspots of floral resource diversity rather than quantity and their nectar supply is underpinned by the contribution of residential gardens. Individual gardeners have an important role to play in pollinator conservation as ornamental plants, usually non-native in origin, are a key source of nectar in towns and cities.

1 | INTRODUCTION

Large-scale changes to land use and management intensity have resulted in the landscape-level depletion of floral resources, which provide food for insect pollinators (Baude et al., 2016; Carvell et al., 2006). A reduction in both the quantity and diversity of floral resources (nectar and pollen) is a major factor contributing towards the declines pollinators are experiencing, particularly in Europe and North America (Goulson et al., 2015; Roulston & Goodell, 2011). Given the key role pollinators play in the functioning of terrestrial ecosystems and their contribution to agricultural productivity (Klein et al., 2007; Ollerton et al., 2011), there is a need to quantify their food supply across entire landscapes.

Nectar supply has been quantified in some rural landscapes (Baude et al., 2016; Flo et al., 2018; Timberlake et al., 2019), but equivalent data for urban settings are lacking (but see Hicks et al., 2016 for nectar and pollen resources in urban flower meadows). This is an important knowledge gap because towns and cities are highly modified environments which are expanding rapidly world-wide (Grimm et al., 2008; Seto et al., 2012). Although urbanisation is regarded as a major threat to biodiversity (Chace & Walsh, 2006; McKinney, 2008; Seto et al., 2012), insect pollinators, particularly bees, can show a surprising degree of tolerance towards urban habitats (Baldock, 2020; Hall et al., 2017; Wenzel et al., 2020). For example, studies in the UK and Germany have found a higher species richness of bees in urban sites compared with surrounding farmland (Baldock et al., 2015; Theodorou et al., 2017, 2020), although contrasting patterns are also reported (e.g. Ahrné et al., 2009; Bates et al., 2011; Lagucki et al., 2017), probably a result of variation in urbanisation and management intensity at the study sites (Wenzel et al., 2020). The comparative success of bees in urban areas is likely to be influenced by the availability of flower-rich green spaces, such as parks and gardens (Baldock et al., 2019; Hülsmann et al., 2015), which can be important sources of nectar and pollen. This is further supported by experiments which recorded bumblebee colonies growing larger in urban and suburban habitats versus agricultural areas (Goulson et al., 2002; Samuelson et al., 2018; but see Milano et al., 2019 for a counter example).

The aim of this study is, for the first time, to quantify the nectar supply of entire urban landscapes, thereby allowing direct comparisons with rural areas, and to investigate the spatial distribution of nectar sugar within cities. Flower counts are typically used as a proxy for nectar and pollen resources (e.g. Baldock et al., 2019; Lowenstein et al., 2018; Matteson et al., 2013, but see Baude et al., 2016; Hicks et al., 2016; Timberlake et al., 2019 for exceptions), with the implicit assumption that each flower provides a similar quantity of food for foraging pollinators. However, this is a major simplification as the amount of nectar and pollen provided by individual flowers of different plant taxa can vary over orders of magnitude (Baude et al., 2016; Hicks et al., 2016). Counts may also provide an especially poor proxy for resource production in urban areas as there is a high proportion of ornamental plants, selectively bred for floral traits that are attractive to people rather than insects, which may provide less nectar and/or pollen (Corbet et al., 2001). Here we combine flower counts with empirical values of nectar sugar production to quantify the nectar supply in urban areas.

Specifically, we asked two questions: (1) How does the nectar supply differ between urban, farmland and nature reserve landscapes? Baldock et al. (2015) reported that pollinator abundance and richness were comparable among these three landscapes, but we do not know how they differ in floral resources. (2) How does the nectar supply differ among the separate land uses that comprise urban landscapes? Towns and cities are heterogeneous patchworks of distinct land uses that differ markedly in their value for insect pollinators (Baldock et al., 2019) and so it is important to understand their relative contributions to landscape-level nectar supply. We also examined the relationship between floral abundance and nectar sugar production to assess the strengths and weaknesses of using flower counts as a proxy for nectar resources.

2 | MATERIALS AND METHODS

To quantify the nectar supply of urban and rural landscapes we combined data on floral abundance with nectar sugar production values (Supporting Information S1). Floral abundance was measured in UK urban and rural areas by Baldock et al. (2015, 2019), and nectar production by Baude et al. (2016), Hicks et al. (2016) and Timberlake et al. (2019) or in this study. Most published nectar sugar values correspond to UK native species, but urban landscapes contain a high proportion of non-native plants (Baldock et al., 2019; Loram et al., 2008). Consequently, we focused our field sampling on the wide variety of non-native species recorded in UK towns and cities.

2.1 | Floral abundance data

To compare the nectar supply between urban, farmland and nature reserve landscapes (question 1) we used floral abundance data previously collected at 36 sites across the UK (Baldock et al., 2015). A representative site was chosen for each of the three landscape types in and around 12 towns and cities. Landscapes comprised a variety of habitats, which were sampled in proportion to their abundance at each site. Thus, urban areas included residential land (containing gardens), allotments, buildings, hard surfaces, public greenspace and woodland; farmland

comprised arable fields, pasture, waste ground, field margins, hedgerows and woodland; nature reserves included woodland, grassland, heathland and wetland. To compare nectar supply among urban land uses (question 2) we used floral abundance data previously collected at 360 sites in four UK cities (Baldock et al., 2019). Cities were divided into ten geographic regions and within each region nine land uses were surveyed: allotments, cemeteries, gardens, manmade surfaces (e.g. car parks and industrial estates), nature reserves, other greenspaces (e.g. amenity grassland), parks, pavements and road verges.

Floral abundance data were collected by systematically sampling along transects and counting the number of floral units (defined as a single flower or collection of flowers following Baldock et al., 2015; Supporting Information S2) for each plant taxon. For the landscape comparison (question 1) floral abundance data were gathered across 100 quadrats (totalling 25 m^2) per site and each site was sampled on four separate occasions between 30 May and 19 September 2011. For the urban land use comparison (question 2) floral abundance data were gathered across 25 quadrats (totalling 25 m^2) per site and each site was sampled on three separate occasions between 15 April and 26 September (twice between 14 May and 26 September 2012 and once between 15 April and 5 September 2013). Baldock et al. (2015) recorded 206 plant taxa across urban, farmland and nature reserve sites and Baldock et al. (2019) recorded 501 plant taxa across sites in nine urban land uses. In total, 536 plant taxa were recorded in the two studies, with 171 taxa present in both.

2.2 | Nectar sugar production data

Each of the 536 plant taxa was assigned a daily nectar sugar production value (mass of sugars produced per floral unit per 24 hr; Supporting Information S3) derived either from empirical values reported in the published literature (230 taxa: Baude et al., 2016; Hicks et al., 2016; Timberlake et al., 2019), measurements made in the field in this study (192 taxa) or predictive modelling where empirical values could not be obtained (114 taxa).

We measured nectar sugar production for 192 of the 536 taxa in the field in March–October 2018 and February–April 2019 using the same methods as Baude et al. (2016), Hicks et al. (2016) and Timberlake et al. (2019), ensuring our values were comparable to those obtained from the published literature. Sampling locations included public and residential gardens, allotments, garden centres and public flower borders in the South of England (Supporting Information S4). Where possible, each taxon was sampled at two or three locations on different days to account for variation due to site, weather and plant variety (following Baude et al., 2016; Supporting Information S5). Pollinators were excluded from flowers to be sampled by mesh bags (pore size 1.4 mm × 1.7 mm) for 24 ± 2 hr, providing a measure of nectar accumulation over a 1-day period. Nectar was then extracted by one of two methods. Where possible, we removed nectar directly using glass microcapillaries (0.5, 1, 5, 10 and 20 μl Minicaps, Hirshmann). Alternatively, where the direct uptake of nectar was not possible as the quantity was too small or viscous, we rinsed nectaries with

0.5–10 μl of distilled water, added with a pipette. Sugar residues were left to dissolve for 1 min before the solution was removed using microcapillaries and the process repeated one further time. The concentration of the solution (C; g of sugars per 100 g solution) was measured using a handheld refractometer modified for small volumes (Eclipse, Bellingham and Stanley). The total mass of sugar produced (s; μg of sugars per 24 hr) was calculated with the formula $s = 10dvC$, where v is the volume collected (μl) and d is the density of a sucrose solution at concentration C and obtained by the formula $d = 0.0037921C + 0.0000178C^2 + 0.9988603$ (Corbet et al., 2001).

Floral abundance data were obtained by Baldock et al. (2015, 2019) by counting floral units rather than flowers. Where the floral unit was a collection of flowers (145 taxa), nectar sugar production was scaled from flower to floral unit level by multiplying by the mean number of open flowers per floral unit. Counts of flowers per floral unit were either collected in the field in this study, obtained from Baude et al. (unpublished data) or in four cases, the floral units were counted in photographs. Nectar sugar values for Asteraceae in Hicks et al. (2016) were already given at the floral unit scale.

For the 114 taxa which lacked published empirical nectar sugar values, and which could not be found for sampling in the field, we estimated nectar sugar production by predictive modelling. Variation in nectar sugar production per floral unit for the empirically measured taxa was analysed using a linear model, which contained plant family, floral unit type, flower shape and floral unit size as explanatory variables (see Supporting Information S6 for a description of the traits and Baude et al., (2016) for a similar modelling approach). The estimates from this model ($N = 326$; $R^2_{adj} = 0.577$) were subsequently used to predict the nectar sugar production values of the plant taxa for which no empirical data were available (see Supporting Information S7 for a validation of our approach). For the landscape comparison (question 1), modelled taxa contributed 3.9% of floral units and 1.1% of nectar sugar and for the urban land use comparison (question 2), 4.9% of floral units and 1.0% of nectar sugar. Results of subsequent statistical analyses were unchanged if modelled taxa were excluded.

Finally, total nectar sugar production for the area of land sampled at each site (i.e. all quadrats combined) was calculated by multiplying the floral abundance of each taxon by its corresponding value of daily nectar sugar production at the floral unit level. Although each site was sampled on four (question 1) or three (question 2) separate occasions to collect floral abundance data, there was insufficient resolution in the dataset to investigate temporal trends in nectar supply. As a result, we pooled estimated nectar sugar production across all sampling visits to a site and divided by the number of visits to report the average daily nectar sugar production per site during the periods May–September (question 1) or April–September (question 2).

2.3 | Data analysis

All analyses were performed using R v.3.5.1 (R Core Team, 2018). Linear mixed models (LMMs) were fitted using R package LME4

(Bates et al., 2015) and diagnostic plots were inspected to validate all models against assumptions of heteroscedasticity and normality of the residuals. P-values for dependent variables were obtained from likelihood ratio tests (R function 'drop1') and pair-wise differences were calculated using post-hoc Tukey's tests (R function 'glht') from R package MULTCOMP (Hothorn et al., 2008). Following Baldock et al. (2015), native status was determined using PLANTATT (Hill et al., 2004), with non-native taxa including both archeophytes and neophytes.

2.3.1 | Question 1: How does the nectar supply differ between urban, farmland and nature reserve landscapes?

To compare the quantity of nectar sugar produced between urban, farmland and nature reserve landscapes we analysed $\log_{10}(x + 1)$ nectar sugar production per sampling site using an LMM containing landscape type as a fixed effect and national region (four regions of the UK) as a random effect to account for any geographic bias in nectar sugar production across the country. We additionally conducted this analysis separately for nectar sugar derived from native and non-native plant taxa. To investigate the strength of the correlation between floral abundance and nectar sugar production we analysed $\log_{10}(x + 1)$ nectar sugar production per sampling site using a linear model (LM) containing $\log_{10}(x)$ floral abundance (number of floral units) as the only dependent variable. To compare the diversity of nectar sources between urban, farmland and nature reserve landscapes we calculated a Shannon diversity index for each sampling site from R package VEGAN (Oksanen et al., 2019) following Baude et al. (2016). The nectar source diversity index (H') was calculated as follows:

$$H' = -\sum_{i=1}^{S} p_i \times \ln(p_i),$$

where p_i is the proportional contribution of plant species i to nectar sugar production per sampling site and S is the total number of plant species per sampling site. Nectar source diversity was analysed using an LMM with the same fixed and random effects as for nectar sugar quantity. Conclusions were unchanged if a Simpson diversity index was calculated instead.

2.3.2 | Question 2: How does the nectar supply differ among urban land uses?

To compare the quantity of nectar sugar produced among urban land uses we analysed $\log_{10}(x + 1)$ nectar sugar production per sampling site using an LMM containing land use and city as fixed effects and city region (40 regions, with 10 in each city) as a random effect to account for any geographic bias (e.g. spatial autocorrelation) in nectar sugar production within cities. We additionally conducted this analysis separately for nectar sugar derived from

native and non-native plant taxa. To estimate each land use's contribution to overall nectar supply at a city scale we multiplied its median site-level nectar sugar production value (an average of sites across all four cities) by the proportion of each city that it comprises by area, with unsurveyed land uses including buildings and roads assigned a nectar production value of zero. To investigate the strength of the correlation between floral abundance and nectar sugar production we used the same approach as above (Section 2.3.1). To compare the diversity of nectar sources among urban land uses, we calculated the diversity index as above (Section 2.3.1) and analysed it using an LMM with the same fixed and random effects as for nectar sugar quantity.

3 | RESULTS

3.1 | Question 1: How does the nectar supply differ between urban, farmland and nature reserve landscapes?
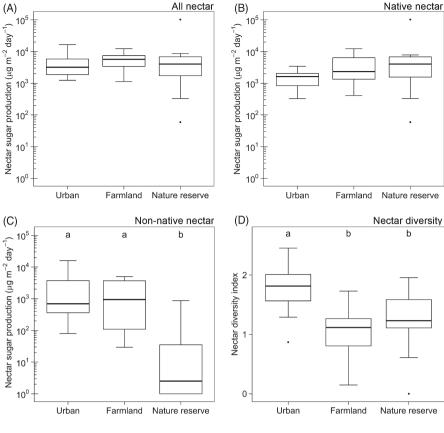
The quantity of nectar sugar did not differ significantly among the three landscape types (LMM: $\chi^2 = 1.01$; $p = 0.60$; Figure 1A), but there were differences in the composition of the plant communities underpinning nectar supply (Figure 2; Supporting Information S8). Nectar sugar production by native taxa did not differ significantly among the three landscape types (Figure 1B), but urban and farmland sites produced significantly more nectar sugar from non-native taxa than nature reserves (Figure 1C; Supporting Information S9) and overall, non-natives comprised 65.6% of the nectar supply in urban sites, 30.0% in farmland and 0.9% in nature reserves. Nectar sugar production varied greatly among sampled sites, spanning the range 58 µg m^{-2} day^{-1} (a broadleaved woodland nature reserve with few flowers recorded) to 102 698 µg m^{-2} day^{-1} (a heathland nature reserve dominated by *Calluna vulgaris*). The diversity of nectar sources differed significantly among the three landscapes (LMM: $\chi^2 = 12.96$, $p = 0.002$), with urban sites producing nectar sugar from a significantly more diverse set of plant taxa than both farmland and nature reserves (Figure 1D; Supporting Information S9). There was a significant positive correlation between the quantity of nectar sugar produced and the number of floral units per site (LM: $F = 30.03$; $R^2 = 0.469$; $p < 0.001$; Supporting Information S10), with floral abundance explaining 46.9% of the variation in nectar sugar production among sites.

3.2 | Question 2: How does the nectar supply differ among urban land uses?

The quantity of nectar sugar differed significantly among the nine urban land uses (LMM: $\chi^2 = 269.72$; $p < 0.001$; Supporting Information S9), but not among the four cities (LMM: $\chi^2 = 0.38$; $p = 0.95$). Gardens produced significantly more nectar sugar than all other land uses except for allotments, while pavements and manmade surfaces produced significantly less nectar than all other

FIGURE 1 Box and whisker plots of the mass (A–C) and diversity (D) of the nectar supply in urban, farmland and nature reserve landscapes. Daily nectar sugar production per square metre was calculated by dividing total nectar sugar production per sampling site by 100 (as 25 m² of land was sampled on four occasions). Data were subsequently transformed ($\log_{10}(x + 1)$) for visualisation on a logarithmic y-axis and are shown for (A) all plant taxa, (B) native plant taxa and (C) non-native plant taxa. Nectar diversity index (Shannon index of nectar sources per sampling site) is shown for all taxa (D). Significantly different landscape types are indicated by different letters (Tukey multiple comparison tests). Boxes show the median, 25th and 75th percentiles; the whiskers extend to $1.5 \times$ the interquartile range; and all outliers are shown
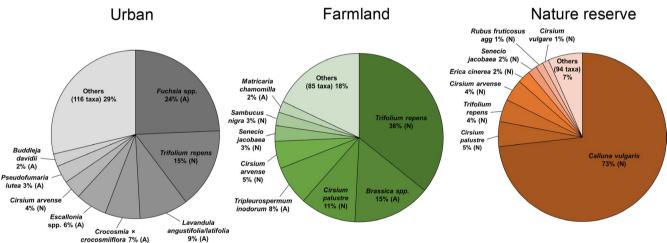

FIGURE 2 Pie charts of the contribution of flowering plant taxa to total nectar supply in urban, farmland and nature reserve landscapes. The eight taxa with the greatest contribution are shown and all other taxa are labelled as 'Others'. The native status of each taxon is indicated by the letter 'N' (native) or 'A' (non-native alien) in parentheses. Although Calluna vulgaris contributed 73% of all nectar sugar in nature reserves, 96% of its production was in a single heathland site, making generalisations about its dominance in UK nature reserves unreliable

land uses (Figure 3A). Even manmade surfaces, the lowest productivity land use, contained some nectar-rich sites (Figure 3A), with flowering shrubs providing 'hotspots' of nectar supply. The high nectar supply in gardens and allotments was largely driven by non-native plants; nectar sugar production by native taxa did not differ significantly among any of the top seven land uses (Figure 3B), while gardens and allotments produced significantly more nectar sugar from non-native taxa than all other land uses (Figure 3C).

Overall, non-natives comprised 69.9% of the nectar supply in allotments and 82.9% in gardens, compared with 3.8% and 4.7% in parks and other greenspaces, respectively. The principal plant taxa contributing to nectar supply in each land use are listed in Supporting Information S11. At a city scale, gardens produced 81.1%–87.6% of all nectar sugar (mean of 85.0% across the four cities), due to their high nectar sugar production per unit area and large area within cities (Table 1). The diversity of nectar sources
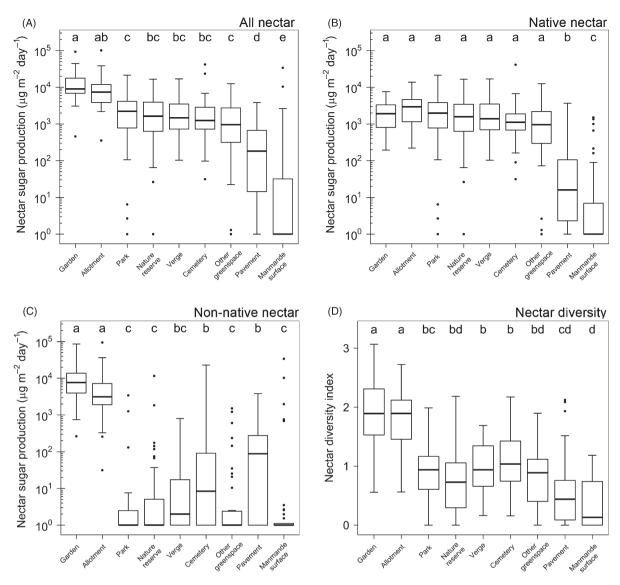
FIGURE 3 Box and whisker plots of the mass (A–C) and diversity (D) of the nectar supply in nine urban land uses. Daily nectar sugar production per square metre was calculated by dividing total nectar sugar production per sampling site by 75 (as 25 m² of land was sampled on three occasions). Data were subsequently transformed ($\log_{10}(x + 1)$) for visualisation on a logarithmic y-axis and are shown for (A) all plant taxa, (B) native plant taxa and (C) non-native plant taxa. Nectar diversity index (Shannon index of nectar sources per sampling site) is shown for all taxa (D). Significantly different landscape types are indicated by different letters (Tukey multiple comparison tests). Boxes show the median, 25th and 75th percentiles; the whiskers extend to $1.5 \times$ the interquartile range; and all outliers are shown

Land use	Nectar sugar production ($\mu g\ m^{-2}\ day^{-1}$)	Percentage of city area (%)	Percentage of city nectar (%)
Garden	8,988 (6,878–17,785)	28.8 (24.2–35.5)	85.0 (81.1–87.6)
Allotment	7,392 (3,849–11,997)	0.7 (0.2–1.0)	1.5 (0.6–2.1)
Park	2,235 (784–4,147)	4.9 (3.1–5.8)	3.6 (2.4–4.7)
Nature reserve	1,633 (631–3,944)	1.8 (0.08–3.8)	1.0 (0.4–2.3)
Verge	1,473 (729–3,498)	1.8 (1.2–2.2)	0.9 (0.7–1.1)
Cemetery	1,248 (722–2,845)	0.8 (0.5–0.9)	0.3 (0.2–0.4)
Other greenspace	960 (315–2,735)	22.5 (18.8–28.0)	7.3 (5.0–10.0)
Pavement	182 (13–675)	4.3 (3.8–5.0)	0.3 (0.2–0.3)
Manmade surface	0 (0–31)	8.2 (6.4–10.3)	0.0 (0.0–0.0)

TABLE 1 A comparison of urban land uses showing nectar sugar production (median and interquartile range across all sites), the percentage of city area that each land use comprises (mean and range among the four cities, from Baldock et al., 2019) and the percentage of nectar production at a city scale that each land use contributes (mean and range among the four cities). Unsurveyed land uses including buildings and roads are not included in this table and were assigned a nectar production value of zero

differed significantly among the nine land uses (LMM: $\chi^2 = 202.97$; $p < 0.001$; Supporting Information S9) and the four cities (LMM: $\chi^2 = 18.73$; $p < 0.001$; Supporting Information S9), with gardens and allotments producing nectar sugar from a significantly more diverse set of plant taxa than all other land uses (Figure 3D). There was a significant positive correlation between the quantity of nectar sugar produced and the number of floral units per site (LM: $F = 563.99$; $R^2 = 0.634$; $p < 0.001$; Supporting Information S10), with floral abundance explaining 63.4% of the variation in nectar sugar production among sites.

4 | DISCUSSION

We found no significant difference in the magnitude of nectar sugar production in urban, farmland and nature reserve landscapes. Urban sites had the highest nectar diversity index, providing nectar sugar from a significantly more diverse set of plant taxa than the other two landscape types. Within urban landscapes, both the magnitude and diversity of the nectar supply differed significantly among land uses. Gardens produced the most nectar sugar per unit area and provide an estimated 81%–88% of nectar at the city scale. The nectar supplies in gardens and allotments were more diverse than all other land uses and were primarily contributed by non-native species. Support for using flower counts as a proxy for floral resource production was mixed: although floral abundance was significantly correlated with nectar sugar production, a large proportion of the variation remained unexplained. In what follows, we first consider the limitations of our approach and then discuss our results in the context of pollinator conservation.

4.1 | Limitations

There are three main limitations to our work. First, the food resource requirements of insect pollinators are more varied than nectar sugar alone. Some pollinators consume pollen as adults (e.g. beetles, hoverflies) and larval diets can include pollen (e.g. bees), other living plant material (e.g. butterflies and moths, hoverflies), other insects (e.g. hoverflies, wasps) and decaying organic matter (e.g. beetles, hoverflies, non-syrphid Diptera; Ball & Morris, 2015; Vaudo et al., 2015; Wäckers et al., 2007). Nectar consumption itself is constrained by compatible morphology between plant and insect, with flower shape an important predictor of visitation among insect species (Stang et al., 2006). Although total nectar sugar is a simplistic measure of food resource availability for insect pollinators, nectar is the main energy source in the diets of adult pollinators and provides a common currency through which to compare the floral resource value of habitats (Baude et al., 2016). Second, quantifying the nectar resources provided by 536 plant taxa required some assumptions and simplifications. A single taxon with a history of cultivation can have many different varieties. For example, the *Dahlia* genus is represented by some 20,000

cultivars (Brickell, 2016). In our study, each taxon derives its nectar production value from one or a few sampled varieties. This is a necessary pragmatic simplification and we found that differences in nectar sugar production between taxa were much greater than between members of the same taxon (which were often different varieties) sampled in two locations (Supporting Information S5). Finally, Baldock et al. (2015, 2019) sampled floral abundance up to a height of 2 m and flowers on trees, shrubs or climbers above this were not recorded. It is possible that flowers on plants more than 2 m in height could produce a significant proportion of the overall nectar on some transects (Somme et al., 2016), but such plants are distributed sporadically, so recording them would require a different sampling method to that used by Baldock et al. (2015, 2019), which allowed for more representative comparisons among landscape and land use types.

4.2 | Implications for pollinator conservation

We did not find clear evidence that urban areas act as resource-rich refuges for insect pollinators within agriculturally dominated rural landscapes, as other authors have suggested (Hall et al., 2017; Samuelson et al., 2018). However, towns and cities contain land uses that are both higher (e.g. gardens and allotments) and lower (e.g. pavements and manmade surfaces) in nectar sugar production than is typical across rural landscapes. Our study reveals the overwhelming importance of residential gardens in providing nectar resources at a city scale. Because they produce the most nectar sugar per unit area and cover the greatest area of any urban land use (24%–36% of cities), gardens supply the vast majority (81%–88%) of nectar sugar produced in cities. Although the magnitude of the nectar supply in urban areas was not greater than in rural landscapes, urban nectar sugar is supplied by a more diverse plant community and not dominated by a small number of taxa, as is common in the countryside (Baude et al., 2016; Timberlake et al., 2019). A diverse array of nectar sources is likely to provide both nutritional diversity of floral rewards and morphological diversity of flowers, which are important determinants of the richness of the pollinator community that can be supported (Stang et al., 2006; Vaudo et al., 2015; Woodard & Jha, 2017). Insect pollinators capable of long-distance foraging (e.g. bumblebees) may be able to visit a combination of urban, farmland and semi-natural areas (such as nature reserves) from their nest site (Goulson et al., 2010; Osborne et al., 2008). If they are sufficiently close, urban areas have the potential to increase the diversity of floral resources in agriculturally dominated landscapes, but there remains a need to understand the extent to which different habitats complement each other by providing different floral resources.

All three sampled landscapes are complex and diverse, making broad-scale comparisons of their floral resources difficult from a relatively small area covered by quadrats, especially given the extreme variability seen in nectar production among different sites. Our comparison of the three landscapes, while large scale, is a relatively

broad-brush approach. In reality, urban landscapes are highly heterogeneous mosaics of different anthropogenic land uses (Baldock et al., 2019; Grimm et al., 2008), as we have discussed; farmland varies with respect to farm type and the degree of management intensity (e.g. arable vs. livestock; high vs. low intensity); and nature reserves are areas with protected status, but are not necessarily managed primarily for pollinators, and can comprise different habitats (e.g. grassland, broad-leaved woodland or heathland). While our study is a robust comparison of the three landscape types, further research into the habitats and land uses within each landscape will enable more specific comparisons to be made.

Research on pollinators in urban landscapes often attempts to explain their abundance or diversity at each sampling site with reference to the extent of nearby green spaces (e.g. Banaszak-Cibicka & Żmihorski, 2012; Sivakoff et al., 2018) or a measure of its reverse, the cover of impervious surfaces (e.g. Ahrné et al., 2009; Fortel et al., 2014). Although floral resources (or its proxy floral abundance) are sometimes measured, this is generally done at a local scale (e.g. Guenat et al., 2019; Theodorou et al., 2017). However, here we show that not all green spaces are alike with respect to their nectar supply: for example, based on median values per unit area, gardens produce four times as much nectar sugar as parks, and allotments six times as much as cemeteries (Table 1). Future studies should consider the quantity of floral resources around pollinator sampling sites in urban areas, rather than proxy variables such as green space extent and impervious surface cover, as it is floral resources which are likely to directly regulate pollinator populations (Roulston & Goodell, 2011). The nectar sugar production values of UK urban land uses, listed here (Table 1), represent a useful asset for researchers aiming to quantify floral resources in urban landscapes.

The high nectar sugar production in gardens and allotments was largely driven by species that are not native to the UK. Although non-native plants are often regarded as less valuable to wildlife than their native counterparts, many such as *Borago officinalis*, *Lavandula* spp. and *Nepeta* spp., are frequently visited by UK pollinators (Baldock et al., 2019; Garbuzov & Ratnieks, 2014; Rollings & Goulson, 2019). Temperate pollination systems tend to be fairly generalised in nature (Memmott, 1999; Waser et al., 1996), thus most flowering plants are visited by broad taxonomic groups of insects (e.g. bees, butterflies or hoverflies), rather than only a few specialist species. Consequently, a non-native plant that evolved in its natural range to attract a group of pollinators also found in the UK is likely to be visited by UK pollinators despite its origin (e.g. *Mahonia japonica* is native to Asia but attracts bumblebees in the UK; Stelzer et al., 2010). Furthermore, given the UK shares pollinator species with continental Europe, interactions between non-native plants of European origin and pollinators in the UK often represent a renewal of associations that have occurred before in evolutionary history (e.g. *Anthidium manicatum* and *Stachys byzantina*; Gallagher & Lucky, 2020). Even exotic plants that have evolved for visitation by pollinators absent from the UK can be important sources of food for UK pollinators. For example, *Fuchsia* species are commonly pollinated by hummingbirds in the Americas (González et al., 2018),

but provide nectar for bumblebees, honeybees and social wasps in UK gardens (N. Tew, pers. obs.). Thus, there is no intrinsic reason to assume non-native plant species are less valuable to most flower-feeding insects than their native counterparts (Garbuzov & Ratnieks, 2014; Majewska & Altizer, 2018; Matteson & Langellotto, 2011), although their prevalence in urban areas could drive changes in pollinator community composition (Seitz et al., 2020; Urbanowicz et al., 2020; Wenzel et al., 2020) and further research into nectar chemistry is needed to establish whether non-natives provide nectar of comparable nutritional quality (Tiedeken et al., 2017; Vaudo et al., 2015).

Urban landscapes contain land uses which differ markedly in both form and function (Dennis et al., 2018; Grimm et al., 2008) and consequently management strategies for conserving pollinators vary among land uses. In land uses that are largely paved and typically of very low nectar value, flowering shrubs can be incorporated to provide long-lived 'hotspots' of nectar in a relatively small space. In pavements and manmade surfaces (including car parks) we found that the non-native shrubs *Berberis* spp., *Buddleja davidi* and *Ceanothus* spp. are responsible for positive outliers in nectar sugar production among city regions (Supporting Information S11). At the other end of the spectrum, gardens and allotments produce a rich and diverse nectar supply, so ensuring these land uses are retained within existing urban landscapes and integrated into new developments is a priority in urban pollinator conservation. Land uses typically covered with short-mown grass, especially parks and other greenspaces (including amenity grassland), have an intermediate value of nectar sugar production. Here, altering the frequency and timing of mowing affects floral abundance (Garbuzov et al., 2015; Johansen et al., 2019; Lerman et al., 2018) and hence nectar sugar production, mediated largely by the three native plants *Trifolium repens*, *Taraxacum* agg. and *Bellis perennis*, which together provide 74%–80% of the nectar in these land uses (Supporting Information S11). In addition, small patches of sown wildflowers can be incorporated into public greenspace to boost nectar supply, with native perennial mixes potentially providing 16 times as much nectar sugar per unit areas as parks and 37 times as much as other greenspaces (Hicks et al., 2016).

5 | CONCLUSIONS

Our results show that, per unit area, the nectar supply in UK towns and cities is comparable in magnitude to farmland and nature reserves, but differs in composition. Urban nectar is supplied by a diverse community of flowering plants, heavily comprised of non-native species. Residential gardens are the key land use underpinning nectar sugar production within urban landscapes, providing both an abundance and diversity of floral resources. By quantifying the nectar supply, rather than relying on proxy variables such as flower abundance, researchers can provide a more ecologically relevant description of the resource value of habitats and landscapes to foraging pollinators and develop evidence-based recommendations for their conservation.

AUTHORS' CONTRIBUTIONS

N.E.T., J.M. and K.C.R.B. conceived the ideas and designed the methodology; N.E.T. collected the data; N.E.T., I.P.V. and K.C.R.B. analysed the data; N.E.T., J.M. and K.C.R.B. led the writing of the manuscript, with I.P.V., S.B., G.N.S. and S.G.P. contributing critically to the drafts; J.M., I.P.V., S.B. and K.C.R.B. acquired funding. All authors gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.41ns1rncm (Tew et al., 2021a) and https://doi.org/10.5061/dryad.sf7m0cg59 (Tew et al., 2021b).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.