RESEARCH ARTICLE

Turnover in floral composition explains species diversity and temporal stability in the nectar supply of urban residential gardens

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Abstract

1. Residential gardens are a valuable habitat for insect pollinators worldwide, but differences in individual gardening practices substantially affect their floral composition. It is important to understand how the floral resource supply of gardens varies in both space and time so we can develop evidence-based management recommendations to support pollinator conservation in towns and cities.

2. We surveyed 59 residential gardens in the city of Bristol, UK, at monthly intervals from March to October. For each of 472 garden surveys, we combined floral abundances with nectar sugar data to quantify the nectar production of each garden, investigating the magnitude, temporal stability, and diversity and composition of garden nectar supplies.

3. We found that individual gardens differ markedly in the quantity of nectar sugar they supply (from 2 to 1,662 g), and nectar production is higher in more affluent neighbourhoods, but not in larger gardens. Nectar supply peaks in July (midsummer), when more plant taxa are in flower, but temporal patterns vary among individual gardens. At larger spatial scales, temporal variability averages out through the portfolio effect, meaning insect pollinators foraging across many gardens in urban landscapes have access to a relatively stable and continuous supply of nectar through the year.

4. Turnover in species composition among gardens leads to an extremely high overall plant richness, with 636 taxa recorded flowering. The nectar supply is dominated by non-natives, which provide 91% of all nectar sugar, while shrubs are the main plant life form contributing to nectar production (58%). Two-thirds of nectar sugar is only available to relatively specialised pollinators, leaving just one-third that is accessible to all.

5. *Synthesis and applications.* By measuring nectar supply in residential gardens, our study demonstrates that pollinator-friendly management, affecting garden quality, is more important than the size of a garden, giving every gardener an

opportunity to contribute to pollinator conservation in urban areas. For gardeners interested in increasing the value of their land to foraging pollinators, we recommend planting nectar-rich shrubs with complementary flowering periods and prioritising flowers with an open structure in late summer and autumn.

KEYWORDS
beta diversity, floral resources, garden, nectar, phenology, pollinator, pollinator conservation, urban ecology

1 | INTRODUCTION

Flower-visiting insects including bees and hoverflies are crucial pollinators of many wild plants and agricultural crops (Klein et al., 2007; Ollerton et al., 2011). Increasing evidence for pollinator declines (e.g. Biesmeijer et al., 2006; Powney et al., 2019; Soroye et al., 2020) has led to a focus on designing and implementing strategies for conserving pollinators (Potts et al., 2016). Urban areas could play a surprisingly important role in such conservation strategies for two main reasons. First, they already cover 2%–3% of the world's land (Liu et al., 2014) and are expanding (Gao & O'Neill, 2020). Second, urban green spaces can support substantial pollinator diversity (Baldock et al., 2019; Normandin et al., 2017), which may be higher than that in surrounding rural areas (Baldock et al., 2015; Theodorou et al., 2017, 2020).

Privately owned residential gardens or yards (hereafter referred to as 'gardens') are a particularly valuable type of urban green space for insect pollinators as they are often (but not always) actively managed by gardeners to provide ornamental displays of flowering plants, which provide pollinators with food in the form of nectar and pollen. As a result, diverse pollinator communities can be found in gardens throughout the world (Baldock et al., 2019; Fetridge et al., 2008; Marín et al., 2020; Martins et al., 2017; Staab et al., 2020). Despite their small individual size, residential gardens collectively cover 16%–36% of cities in different countries (Baldock et al., 2019; Colding et al., 2006; Loram et al., 2007; Mathieu et al., 2007; Ossola et al., 2021) and provide an estimated 85% of nectar in urban areas in the UK (Tew et al., 2021). Consequently, gardens offer a unique opportunity for pollinator conservation where the combined action of many individuals can have a major impact on foraging resources at a landscape scale (Goddard et al., 2010).

Gardens vary substantially in size, shape, topography, amount of sunlight and soil type (Loram et al., 2007; Matteson & Langellotto, 2010). In addition, management by gardeners differs due to the many and diverse motivations for gardening, this being explained in part by demographic and socioeconomic factors (Goddard et al., 2013; Lindemann-Matthies & Marty, 2013; Philpott et al., 2020). As a result, the abundance and composition of flowering plants is very variable among gardens, with some comprised of flower-rich borders and others dominated by short mown grass or hard surfaces (Goddard et al., 2013; Loram et al., 2008). Consequently, the quantity of floral resources available to insect

pollinators is likely to differ substantially from one garden to the next, as is the temporal pattern of resource production due to differences in flowering phenology among species. The seasonal timing of floral resources is often overlooked, but is an important factor determining the success of insect pollinators in temperate climates (Guezen & Forrest, 2021; Timberlake et al., 2020). To understand the quality of the garden habitat for foraging pollinators and identify opportunities for its enhancement, we need to quantify variation in the supply of floral resources among individual gardens.

In this study, we investigate for the first time how the nectar supply of residential gardens varies in space and time and use our results to develop evidence-based management recommendations for pollinator conservation in urban areas. Nectar sugar is the main energy source for adult pollinators, particularly important for powering their flight muscles (McCallum et al., 2013), but nectar resources have declined in rural areas due to land-use change (Baude et al., 2016). We focus on three characteristics of the nectar supply in gardens. (a) Magnitude: we predict substantial variation in nectar sugar production among gardens and an overall peak in summer when we expect more plants to be in flower. (b) Temporal stability: we predict that individual gardens will vary in their seasonal patterns of nectar sugar production such that not all gardens will peak at the same time of year. However, complementarity among gardens should produce a relatively stable supply of nectar throughout the year at the scale of an urban landscape. (c) Diversity and composition: given gardeners can choose from a wide variety of species when planting, we predict substantial turnover in species composition among gardens.

2 | MATERIALS AND METHODS

2.1 | Selecting gardens to survey

We surveyed residential gardens in Bristol, a city of around 460,000 inhabitants (Office for National Statistics, 2019) in Southwest England, UK, and stratified our sampling by both geographical location and neighbourhood income. Six separate regions of the city were chosen for garden surveys (see Appendix S1), with each region corresponding to an Output Area (a census reporting unit containing 101–123 households). Two regions were each chosen to represent areas of relatively low (band one: £19,149 and £21,215),

intermediate (band two: £25,357 and £28,677) and high (band three: £41,308 and £44,992) median annual income (Baldock et al., 2019).

We obtained permission to survey residential gardens by posting a flyer advertising the study to all properties in our chosen six regions and subsequently visiting properties to talk to residents (see Appendix S2). Following this, we obtained permission to survey 59 gardens continuously from March to October, these encompassing a wide range of sizes and planting styles. Although we tried to ensure we surveyed an equal number of gardens in each income band, there were differences in the number of properties we gained permission to access (band one: 12; band two: 23; band three: 24), but this imbalance did not affect our conclusions (see Appendix S3).

2.2 | Surveying gardens

We visited each of the 59 gardens once per calendar month between 4 March and 29 October 2019 to record floral abundance. Thus, each garden was visited eight times, with 472 garden surveys conducted. The period from March (early spring) to October (mid-autumn) covers the vast majority of the UK pollinator flight season. Although some gardens contain floral resources in late autumn and winter (November–February), pollinator activity is low at these times (Ball & Morris, 2015; Falk, 2015). We ensured gaps between visits to the same garden were close to one calendar month, with a mean gap of 30.7 days ($n = 413$; range = 25–42 days; 97% of gaps 25–35 days inclusive). For logistical reasons, we usually visited multiple gardens in the same region on the same day, but we visited each region on 2–6 days spread across each month to ensure there was no systematic bias in sampling date among regions.

On the first visit, we mapped each garden to measure its total area. On this and each subsequent visit, we identified all plant taxa in flower as far as possible (to species, species aggregate, hybrid or genus) and counted all open floral units within the boundaries of each garden (with no height limit and including flowers on plants hanging over boundaries into gardens). We excluded grasses (Poaceae) as they offer no nectar resources. Floral units were defined as a single flower or collection of flowers (e.g. a capitulum for Asteraceae) that a pollinator can walk within but must fly between (e.g. Baldock et al., 2015; Carvalheiro et al., 2008; see Appendix S4). Floral units were either counted individually in a garden using a handheld tally counter or estimated by sub-sampling and then multiplying up (e.g. for flowering shrubs and trees). For flower-rich lawns, we estimated floral units using quadrats (0.5 × 0.5 m) to quantify floral abundance for a fixed area, which we then scaled up to the area of the entire lawn.

2.3 | Nectar sugar production data

Each of the 636 plant taxa we recorded flowering in gardens was assigned a daily nectar sugar production value (mass of sugars produced per floral unit per 24 hr) derived either from empirical values reported in the published literature (181 taxa; Baude et al., 2016; Hicks et al., 2016; Timberlake et al., 2019), measurements we made in the field (263 taxa), or predictive modelling where empirical values could not be obtained (192 taxa). Our approach for assigning nectar sugar values to plant taxa (see Appendix S5) followed that of Tew et al. (2021).

We measured nectar sugar production at field sites in Southern England (not the 59 gardens we surveyed; see Appendix S6) for 263 taxa 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). We enclosed flowers with mesh bags (pore size 1.4 mm × 1.7 mm) for 24 ± 2 hr and subsequently extracted accumulated nectar using glass microcapillaries (0.5, 1, 5, 10 and 20 μl Minicaps; Hirshmann), rinsing nectaries with distilled water to dissolve sugar residues where necessary. 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, Tunbridge Wells, UK) and the mass of sugar produced (s; μg of sugars per 24 hr) 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). We sampled 10–52 flowers for 255 plant taxa (1–9 for 8 taxa) and focused our field sampling of nectar on plants commonly found in UK gardens, which we selected in part based on data from Baldock et al. (2019).

Where the floral unit was defined as a collection of flowers (125 taxa), nectar sugar production was scaled from flower to floral unit level by multiplying by the mean number of open flowers per floral unit (see Appendix S5). For the 192 taxa which lacked published empirical nectar sugar values, and which could not be found in sufficient numbers for sampling in the field, we estimated nectar sugar production using the predictive modelling approach employed by Tew et al. (2021). 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 Appendix S7). The estimates from this model ($N = 318$; $R^2_{adj} = 0.537$) were subsequently used to predict the nectar sugar production values for the plant taxa for which no empirical data were available (see validation in Appendix S8). Finally, daily nectar sugar production per monthly visit was calculated for each garden by multiplying the number of floral units of each taxon by its corresponding value of daily nectar sugar production.

2.4 | Data analysis

All analyses were performed using R v.4.0.3 (R Core Team, 2020). Generalised additive mixed models (GAMMs) were fitted using R package 'MGCV' (v.1.8-33; Wood, 2017) and diagnostic plots (generated with R function 'gam.check') were inspected to validate models

against assumptions of heteroscedasticity and normality of the residuals. The degree of smoothness of the regression spline was selected by comparing Akaike's information criterion (AIC) among candidate models (see Appendix S9).

2.4.1 | Magnitude of the nectar supply through the year

To estimate 'annual' (March–October) nectar sugar production for each garden, we multiplied the mean daily nectar sugar mass for the eight survey visits by the number of days between 1 March and 31 October inclusive. To describe the nonlinear trend in nectar sugar production through the sampling period, we fitted a GAMM with day of the year modelled with a thin-plate regression spline. A Gamma error family with log link function gave the best fit for the data. The model also included median household income (a numeric value for each of the six sampled regions in Bristol) and garden area as fixed effects (linear fits) and the code for each garden as a random effect, this accounting for the repeated sampling of gardens (see Appendix S9).

2.4.2 | Temporal stability of the nectar supply

To investigate how the temporal stability of the garden nectar supply (i.e. consistency between months of the year) varied with the flowering plant richness of individual gardens, we regressed the coefficient of variation (standard deviation/mean) in monthly nectar sugar production onto flowering plant richness. The coefficient of variation (CV) is commonly used as a measure of instability in ecology (Doak et al., 1998), with a smaller value indicating greater stability. Next, we investigated how the total number of gardens a pollinator can visit affects the temporal stability of the overall nectar supply, using a simulation approach. We drew random combinations of gardens from the 59 we surveyed (with replacement, so gardens could be selected multiple times) to give samples of 1–100 gardens and iterated this process 1,000 times for each sample size (1–100 gardens). For each iteration, we summed across gardens to give total nectar sugar per month and calculated CV for this aggregated supply. A pollinator flying 100 m from a central point within each of our six surveyed regions of Bristol can visit 60–181 gardens (mean of 93; data from inspecting satellite imagery). Thus, 100 gardens are accessible well within the typical foraging ranges of flower-visiting insects (Greenleaf et al., 2007; Wratten et al., 2003).

2.4.3 | Diversity and composition of the nectar supply

To describe the nonlinear trend in flowering plant richness through the sampling period, we fitted a GAMM as described

above (Section 2.4.1; see Appendix S9). We estimated beta diversity across gardens by calculating Sørensen dissimilarity and partitioning it into turnover and nestedness components, using R package 'BETAPART' (v.1.5.2; Baselga & Orme, 2012). The Sørensen dissimilarity index describes the extent to which different sites (i.e. gardens) share species (perfect similarity = 0; perfect dissimilarity = 1).

The native versus non-native status of flowering plants was determined using the online plant atlas PLANTATT (Hill et al., 2004) and plant life form was determined using Brickell (2016), with each taxon categorised as an herbaceous plant, tree, shrub or woody climber. We grouped plants into those with 'generalised' or 'specialised' flower structures according to the accessibility of the nectar provided for pollinators. Generalised flowers have an open structure with nectar accessible to all short- and long-tongued insects (e.g. *Bellis perennis*). Specialised flowers in contrast offer nectar rewards that cannot be accessed by all pollinators. In most cases, this is due to a long corolla tube which requires a long tongue (e.g. *Lamium album*) and in others a physical obstacle which requires sufficient force to manipulate (e.g. *Lotus corniculatus*). Although this dichotomy is necessarily simplistic, categories were decided from a combination of corolla measurements and observations of pollinator visits.

3 | RESULTS

In total, we recorded over two million floral units (2,061,703) belonging to 636 plant taxa in 98 families in the 59 surveyed gardens. Garden area ranged from 31.3 to 407.7 m^2, with a mean of 156.4 m^2 (±12.7 SE) and a combined area of 0.92 ha. Taxa with empirical values of nectar sugar accounted for 91.9% of the total supply and conclusions drawn from subsequent statistical analyses were unchanged if taxa assigned modelled nectar values were excluded.

3.1 | Magnitude of the nectar supply through the year

Total annual (March–October) nectar sugar production per garden varied from 2.3 to 1,661.9 g (mean 395.5 g ± 45.2 SE). The distribution of annual nectar supply was positively skewed, with the top 13 gardens (22%) accounting for 51% of the total nectar sugar (Figure 1A). Gardens produced a mean of 3.2 g (±2.7 SE) of nectar sugar per square metre across the sampling period (range 0.03–10.80 g). A generalised additive mixed model described a significantly nonlinear trend in nectar supply through the year (GAMM: $F_{6,6}$ = 16.72; $p < 0.001$), with a predicted peak of 5 July and periods of lower supply in early spring (March) and from late summer into autumn (August–October; Figure 1B). There was a significant positive correlation between nectar sugar production and median household income (GAMM: $t = 2.87$;
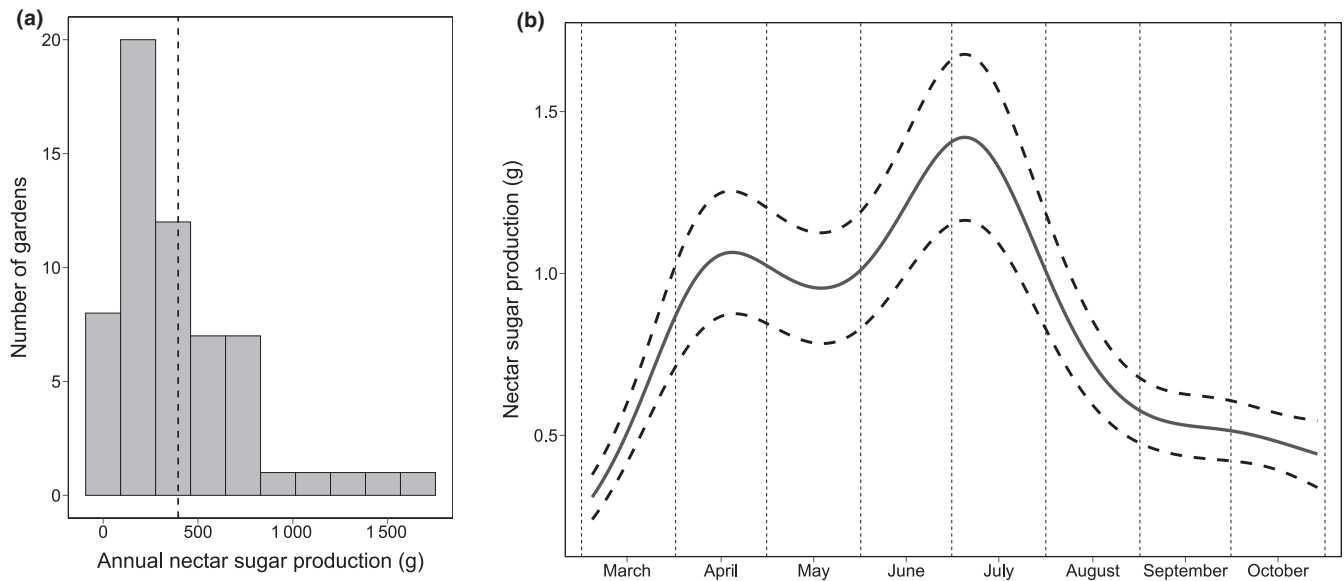
FIGURE 1 Spatial and temporal patterns in the magnitude of the nectar supply. (A) A histogram of annual (March–October) nectar sugar production per garden, with the mean (396 g) indicated by a dashed line. (B) Nectar sugar production per garden plotted through the sampling year, showing the prediction (using median values of household income and garden area) from a generalised additive mixed model (solid line) and boundaries 1 *SE* above and below the prediction (dashed lines)
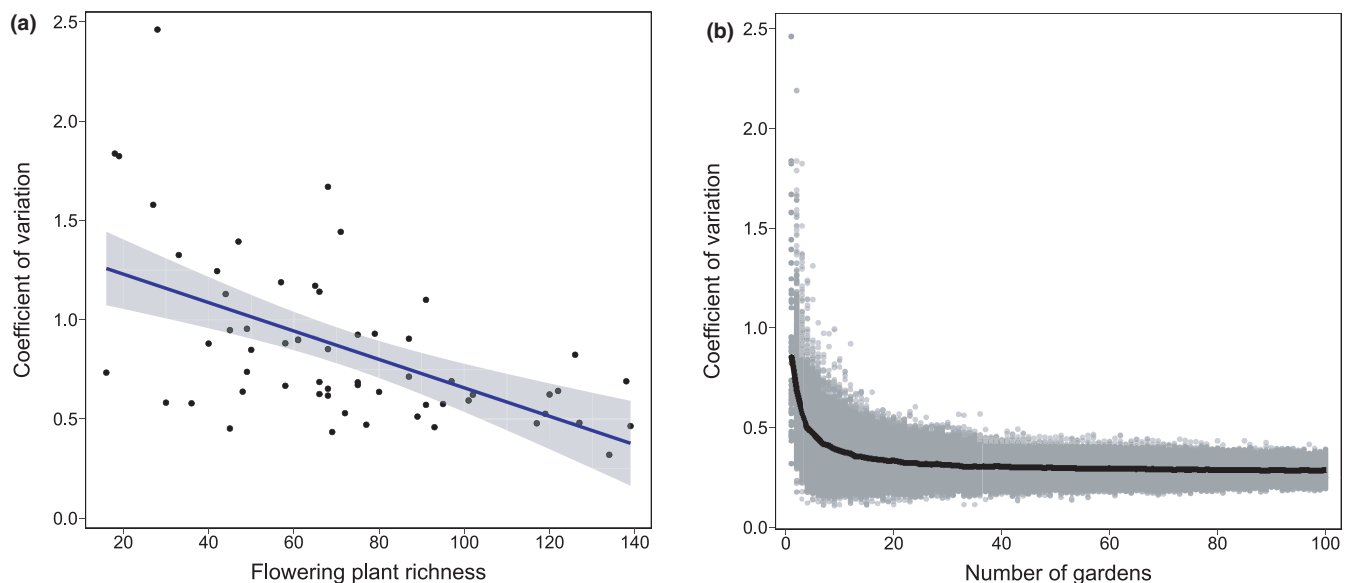
FIGURE 2 Patterns of temporal stability in the nectar supply. (A) The relationship between flowering plant richness and the coefficient of variation in monthly nectar sugar production (linear regression line in blue and shaded area covering 1 *SE* around the prediction). (B) The simulated relationship between the number of gardens and the coefficient of variation in their aggregated monthly nectar sugar production. Grey points represent iterations of our simulation and the mean line across iterations is shown in black

$p = 0.004$), but not between nectar sugar production and garden area (GAMM: $t = 0.92$; $p = 0.358$). Together, day of the year, income and garden area explained 13.2% of the variation in nectar sugar production. The temporal pattern of nectar supply varied among individual gardens, with 22 (37%) peaking outside of May–July and at least one garden peaking in each month. The mean monthly nectar sugar production per garden varied by a factor of two across the year (from 2.2 g in July to 1.1 g in October).

3.2 | Temporal stability of the nectar supply

There was a significant negative correlation between flowering plant richness in gardens and the coefficient of variation in monthly nectar sugar production (Linear model: $F_{1,57} = 24.67$; $R^2 = 0.302$; $p < 0.001$; Figure 2A); hence, gardens with richer floras tended to have a more stable supply of nectar through the year. Our simulations showed the more gardens a pollinator can

visit, the more stable the overall supply of nectar through time (Figure 2B). The coefficient of variation in nectar supply among months rapidly declines with an increasing number of gardens, with mean CV across iterations halving between one and seven gardens (Figure 2B). Thus, complementarity among many gardens in residential areas smooths temporal variability in their combined nectar supply.

3.3 | Diversity and composition of the nectar supply

A generalised additive mixed model described a significantly non-linear trend in flowering plant richness through the year (GAMM: $F_{2,2} = 317.92$; $p < 0.001$), with a predicted peak of 7 July and periods of lower richness in spring (March–May) and autumn (September–October; Figure 3). Neither median household income (GAMM: $t = 1.58$; $p = 0.115$) nor garden area (GAMM: $t = 1.92$; $p = 0.056$) correlated significantly with flowering plant richness. The temporal pattern of flowering plant richness was relatively consistent, with 50 of the 59 gardens peaking in the summer (June–August) and none peaking in March or October. Beta diversity was very high (Sørensen dissimilarity 0.96) and driven by turnover among gardens rather than nestedness (turnover component 98%). Thus, gardens tended to share a very low proportion of their taxa and the floral composition of low richness gardens was not generally a subset of that in higher richness gardens. This was reflected in the incidence frequencies of taxa, with only 20 taxa (3.1% of the total) recorded in at least half of gardens (see Appendix S10) and 203 taxa (31.9% of the total) only found in a single garden. Half of the total nectar supply was provided by 13 taxa, three-quarters by 43 taxa and 95% by 154 taxa (see Appendix S11).

The composition of plant species underpinning nectar sugar production varied greatly through the year, reflecting different flowering periods among taxa (Figure 4; see Appendix S11). *Pieris* species provided the most nectar of any single taxon in March (31.0%) and April (26.1%) while *Fuchsia magellanica* was dominant from July to October (32.3%–52.1%). Non-native taxa (77% of all taxa) contributed 90.5% of total nectar sugar production, a proportion which remained relatively consistent through the year (see Appendix S12). Shrubs produced 57.5% of nectar (more in spring and autumn; see Appendix S12), herbaceous plants 33.5% and the contributions of woody climbers (6.2%) and trees (2.7%) were lower. Around two-thirds (66.4%) of nectar was provided by flowers with a specialised structure, with just one-third (33.6%) accessible to all pollinators. This pattern changed through time, with specialised flowers providing 73.9%–82.6% of nectar in July–October (see Appendix S12).
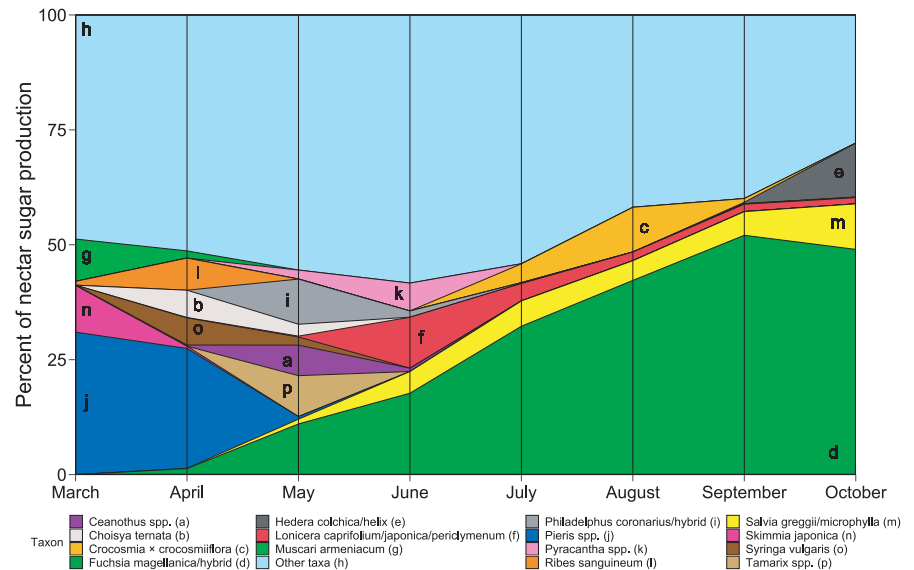
4 | DISCUSSION

Garden nectar production peaked in mid-summer, but individual gardens differed markedly in both the magnitude of their nectar supply and its temporal pattern. Most of this variation was not explained by our model, indicating the importance of additional factors in determining nectar among gardens. The finding that garden size did not correlate significantly with nectar sugar production suggests that the quality of the garden habitat, driven by individual management decisions, is of primary importance. Nectar production was more stable through time in gardens with greater flowering plant richness and, at larger spatial scales temporal stability in the nectar supply rapidly emerges if pollinators forage across multiple gardens. In what follows we first consider the limitations of our work and then discuss our results in the context of urban pollinator conservation.
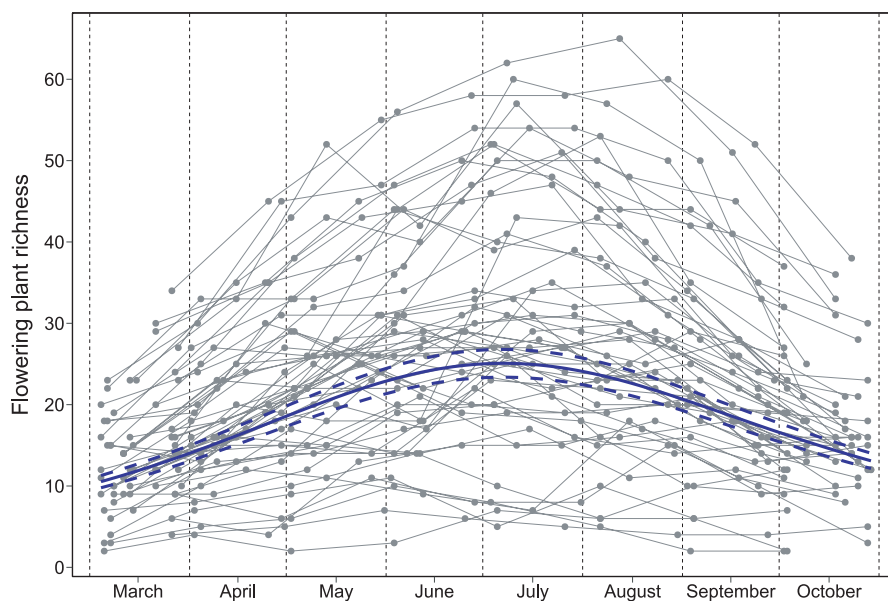
FIGURE 3 Flowering plant richness plotted for each garden through the sampling year (with lines joining points for individual gardens), showing the prediction (using median values of household income and garden area) from a generalised additive mixed model (solid blue line) and boundaries 1 *SE* above and below the prediction (dashed blue lines)

FIGURE 4 The contribution of plant taxa to monthly nectar sugar production plotted through the sampling year, with the percentage indicated by the height of a coloured polygon. The 15 displayed taxa provided >5% of nectar sugar in at least one month, with the remainder included in the 'Other taxa' category

Taxon

Ceanothus spp. (a)	Hedera colchica/helix (e)	Philadelphus coronarius/hybrid (i)	Salvia greggii/microphylla (m)
Choisya ternata (b)	Lonicera caprifolium/japonica/periclymenum (f)	Pieris spp. (j)	Skimmia japonica (n)
Crocosmia × crocosmiiflora (c)	Muscari armeniacum (g)	Pyracantha spp. (k)	Syringa vulgaris (o)
Fuchsia magellanica/hybrid (d)	Other taxa (h)	Ribes sanguineum (l)	Tamarix spp. (p)

4.1 | Limitations

There are two main limitations to our study of nectar supply in residential gardens. First, insect pollinators require additional resources to nectar sugar alone, which can include pollen, extrafloral nectar and honeydew, nest sites, prey items and food plants for larvae (Wäckers et al., 2007). Given nectar sugar mass and total pollen volume both correlate with floral abundance (Hicks et al., 2016), the broad patterns we observe in nectar supply are likely to reflect those of pollen production. Currently, there is insufficient published pollen data to have included it in this study. Nevertheless, nectar sugar is a general energy source required by the vast majority of adult pollinators so it provides a common currency through which to compare the floral resource value of habitats (e.g. Baude et al., 2016; Timberlake et al., 2019). Second, we only surveyed gardens in a single city (Bristol, UK) in a single year (2019). Residential gardens cover 28% of Bristol by area (Baldock et al., 2019), putting it within the range seen for cities worldwide (e.g. 16% in Stockholm, Sweden; Colding et al., 2006 and 36% in Dunedin, New Zealand; Mathieu et al., 2007). In addition, there was no significant difference in the nectar sugar production of urban land uses between Bristol and three other UK cities (Tew et al., 2021), but there is no equivalent data for non-UK cities to make comparisons. Both mean annual temperature and total rainfall for Bristol in 2019 were typical of those in the past decade (Met Office, 2020), so we expect the patterns we observed in 2019 will be representative of those in other years. While the precise shape of the seasonal nectar supply curve and the contributions of specific plant taxa will differ in other cities and years, the general findings of extreme variability and turnover among single gardens but temporal stability across multiple gardens are very likely to apply in other cities because the principle that gardens comprise many small habitat patches which differ independently in their management remains true wherever they are located.

4.2 | Nectar supply in gardens

There was substantial variation in the magnitude of nectar production among individual gardens (the scale at which management decisions are made). In our sample, the highest-nectar garden produced more than 700 times more sugar than the lowest-nectar garden during our survey period, but we found that garden size did not correlate significantly with nectar sugar production, which emphasises the importance of management decisions for nectar supply rather than total area per se. The highest-nectar gardens tended to be in more affluent regions (four of the top five nectar producing gardens were in income band 1) and contained ornamental flower borders, while the lowest-nectar gardens were likely to be in regions of lower income (four of the bottom five in income band 3) and typically lacked flower-rich borders. There was no clear negative role of hard surfaces like decking and paving in place of lawns because we observed that herbaceous plants and shrubs in pots or peripheral borders were usually the major nectar source rather than flower-rich lawns. Our study shows that it is not necessary for a gardener to have a large garden to provide pollinators with a large supply of nectar because it is how they choose to garden which is most important. However, a lack of gardener knowledge of which species are nectar rich could lead to suboptimal outcomes for pollinators even where the necessary motivation exists (Lindemann-Matthies et al., 2021).

Nectar production peaked in mid-summer, when UK pollinator abundance is also highest (Balfour et al., 2018), but patterns among individual gardens were idiosyncratic with at least one garden peaking in each month from March to October. It was common for a single flowering plant taxon (often a tree or shrub) to provide the majority of a garden's nectar sugar in a particular month, contributing to the variability in temporal patterns within and among gardens. Because each garden is managed by a single individual or group of individuals, temporal patterns of nectar supply vary among gardens in a relatively independent fashion. As a result, extreme temporal

variation in nectar production tends to average out when summed across many gardens, resulting in an overall supply that is more stable through time, an example of the portfolio effect (Schindler et al., 2015). Across our 59 surveyed gardens, the mean monthly nectar sugar production only varied by a factor of two through the sampling year. This contrasts with patterns in rural farmland, where temporal peaks may be more than 10 times as great as troughs in nectar supply (Timberlake et al., 2019). Because urban gardens are present at such a high density, the portfolio effect smooths temporal variability in their aggregated supply at a scale relevant to foraging pollinators. Hence, unless there are strong barriers limiting dispersal in urban areas, pollinators foraging in residential regions of towns and cities have access to a much more stable and continuous supply of nectar through the year than those in rural farmland.

The flowering plant richness of residential gardens is extremely high; we recorded 636 taxa from 98 families flowering in less than one hectare of land. This phenomenal richness (which is higher than in semi-natural habitats; e.g. Vessby et al., 2002) is driven by extreme turnover in species composition among gardens (Loram et al., 2008). Individual gardens tend to have relatively distinct floras (only 3% of taxa were recorded in half the gardens) because gardeners have a wide variety of (native and non-native) species to choose from when planting and their active management (e.g. 'weeding') prevents plants being outcompeted (Loram, Thompson, et al., 2008). The value of gardens as a habitat type is an emergent property, resulting from many small patches of land being managed independently,

emphasising the importance of understanding landscape context for biodiversity conservation in urban areas (Goddard et al., 2010). Being mobile, insect pollinators have the potential to take advantage of the nectar supplied by gardens despite their patchy distribution in fragmented urban landscapes, but differences in diet, larval requirements, dispersal capability and nesting behaviour among taxa will affect the composition of pollinator communities that can be supported (Seitz et al., 2020; Wenzel et al., 2020).

4.3 | Management recommendations

Shrubs, climbers and trees provided two-thirds of all nectar as their physical structure results in a three-dimensional arrangement of flowers, allowing a large number to be produced within a relatively small area of land. Ornamental shrubs, climbers and trees with nectar-rich flowers are therefore a space-efficient way to boost the garden nectar supply during their flowering periods. Gardens with higher flowering plant richness provide a more stable supply of nectar sugar through time, but by actively selecting nectar-rich species with complementary phenological profiles gardeners can achieve this result more efficiently with respect to cost and space (Table 1). An additional consideration when planting for pollinators is flower structure, which determines the accessibility of floral resources to different insects (e.g. Stang et al., 2006). From July to October, 74%–83% of nectar sugar was supplied by flowers that are not accessible to all pollinators (especially *Fuchsia magellanica*, *Lonicera*

Seasonal period	Recommended plants	Native status	Flower structure
Early spring (March)	*Helleborus* spp.	N or A	S
	Pieris spp.	A	S
	Pulmonaria spp.	N or A	S
	Salix spp. (willow)	N or A	G
	Skimmia japonica	A	G
Mid to late spring (April–May)	*Aquilegia vulgaris*	N	S
	Ceanothus spp.	A	G
	Malus spp. (apple)	N or A	G
	Prunus avium (cherry)	N	G
	Ribes spp. (currants)	N or A	G or S
Early to mid summer (June–July)	*Campanula* spp. (bellflower)	N or A	G
	Geranium spp. (cranesbill)	N or A	G or S
	Lavandula spp.	A	S
	Lonicera periclymenum (honeysuckle)	N	S
	Pyracantha coccinea (firethorn)	A	G
Late summer to autumn (August–October)	*Echinacea purpurea* (coneflower)	A	G
	Hedera helix (ivy)	N	G
	Origanum vulgare	N	G
	Sedum spp.	N or A	G
	Verbena bonariensis	A	S

TABLE 1 Recommended plants for different seasonal periods in UK gardens. Listed plants are nectar rich, attractive to flower-visiting insects and easily acquired by gardeners. Taxa are described as native ('N') or non-native alien ('A') and as having a generalised ('G') or specialised ('S') flower structure (or including members of both categories). Gardeners should avoid invasive plants, which can escape from gardens and spread extensively in rural habitats

and *Salvia* species, which have long corolla tubes), so we recommend prioritising the planting of taxa which produce relatively open flowers in late summer and autumn to ensure sufficient food for short-tongued solitary bees and Diptera (Table 1).

5 | CONCLUSIONS

Our study demonstrates that urban residential gardens differ markedly in the magnitude and temporal pattern of nectar supply, but bigger gardens are not necessarily better for feeding pollinators. Instead, the management decisions made by individuals are particularly important, with gardeners able to control habitat quality if not quantity. By visiting multiple gardens which differ independently in plant species composition, pollinators have the potential to access a diverse and continuous supply of nectar in urban landscapes.

CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.

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

DATA AVAILABILITY STATEMENT
Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.44j0zpcfd (Tew et al., 2022a) and https://doi.org/10.5061/dryad.15dv41nzg (Tew et al., 2022b).

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