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Rarity begets rarity: Social and environmental drivers of rare organisms in cities

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Abstract

Cities are sometimes characterized as homogenous with species assemblages composed of abundant, generalist species having similar ecological functions. Under this assumption, rare species, or species observed infrequently, would have especially high conservation value in cities for their potential to increase functional diversity. Management to increase the number of rare species in cities could be an important conservation strategy in a rapidly urbanizing world. However, most studies of species rarity define rarity in relatively pristine environments where human management and disturbance is minimized. We know little about what species are rare, how many species are rare, and what management practices promote rare species in urban environments. Here, we identified which plants and species of birds and bees that control pests and pollinate crops are rare in urban gardens and assessed how social, biophysical factors, and cross-taxonomic comparisons influence rare species richness. We found overwhelming numbers of rare species, with more than 50% of plants observed classified as rare. Our results highlight the importance of women, older individuals, and gardeners who live closer to garden sites in increasing the number of rare plants within urban areas. Fewer rare plants were found in older gardens and gardens with more bare soil. There were more rare bird

species in larger gardens and more rare bee species for which canopy cover was higher. We also found that in some cases, rarity begets rarity, with positive correlations found between the number of rare plants and bee species and between bee and bird species. Overall, our results suggest that urban gardens include a high number of species existing at low frequency and that social and biophysical factors promoting rare, planned biodiversity can cascade down to promote rare, associated biodiversity.

INTRODUCTION

An enormous body of literature supports the hypothesis that species-level diversity promotes ecosystem services and human well-being and therefore should be conserved (e.g., Haines-Young & Potschin, 2010; Sandifer et al., 2015). However, biodiversity and associated ecosystem services are rapidly declining at a global scale and urbanization, through its associated land-use change impacts, is one of the primary causes (Eichenberg et al., 2021; Hansen & Pauleit, 2014; Loreau et al., 2001; Taylor & Hochuli, 2015). Urbanization often negatively impacts species diversity because it is associated with land-use conversion and habitat loss and is increasing rapidly with the 53% of the human population currently residing in cities expected to escalate to 60% by 2030 (Liu et al., 2016; McKinney, 2006; United Nations, 2018). In addition to habitat losses, the structure and integrity of remaining habitats can be altered in urban environments so that they provide fewer resources and become inhospitable for some organisms, particularly specialists. Development of urban spaces (e.g., gridded streets, water and power infrastructure) is known to drive the functional homogenization of ecological environments and communities across multiple scales (Aronson et al., 2017; Groffman et al., 2014). This is because in cities, human disturbance including land-use change is theorized to select for more adaptable, generalist species. However, human activities including international trade, horticulture, and recreation also encourage higher rates of introductions of nonnative species, a potential source of diversification. Yet generalist species tend to be introduced in greater numbers and may have higher establishment success in highly disturbed environments (Clavel et al., 2011). The greater flexibility of generalist species to adapt to novel conditions may give them a selective advantage in urban environments.

Although a small number of dominant species, whether generalist or not, is often sufficient to support ecosystem function (Schwartz et al., 2000), there is a growing consensus that less common and rare species are vital to maintain a broad range of ecosystem functions and services (Ives et al., 2016; Leitão et al., 2016; Lyons et al., 2005; Lyons & Schwartz, 2001). Ecosystem function can be specific to the urban environment (e.g., storm water management), but for many such as pest control and pollination, function in urban settings is equivalent to their analogs in nonurban environments, although they may have different target pest, host populations, or perceived values by human managers. Rare species, those represented by a few individuals within a particular habitat, may add temporal variability in species abundance, and may contribute to aggregate the effects of biodiversity on ecosystem function (Lyons et al., 2005). Even in high-diversity ecosystems such as coral reefs, rare species have been reported to support the most vulnerable functions (Mouillot et al., 2013). Whereas rare species contribute to the functional structure of species assemblages (Leitão et al., 2016), they are often highly vulnerable to environmental changes themselves, including those associated with urbanization. Theory suggests that both habitat loss and prolonged and heightened levels of disturbance such as those found in cities can lead to functional homogenization as generalist species replace specialists (Clavel et al., 2011; Harrison et al., 2019). Yet rarity is most often defined by extinction risk, a metric that may be confounded with habitat preference in relatively pristine, high-diversity ecosystems where human management and disturbance is minimized (Lawler et al., 2003; Leitão et al., 2016). Species certainly exist at low frequency in cities, but little information is known about the composition and drivers of rarity in urban environments that are homogenized and heavily managed. Therefore, in this study, we define an organism as rare based on frequency of occurrence alone.

Cities have the potential to play an important role in the conservation of rare species through the planning and management of urban green spaces. Planned

biodiversity in the form of cultivated and intentionally planted vegetation in gardens may have effects on associated biodiversity of wild plants and animals, both native and introduced, in cities. Although researchers and the public tend to equate urban spaces with low diversity ecosystems composed of cosmopolitan species that are largely nonnative and generalist, recent work indicates that urban greenspaces can harbor surprisingly high levels of endemic biodiversity (Aronson et al., 2017). Urban greenspaces include natural, seminatural, and artificial ecological systems within and around a city (Cilliers et al., 2013). Urban gardens are especially notable for their documented ability to harbor biodiversity. The high abundance of managed flowering plants and prolonged growing season maintained by irrigation and fertilization in urban gardens creates habitat for a diversity of wildlife (Aronson et al., 2017; Clucas et al., 2018; Colding et al., 2006; Faeth et al., 2005; Mata et al., 2017; Smith et al., 2006). We know that biodiversity of primary producers can cascade up to increase biodiversity of higher trophic levels with consequences for ecosystem services. Researchers have documented this trend in both natural and human-managed systems, particularly in agricultural settings where trophic cascades in pest control systems is a major focus (Bruno & Cardinale, 2008; Tilman et al., 1997). Plant species within urban gardens underpin the delivery of many ecosystem services in these systems (Borysiak et al., 2017; Potter & LeBuhn, 2015), particularly for mobile ecosystem service-providing organisms, such as pest-predating birds and pollinating bees (Kremen et al., 2007). In cropping systems, the aggregate contribution of less common bee species is essential to sustain pollination services (Kremen et al., 2002). Similarly, rare bird species may provide predation services that help keep some pests under control (Maas et al., 2015). Researchers have hypothesized that the abundance and diversity of planned plant biodiversity in gardens impact associated wild urban bee and bird biodiversity but these studies do not focus on rare species and it is unclear whether the effects of biodiversity and abundances are separable (Fortel et al., 2014; Mayorga et al., 2020; Potts et al., 2016; Scheper et al., 2014). Beyond species-level contributions, crops have been artificially selected into cultivars that may become unique ecological partners for other taxa (Hauri et al., 2021). Cultivars are typically characterized by structural and chemical differences with ecological consequences; for example, cauliflower has been selected for mutant, sterile flowers that do not attract the same pollinators as wild mustard plants, despite being the same species, *Brassica oleracea* (Jahan et al., 2013). Urban gardens host a high degree of cultivar diversity but the contributions from rare cultivars to specialist, mobile ecosystem service providers such as pollinators or pest-predators may be undervalued because cultivars are not distinct species and often ignored in biodiversity studies (Dixon & Aldous, 2014; Ong & Fitch, 2020). Although studies documenting the importance of urban gardens for biodiversity continue to accumulate, these studies do not focus on rare organisms that occur at very low frequency. Understanding how management of urban gardens can be carried out to support rare organisms in cities will be particularly important as urbanization and functional homogenization proceeds at a rapid pace.

Because plots within urban gardens are managed by a multitude of people from different backgrounds, ages, and socioeconomic statuses, gardens face a complex set of social, cultural, and economic factors that govern how they are managed (Aronson et al., 2017). Extensive work in the social sciences show that urban gardens may be especially influenced by factors such as gender (Philpott et al., 2020), education (Shava et al., 2010), and economic status (Hope et al., 2003; Iuliano et al., 2017; Kinzig et al., 2005; van Heezik et al., 2013). Interestingly, there is a limited understanding of how these social and biophysical factors interface to support rare plant and animal species in urban contexts (Lepczyk et al., 2017; Ong & Fitch, 2020). Individual gardeners make decisions about plant diversity (Gregory et al., 2016), soil management, and applications of irrigation and agrochemicals based on their perceptions and desires for their garden plots (Clarke & Jenerette, 2015). For example, higher income has been associated with higher ornamental plant diversity in gardens (Clarke & Jenerette, 2015). The levels of labor and experience of gardeners can also influence the prevalence and diversity of weeds or ambient vegetation that is not specifically curated in garden plots. Greater labor tends to decrease weed abundance (Philpott et al., 2020). Because plant diversity has been linked with socioeconomic (Hope et al., 2003) and linguistic diversity (Romaine & Gorenflo, 2017), certain gardener traits may also select for rare plant species. Yet the broader connection between socioeconomic variables, plant biodiversity, and the ability of gardens to support associated wild rare species remains understudied.

Clearly, urban gardens have significant potential to support biodiversity and functional diversification in an increasingly urban world. Yet studies on rare organisms in cities are themselves few and far between. In this paper, we begin to address existing gaps in the literature by asking which species and cultivars are rare in urban gardens, to what extent are they rare, which socio-environmental factors drive increased numbers of rare species and cultivars and can planned plant rarity beget associated bee and bird rarity.

MATERIALS AND METHODS

Study region

We worked in 18 urban community gardens in three counties (Santa Clara, Santa Cruz, and Monterey) in the central coast region of California. The gardens differ in local habitat (structural and compositional diversity of both crop and noncrop species) and landscape context (amount of natural, agricultural, and urban land cover in the surrounding area). All gardens had been cultivated for five to 47 years and range from 444 to 15,525 m^2 in size. All the gardens use organic management practices and prohibit the use of chemical pesticides and insecticides. Gardens were chosen because they represent sites across a gradient of urban, natural, and agricultural landscapes and were separated from each other by ≥2 km, the farthest distance between gardens was 90 km and the closest was 2 km (Cohen et al., 2022; Egerer et al., 2017; Philpott & Bichier, 2017). Gardener demographic data indicated that gardeners are diverse in their make-up, covering a range of family sizes, education, salary, and food insecurity levels (Egerer et al., 2017; Philpott et al., 2020).

Data collection

We provide the following framework (Figure 1) to help visualize the specific set of questions posed in this study and the data and analyses used to address them. First, we ask which gardener characteristics (Q1) and which local and landscape garden features affect the number of rare plants (Q2a) and rare bird and bee species (Q2b) in urban community gardens. We include cultivars as distinct types per Reiss and Drinkwater (2018). Subsequently, we ask if there is an association between the number of rare plants and the number of rare bird and bee species (Q3) and if the number of rare bird and bee species are also related to one another (Q4).

The data analyzed for this research was collected in two summer field seasons (2015, 2017), from May to September, which is the peak urban garden growing season for the region. Gardener characteristics data (defined below) and gardener self-reported plant data were collected in summer 2017 to address Q1 (Figure 1). Direct sampling of biodiversity (plants, bees, birds) and garden characteristics was done in summer 2015 to address Q2–4 (Figure 1). Although structural equation modeling (SEM) was considered, there is no direct way to compare data from 2017 and 2015 because of the methodological differences outlined below. Therefore, separate statistical analyses are conducted for 2017 and 2015 data. We can test the relationship between gardener characteristics and number of rare
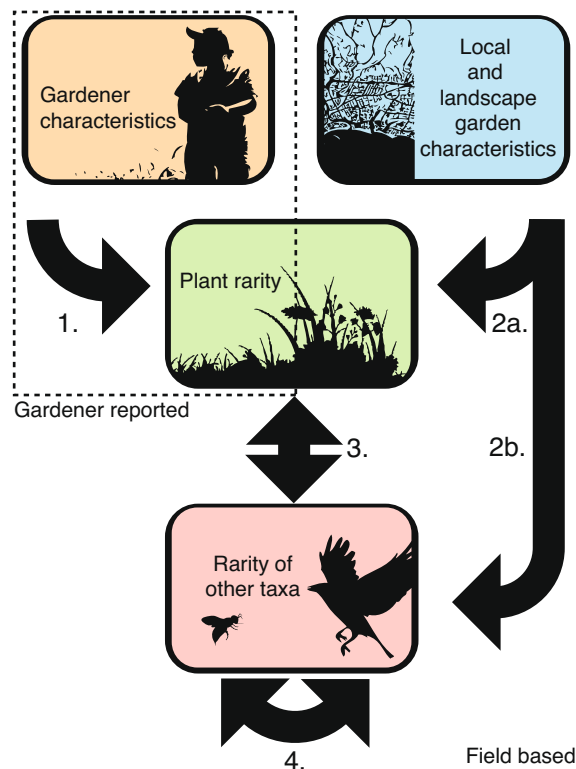
FIGURE 1 Overarching research framework. Each numbered arrow indicates the direction of each hypothesized relationship that we tested in our study, including: 1. Gardener characteristic effects on number of rare plants reported by gardeners. 2a. Local and landscape-level garden characteristic effects on number of rare plants directly surveyed in the field. 2b. Local and landscape-level garden characteristics effects on number of rare bird and bee species directly observed in the field. 3. Number of rare plant effects on number of rare bird and bee species directly observed. 4. The relationship between number of rare bird and bee species observed. The box outlined in dashed lines indicates that gardener-reported data were used to assess study questions. Analyses outside of dashed box used field-based data.

plants because gardeners reported in our surveys what plants they grew. We cannot directly test how gardener characteristics influenced the number of rare bird and bee species because gardeners were not asked about these species. Instead, we infer the effects of gardener characteristics on bees and birds indirectly through the overall research framework in Figure 1. We explain the specific methods for each type of data collection and the analysis below.

Gardener characteristics data

We surveyed gardeners from 18 urban community gardens during the 2017 summer field season. Survey questionnaires collected information on gardener demographic information as well as gardening experience and use data

(Table 1). Specifically, we surveyed 185 gardeners in total, or six to 14 gardeners per garden (9.5%–65% of the gardener population in a site). We only included surveys in our analysis if plant information on the survey was completed ($n = 162$). We administered surveys in English ($n = 123$), Spanish ($n = 38$), and Bosnian ($n = 1$) and either read the survey out loud in person ($n = 138$) or by telephone ($n = 1$), and either had the gardener fill out the survey themselves ($n = 21$) or had a gardener read the survey to another gardener ($n = 1$). Two of the surveys did not have information on the method of survey administration. We also note that despite our best efforts to survey gardens equally, uneven gardener availability resulted in unequal gardener sampling across the 18 community gardens, requiring us to calculate the number of rare plants in gardener-reported data (2017) by gardener surveys rather than by garden as was done in direct field-based data (2015) described in the following sections.

Gardener-reported plant data

Gardeners were asked to identify and list the plants that they planted in their plots. We then classified gardener-reported plants into either crop or ornamental species. Crop species included fruits, vegetables, herbs, and other consumable plants. Ornamental species included plants grown for decorative purposes, such as flowers and nonfood providing crops. Although we included plant cultivars as distinct types, gardeners varied in the level of cultivar specificity provided, which we acknowledge is a limitation to our study. We looked up scientific names for common names provided and supplemented these results with direct field-based plant data in which researchers identified species and cultivars in the field using methods described in detail in the following paragraphs.

Garden characteristics data

Landscape-level garden data

For each garden, we measured the surrounding landscape composition within buffers surrounding gardens at the 0.5-, 1-, and 3-km scales. We used the 2011 National Land Cover Database (NLCD) (Jin et al., 2015) to calculate the percentage of urban NLCD land cover class using ArcGIS (v. 10.1) (ESRI, 2011). Urban land cover was

TABLE 1 Gardener characteristics (sociodemographic and gardener experience/use data) collected within the survey.

Gardener characteristics collected from the survey	Explanation of variable and coding methodology
Age	Age of survey participant, gardeners provided exact ages at time of data collection
Family size	Number of people in the family. Converted to ordinal format with: 0 additional members (1); 1–3 family members (2); 4–6 family members (3); 7–10 family members (4); and more than 10 additional members (5)
Gender	Converted to ordinal format with: female (1) and male (2)
Income	Converted to ordinal format with: "prefer not to say" (0); $0 to $10 K (1); $10 to $20 K (2); $20 to $30 K (3); $30 to $40 K (4); $40 to $50 K (5); $50 to $75 K (6); greater than $75 K (7)
Education	Converted to ordinal format with: no schooling (0); Elementary School (1); Middle School (2); High School (3); Vocation/Associates Degree (4); Bachelor's Degree (5); Master's Degree (6); Professional Degree (7); Doctorate (8)
Languages spoken	Number of languages besides English spoken
Food insecurity	Self-reported levels of food insecurity with: low (1); medium (2); high (3) were used in the regression analyses for species richness and pounds of food produced
Distance from garden	Distance the gardener lives from the garden. Converted to ordinal format with <1 mile (1); 1–5 miles (2); 5–10 miles (3); >10 miles (4)
Years gardening	Number of years of gardening experience; provided as exact number of years of experience. If the gardener provided a range, the middle of the range was taken
Hours in garden	Number of hours spent in the garden per week; provided as an exact number. If the gardener provided a range, the middle of the range was taken
Species/cultivar richness	Gardeners listed all the plants they intentionally grew in their plots. Total plant species richness is the total number of plant species/cultivars grown. Ornamental and crop plants were classified by researchers and the number of plants in each category were counted

Note: The left column provides the abbreviated terms used in the following tables and in the analysis. The right column explains what type of data were collected and how these factors were coded and calculated for the analysis.

calculated by combining developed low-, medium-, and high-intensity developed land. Urban land cover is correlated with many other land-use categories (e.g., natural land), therefore we chose to focus on only urban land cover in our models because we were most interested in the effects of urbanization on biodiversity; furthermore, urban land cover has been a significant predictor of biodiversity in previous analyses of these gardens (Egerer et al., 2017; Quistberg et al., 2016). Urban cover at the 1-km scale best predicted pooled species rarity across taxa, exhibiting the lowest AIC of all the scale models (Appendix S1: Table S1), therefore the 1-km spatial scale was used for all subsequent analyses.

Local-level garden data

To collect local-scale garden characteristics, we established a 20 × 20 m plot in the center of each garden. In this plot, we measured canopy cover using a spherical densiometer at the center and N, S, E, and W edges of the plot, counted the number and species of trees and shrubs, and counted the number of trees or shrubs in flower within the plot. We determined age and size of each garden by examining historic Google Earth images and noting the first appearance of the gardens, and then we used ground-truthed GPS points taken from each garden to calculate size. For a few of the gardens older than 35 years, we used historical information gained through community resources or discussions with farm management to determine age.

We measured ground characteristics using four 1 × 1 m subplots within the 20 × 20 m plots. The 1 × 1 m subplots were randomly placed anywhere (including pathways) within the 20 × 20 m plots. Within each 1 × 1 m subplot, we measured the height of the tallest herbaceous vegetation and estimated ground cover composition (percent bare soil, rocks, leaf litter, grass, mulch).

We repeated sampling once per month between May and September 2015 and calculated the mean value for each environmental variable for each garden at each time point.

Field-based biodiversity data

Field-based plant data

We measured plant biodiversity using the same four 1 × 1 m subplots within the 20 × 20 m plots. Within each subplot, we identified the species and cultivars of all herbaceous plants and measured the percentage cover for each species and cultivar. This was measured once per month for five sampling periods, separated by roughly 21 days. As with gardener-reported plant data, researchers classified field-based plant data into either crop or ornamental species and cultivars. Plants that did not fit crop or ornamental categories were designated weeds. Gardeners were not asked to report any weeds, therefore not classified in gardener-reported plant data.

Bird data

All bird surveys were conducted by one observer (P. Bichier) at each sampling period (see Mayorga et al., 2020). In each garden, this person performed a 10-min point count. Due to the small sizes and irregular shape of some gardens, fixed-radius point counts were not used. Instead, the observer stood approximately at the center of each garden and recorded all birds seen or heard within the garden. We assumed that birds within 30 m that were heard but not seen were in the plot unless visually observed to be outside of the plot. Each site was visited during different times during daylight hours (i.e., morning, afternoon, evening) across sample periods to reduce bias in the survey. All birds that were seen or heard inside the garden were identified, and totals were calculated for each round.

Bee data

We sampled bees with both elevated pan traps and hand netting (Grundel et al., 2011), using 400-ml plastic bowls (yellow, white, and blue) painted with Clear Neon Brand and Clear UV spray paint for pan traps (see Quistberg et al., 2016). We placed pan traps from ~8:00 to 11:00 AM and collected traps between 4:00 and 7:00 PM on the same day, and sampling was repeated five times across the summer. We placed three 1-m tall PVC pipes in the ground in a triangle formation, 5 m apart within each of the 20 × 20 m plots and placed one bowl of each color on top of PVC tubes (Tuell & Isaacs, 2009). We filled bowls with 300 ml of water and 4 ml of unscented Dawn dish soap. In addition, we sampled bees using aerial nets at each site for a total of 30 min per site, not including handling time. We netted bees that were observed on flowers, within 20 m of and inside the 20 × 20 m plots in each site. We stored all captured bees for later identification. We performed bee identifications with reference to online resources, image databases, books, and dichotomous keys (Ascher & Pickering, 2020; Frankie et al., 2014; Gibbs, 2010; Michener, 2007). We identified all specimens to the highest taxonomic level possible or designated morphospecies. We compared our specimens to those held in the Kenneth S. Norris Center for Natural History on the University of California, Santa Cruz campus. All voucher specimens are housed in the Philpott Laboratory at the University of California, Santa Cruz.

Defining rarity

We considered a species or cultivar as rare if it occupied less than or equal to 1% of all samples ($n = 18$

garden samples for field-based data for each of five sampling rounds and $n = 185$ gardener survey samples for gardener-reported data; as per Lyons et al., 2005). In our study, a rare species or cultivar was found in only one of all 18 sites sampled (1/18 is less than or equal to 5%, which is the lowest occurrence rate possible for our sample size) or was reported in only two of all 185 gardener surveys (2/185 rounds down to 1%) for gardener-reported plant data. To assess whether we adequately sampled the biodiversity of each taxon and sampling scheme, species accumulation curves were produced for the gardener-reported plant data and field-based plant, bird, and bee biodiversity data (Appendix S1: Figures S1–S4). We tallied the number of rare species and cultivars and compared this with total numbers of species and cultivars documented for each taxonomic group and sampling protocol to determine the extent of rarity we observed in urban gardens. Full lists of rare and common species/cultivars and their frequencies are available in Appendix S1: Tables S2–S9.

Analysis

We constructed four generalized linear mixed models (GLMM) that together address our questions in Figure 1 (Bolker et al., 2009). We used these four models to predict the number of rare gardener-reported plant, field-based plant, bird, and bee species as a function of the following fixed and random effects:

$$r_{\text{plant−reported 2017}} \sim \text{gardener characteristics} + (1|\text{garden}) + \xi \quad (1)$$

$$r_{\text{plant−field 2015}} \sim \text{garden characteristics} + r_{\text{bee}} + r_{\text{bird}} + (1|\text{round}) + \xi \quad (2)$$

$$r_{\text{bee}} \sim \text{garden characteristics} + r_{\text{plant−field 2015}} + r_{\text{bird}} + (1|\text{round}) + X \quad (3)$$

$$r_{\text{bird}} \sim \text{garden characteristics} + r_{\text{bee}} + r_{\text{plant−field 2015}} + (1|\text{round}) + X \quad (4)$$

where r is the number of rare plants reported by gardeners or rare plants, bee, and bird species observed in field-based surveys. We used garden as a random effect for gardener-reported data (Equation 1) and sampling round as a random effect for field-based data (Equations 2–4) because the number of rare species is calculated by garden for field-based data and by survey for gardener-reported data. We assumed Poisson error

distributions, ξ, for plant count data and transformed our rare bird and bee observations into a binomial presence/absence variable as most counts (97.6% of rare birds and 98.9% of rare bees) were 1 or 0. Therefore, we assumed binomial error distributions, X, for the bird and bee count data.

Our fixed effects include gardener, garden characteristics, and cross-taxonomic effects. Gardener and garden characteristics are composed of several variables detailed below. For all fixed effects, we utilized a variance inflation factor cut-off of three to remove any collinear variables (Zuur et al., 2009). Categorical variables were coded in an ordinal format when appropriate (see Table 1) as per (Hildebrand et al., 1977). All analyses and figures were run and generated using the R environment using packages *tidyverse*, *lme4*, *ggpubr*, *car*, *corrplot*, and *vegan* (Bates et al., 2015; Fox and Weiberg, 2019; Kassambara, 2020; Oksanen et al., 2020; R Core Team, 2016; Wei & Simko, 2017; Wickham et al., 2019).

Gardener characteristics
We used the sociodemographic variables described in Table 1 as fixed effects to predict the number of gardener-reported rare plants (Equation 1). After removing collinear variables, the final fixed effects for gardener traits included age, number of people in the family, gender, number of languages other than English, distance of home to the garden, income, education, number of years gardening, number of hours gardening, and food insecurity.

Garden characteristics
Several local and landscape-level garden characteristics were measured and broadly divided into three groups: permanent garden and landscape variables, woody vegetation variables, and ground cover variables. In each group, we tested for collinearity between variables, and then among collinear sets of variables, we retained variables for final models based on perceived importance for the taxa in this system (Burks & Philpott, 2017; Quistberg et al., 2016). For example, in the permanent garden and landscape group, size and age of gardens are anticipated to influence the biogeography and microclimates experienced by taxa at garden sites (Potter & LeBuhn, 2015; Smith et al., 2005). We are also interested in urbanization, therefore selected the variable percent urban cover over the variable percent agriculture cover, which were correlated. We chose percent canopy cover for vegetation characteristics because this is a widely used metric in other studies, it is positively correlated with the number of trees and shrubs, and we did not want to use the number of trees and shrubs because this variable is also a component of our dependent variable, the number of rare plant

species. In the category of ground cover, we chose percent bare soil because there is evidence from the published literature that many bee species are strongly influenced by this metric and it is negatively correlated with percent mulch and straw (Quistberg et al., 2016). We excluded percent herbaceous plants in this category because of the potential conflict with our dependent variable, the number of rare plant species and cultivars. The same garden characteristic variables were used to predict all rare taxa using (Equations 2–4). From here onwards, we only discuss variables that were retained in our final models. These include garden age, garden size, percent urban at 1 km, percent canopy cover, and percent bare soil.

Testing whether rarity begets rarity

Because we are interested in whether the number of rare plants, birds, and bees are associated, our GLMMs also include the number of rare plant, bird, and bee species as explanatory variables when appropriate (Equations 2–4). In addition to these models, which test for potential causal relationships, we ran Pearson's *r* tests to assess correlations between the numbers of rare species across taxa (Appendix S1: Figure S1). When correlating each pair of taxa, we constrained our analysis to include only data that were collected during the same sampling rounds and gardens.

RESULTS

Rare species numbers and descriptions across taxa

Gardeners reported growing a total of 190 plants, which included 183 distinct species. Of those, 75 plants, which included 74 distinct species, were rare (Table 2). Rare plant species belonged to several families including, but not limited to, Apiaceae, Asteraceae, Poaceae, Lamiaceae, and Papaveraceae (Appendix S1: Table S2). Many of the rare crop species

(e.g., *Ribes uva-crispa*, *Prunus avium*, *Colocasia esculenta*, *Benincasa hispida*) were reported only once by all surveyed gardeners.

We observed 295 total plants, which included 267 distinct species in our field-based plant surveys. Of those, 159 plants, which included 156 distinct species, were classified as rare (Table 2). We note that a rare plant could be recorded more than once at a different sampling time or spatial in-garden replicate but never in more than one garden for field-based data. The number of duplicate common plant species totaled seven and 28 for gardener-reported and field-based data, respectively. Of those plants that were classified rare, only one and three cultivars were a duplicate species in gardener-reported and field-based data, respectively (Table 2). Rare plants came from a wide range of taxonomic plant families including Amaryllidaceae, Apocynaceae, and Ranunculaceae (Appendix S1: Table S3). There were very few similarities in rare plants across gardener-reported and field-based data (i.e., *Stevia rebaudiana*, *Vitis vinifera*, *Xerochrysum bracteatum*, *Papaver* sp.). Rare field-based plants included many weed species that were not reported by gardeners (Table 2; Appendix S1: Tables S2–S3).

We found 52 bee species and morphospecies and we classified 12 as rare. Our rare bees exhibit a wide range of phenotypic traits (Cohen et al., 2022). They include both generalist and specialist bees, bees exhibiting oligolecty and polylecty, and bees nesting aboveground and belowground (Table 2; Appendix S1: Table S4). We recorded 57 bird species and determined that 13 were rare in this system (Table 2; Appendix S1: Table S5). Many of the rare bird species prefer woodlands or semiopen habitat.

Gardener characteristics promoting rare plants: Q1

We found that gender was a significant predictor of the number of rare plants, with women planting more rare plants than men (Figure 2; Table 3). Age was also

TABLE 2 Total number of species across taxa lists as well as the number of species and cultivars, for plants only, considered rare in our study.

Category	Total no. plants	No. plants considered rare	Total no. species	No. species considered rare
Gardener-reported plants: (including crops and ornamental)	190	75	183	74
Field-based plants: (including crops, ornamentals, and weeds)	295	159	267	156
Field-based bees	...	...	52	12
Field-based birds	...	...	57	13
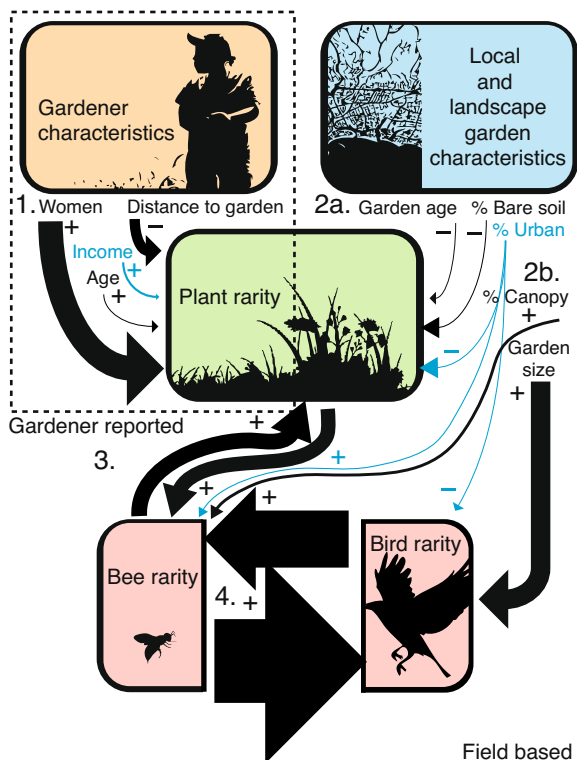
FIGURE 2 Visualization of results from generalized linear mixed effects (GLMM) models. Black arrows indicate the direction (arrowheads) and effect size (width of arrows) for significant ($p \leq 0.05$) predictors of plant, bird, and bee rarity (number of rare species and cultivars for plants). Blue arrows indicate partially significant effects ($0.05 < p \leq 0.10$). See Figure 1 for further details.

significant, with older gardeners tending to plant more rare plants (Figure 2; Table 3). Distance between place of residence and the garden was a significant predictor of rare plants, with gardeners who lived closer to the garden planting greater numbers of rare plants than those residing further away. Income had a marginally positive impact on number of rare plants (Figure 2; Table 3).

Garden characteristics promoting rare plants, birds, and bees: Q2a and 2b

Garden age negatively impacted the number of rare plants, with younger gardens having greater numbers of rare plants (Figure 2; Table 3). Percentage bare soil also reduced the number of rare plants so that gardens with less bare soil harbored greater numbers of rare plants. The percentage of built urban cover within 1 km of the garden had a marginally negative effect on rare plants (Figure 2; Table 3).

Both local and landscape garden characteristics were significantly associated with the number of rare bird and bee species. The number of rare bird species was greater in larger gardens and there were more rare bee species in gardens with a higher percentage of tree canopy. The percentage of built urban cover at the 1-km radius had a marginally negative effect on the number of rare bird species and marginally positive effect on the number of bee species (Figure 2; Table 3).

Does rarity beget rarity: Q3 and 4

For field-based data, the number of rare plants was positively associated with the number of rare bee species (effect size estimate $= 0.54$, $p = 0.014$), but the number of rare bird species was not associated with plants. Additionally, the number of rare bird species had a large positive association with the number of rare bee species (effect size estimate $= 2.14$, $p = 0.054$). Rare bees also strongly predicted rare birds (effect size estimate $= 3.14$, $p = 0.019$) (Figure 2, Table 3; Appendix S1: Figure S1).

DISCUSSION

A discussion around how "rarity" is defined is always context dependent. Rare species defined within this system may not be so in other ecological systems or at different scales or times (Flather et al., 1997; Lawler et al., 2003). In this paper, a rare species occurred infrequently across the landscape or was reported by few gardeners. It is important to note that we have known for some time that most species on earth are rare, with fewer species considered common (Gaston, 2008). Here we find that this is also true in our urban garden sites, with 53.8% of the plants in field-based data, 39.5% of the plants in gardener-reported data and nearly a quarter of the total bee (22.8%) and bird species (23.1%) classified as rare in our urban garden sites (Table 2; Figure 3). Previous work concentrating in landscapes where human impact is limited have found that rare organisms are highly susceptible to climate change and habitat disturbance and are most commonly found in specialized niches (Irl et al., 2017; Vincent et al., 2020). Our results indicate that urban gardens harbor many rare organisms, but that the composition and drivers of rare species assemblages may be quite different in urban settings.

Role of gardener characteristics in promoting rare plants

We found that gender, age, and distance to a garden from a gardener's home played significant roles in influencing the number of rare plants found in the garden plots.

TABLE 3 Model results

| Predicted variable	Predictor variable	Estimate	SE	z	p
Q1: Which gardener characteristics are predictive of number of rare plants?					
	Gender (woman = 0)	−0.92	0.27	−3.43	0.0006***
	Gardener age	0.02	0.01	2.16	0.030*
	Distance to garden	−0.39	0.20	−1.94	0.052*
	Gardener income	0.08	0.05	1.67	0.095°
Q2a: Which local and landscape-level garden characteristics are predictive of number of rare plants?					
	% Bare soil	−0.01	0.00	−2.82	0.005**
	Garden age	−0.02	0.01	−2.53	0.011*
	% Urban at 1 km	−0.01	0.00	−1.89	0.058°
Q2b: Which local and landscape-level garden characteristics are predictive of number of rare bird and bee species?					
Rare birds	Garden size	0.73	0.28	2.64	0.008**
Rare birds	% Urban at 1 km	−0.02	0.01	−1.77	0.077°
Rare bees	% Canopy	0.11	0.05	2.13	0.034*
Rare bees	% Urban at 1 km	0.04	0.02	1.91	0.056°
Q3: Are number of rare plants predictive of numbers of rare bird and bee species and vice versa?					
Rare plants	Rare bees	0.54	0.22	2.46	0.014*
Rare plants	Rare birds	0.17	0.27	0.64	0.520
Rare bees	Rare plants	0.59	0.24	2.42	0.016*
Rare birds	Rare plants	0.08	0.26	0.32	0.750
Q4: Do numbers of rare bee and bird species predict one another?					
Rare bees	Rare birds	3.14	1.34	2.35	0.019*
Rare birds	Rare bees	2.14	1.12	1.92	0.054*

Note: Analyses with rare plants as the predicted variable were performed using a generalized linear mixed effects model (GLMM) with Poisson distribution and garden or sampling round as a random effect. Analyses with rare bird or rare bees as the predicted variable were performed using a GLMM with a binomial distribution and sampling round as a random effect. Significance values: °, ≤0.10; *, ≤0.05; **, ≤0.01; ***, ≤0.001.

Specifically, women tended to plant more rare plants (Figure 2). This resonates with findings from other studies in which gardens managed by women host a larger diversity of species per unit area (Reyes-García et al., 2010) potentially because they also tend to cultivate a higher proportion of ornamental plants (Philpott et al., 2020). Furthermore, women report a larger diversity of uses (ornamental, medicinal, religious) for the plants they grow in gardens than men (Reyes-García et al., 2010). Environmental theory suggests that women, who display greater proenvironmental attitudes and behavior than men on average, could include a wider variety of plants in their plots to promote wildlife, sustainability, and human well-being (Milfont & Sibley, 2016).

Age of gardeners was also found to be a significant positive predictor of the number of rare plants found in the garden plots with older gardeners cultivating a greater number of rare plants. Other studies on urban gardens have found a positive correlation between the age of the gardener and plant species richness and diversity, with more diversified gardens belonging to older gardeners (Bernholt et al., 2009; Naigaga et al., 2020). Previous sociodemographic work within the same dataset found that total plant composition differed with age (Philpott et al., 2020). Among gardeners surveyed, 45% were more than 60 years old, with many already retired. Age and retirement potentially indicate greater time available to garden. Older gardeners tended to have more years of gardening experience as well, whereas younger gardeners (22–50 years of age) tended to spend less time in gardens and were mostly motivated by food, potentially leading to a more restricted set of plants.

In addition, we found that gardeners who live closer to their community garden (<1 km) may plant more rare plants than those who live far away (>5 km). The proximity of the household to the garden may increase the time gardeners spend in the gardens as leisure spaces and may promote stewardship of the land, resulting in efforts to beautify, maintain, and diversify the garden. We have found in our previous analysis of the same system
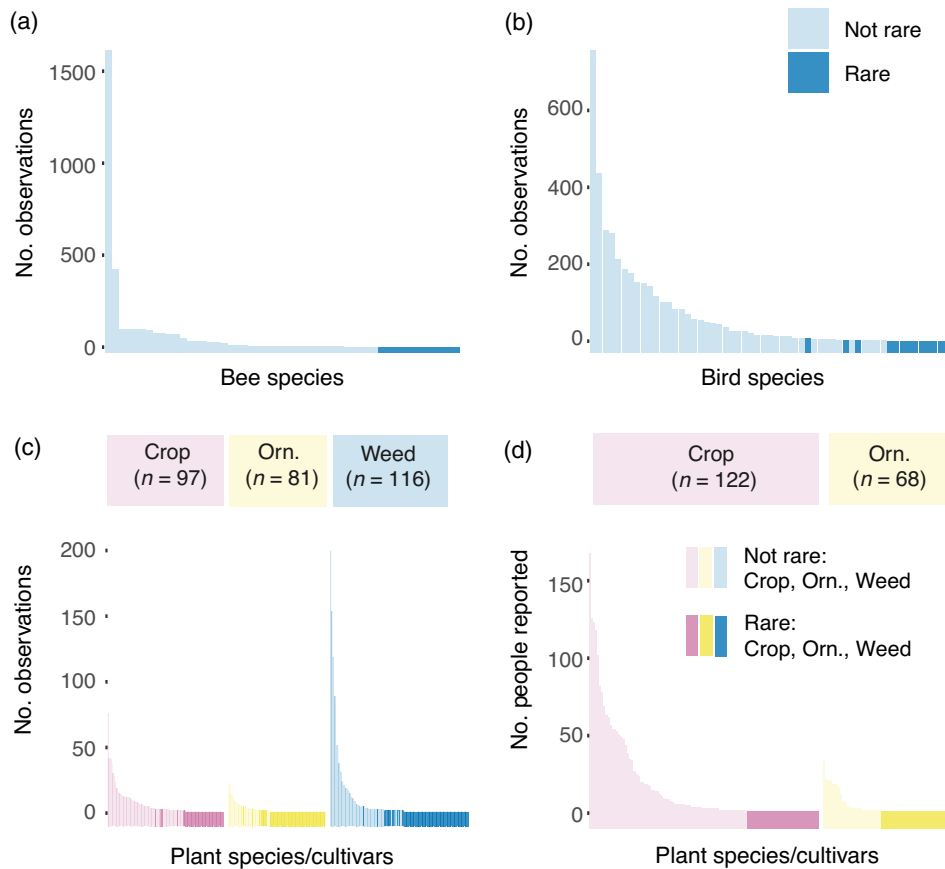
FIGURE 3 Ranked species and cultivar frequency plots. Panels (a) and (b) show the total number of observations of all bee and bird species across each site for field-based data. Panel (c) displays the total number of times each plant was observed across all 1 × 1 m subplots in all site samples across the growing season. We divided this plot by plant type: crop, ornamental, weed. Panel (d) shows the total number of times a gardener reported growing a plant in their garden. Again, we divided this plot by plant classification. Because plants were self-reported by gardeners, we did not collect any weed data.

(Philpott et al., 2020) that time spent in gardens does enhance overall plant species richness, which we show here may also extend to greater numbers of rare plants. Because home values in neighborhoods with urban gardens tend to increase (Voicu & Been, 2008), gardeners who include more rare plants for aesthetic reasons may also benefit by enhancing the value of their communities.

We also found a marginal, positive effect of income on number of rare plants that is supported by previous studies. Gardeners with more income may be able to devote more financial resources to promoting rare species, particularly ornamentals.

Role of garden characteristics in promoting rare plants, bees, and birds

Plants

The number of rare plants was influenced by several garden management features. First, garden age was a significant predictor, with younger gardens harboring more rare plants. One potential explanation for this pattern may be that managers and gardeners in younger gardens have not had the time and resources to create highly defined plots and pathways, and therefore our surveys captured greater ambient vegetation (e.g., peripheral vegetation on pathways, that is weeds) within the garden landscape. Older gardens may benefit from a larger, more consistent workforce of volunteers, gardeners and managers that keep up with maintenance and consequently reduce the number of rare plants that were more commonly found in messier, younger gardens. For example, our oldest garden, The Alan Chadwick Garden on the University of California, Santa Cruz campus, is serviced by large groups of student interns, apprentices, and paid staff that maintain weeds, potentially reducing the numbers of rare plants observed in our study. The percentage of bare soil cover was also a significant predictor, with less bare soil cover supporting more rare plant species (Figure 2; Table 3). Our field survey of plants included plants sampled in pathways and unmanaged shared spaces within the garden. Gardens with less bare soil

ONG ET AL.

generally have greater vegetation cover and potential to harbor more ambient species. Additionally, we found that more urban cover in the landscape had a marginally negative association with the number of rare plants in a garden (Table 3). Whereas high plant species richness has been found in moderately urbanized areas with high habitat heterogeneity (McKinney, 2008; Schmidt et al., 2014), urban landscapes dominated by impervious cover may not be hospitable for many plant species, including rare plants occurring in our garden sites. We expected cultivar diversity to spill over to increase the number of rare plants observed, but most of the rare plants classified in this study were distinct species, with only four rare cultivars representing a repeated species (Table 2; Appendix S1: Table S3). Although including cultivars in our study added some diversity overall, rare plants tend to include mostly distinct species. The high contribution of weeds, which were all considered distinct species, to rare plant counts may explain this result. Although not the focus of this study, we note that the majority of plants documented in the study were nonnative at 91%, with only 9% native California species. Of the rare plants classified, five of them were native, ~3%. Rare plants in urban gardens are cultivated and therefore may represent higher levels of nonnative species as people grow crop and ornamental plants from many parts of the world.

Bees

We add to the growing evidence that urban garden management can influence bee species richness (Hall et al., 2017; Matteson & Langellotto, 2010; Verboven et al., 2012). We found that gardens with more canopy cover support more rare bee species. Because some of the rare bee species we documented nest in plant stems and have limited foraging ranges (e.g., *Megachile relativa* [Medler & Koerber, 1958]), the availability of nesting sites may be particularly important for predicting the presence of these bees. Nesting resources structure wild bee communities in rural agricultural systems (Potts et al., 2005; Sardiñas & Kremen, 2014), but more research is needed to discern how bee species utilize nesting resources in urban environments. We also found a marginally significant trend suggesting that gardens surrounded by more urban land cover supported a higher richness of rare bee species ($p = 0.056$; Table 3). One possible explanation is that landscapes with increasing urban cover may promote greater bee foraging within floral-rich urban gardens, as previously documented in this system (O'Connell et al., 2020). Our rare bees have short foraging ranges; therefore, colonization and dispersal are likely to be limited to their local environment.

An examination of the phenotypic traits characteristic of the rare bees in this system may explain why

urbanization positively impacted rare species. One might expect that most rare bees in this system would be specialists because specialists rely on a narrow range of plant partners that may not be available in urban agricultural systems. However, we found that rare bees included many polylectic species (bees that collect pollen from a variety of plant species). These included bees in the genus *Halictus*, known to tolerate and utilize a wide range of floral resources (Cane, 2015), and *Lassioglossum incompletum*, a hypergeneralist that although generally common in this region, were rare in the gardens. Although habitat change is often associated with colonization by generalist species who can take advantage of many plant partners (Rand & Tscharntke, 2007; Rocha & Fellowes, 2020), our findings suggest that generalist species can still be rare in an urban system. Many scientists argue that the introduction of the European honey bee, *Apis mellifera*, a common practice in urban gardens, is causing competitive displacement of native bee communities (Paini, 2004). *A. mellifera* was by far the most abundant species observed in our study at greater than 1500 observations. This could help explain the hard skew and long tail in our bee distribution resulting in 23% of our bee species classified rare but many more nearing that classification (Figure 3; Appendix S1: Table S4). As opposed to plants, we note that all the bee species classified rare in this study were also native to the area.

Birds

Garden size was a significant predictor for rare bird species with larger gardens supporting more rare bird species (Table 3). This result may be due to a larger garden providing more shrubs and trees as resources for bird species and more area for bird prey. Birds require large areas of land for their habitat and food requirements and often rely on shrub and tree species richness (Paker et al., 2014). Larger urban habitat fragments including urban gardens tend to support greater bird abundance and richness (Crooks et al., 2004, Dale, 2018, Mayorga et al. 2020), which may increase the probability that rare bird species occur. The importance of garden size in our study may also be a factor of the sampling protocol. Within the protocol, all birds inside the garden were counted and birds outside the garden were not included in the sample. This may mean that more birds were counted in larger gardens, as some gardens were 20 times larger than other gardens, which is a limitation of the study. Furthermore, all data was used regardless of the distance of the bird from the observer.

Of the 57 bird species recorded, 13 were considered rare in the gardens (Appendix S1: Table S4), all of

which are currently listed as species of least concern by the International Union for Conservation of Nature (IUCN, 2021). The majority of the birds classified as rare in our study are only present in Northern California seasonally and could be temporally rare (Sibley, 2016). Northern California is the summer breeding ground for most, with the exception of the Western Tanager (*Piranga ludoviciana*), which passes through when migrating and the Pine Siskin (*Spinus pinus*), which utilizes the area during its nonbreeding season (Sibley 2016). None of the rare bird species are found primarily in garden or urban habitats. Some are more commonly found near water, including the Cliff Swallow (*Petrochelidon pyrrhonota*), Wilson's Warbler (*Cardellina pusilla)* and the Willow Flycatcher (*Empidonax traillii)* (Sibley, 2016). Many are found primarily in forest habitats and are dependent on trees that are lacking in urban gardens including Sharp-shinned Hawk (*Accipter striatus*), *C. pusila*, Stellar's Jay (*Cyanocitta stelleri*), *E. traillii*, the Band-tailed Pigeon (*Patagioenas fasciata*), *P. ludoviciana*, the Glue-gray Gnatcatcher (*Polioptila caerulea*) and *S. pinus* (Reynolds, 1983; Sibley, 2016).

Although some species, such as the American Kestrel (*Falco sparverius*), Tree Swallow (*Tachycineta bicolor),* *P. fasciata*, *C. pusila*, *E. traillii* and Purple Finch (*Haemorhous purpureus*) are historically common and have extensive ranges, they have experienced declines either in the recent past or present (Dunn, 2002; IUCN, 2021). Some of these declines have been linked to human activities including the spread of West Nile virus, the clearing of forests and competitive displacement by house sparrows (*Passer domesticus*), which are very common in disturbed habitats and are now also experiencing declines (Dunn, 2002; Jernelöv, 2017; Smallwood et al., 2009; Stanton et al., 2016). The classification of some of these common species as rare in this study may be cause for concern (Neeson et al., 2018). Deforestation may be pushing some bird species into smaller patches of habitats including those such as our urban gardens, explaining why garden size may be the only significant predictor of the number of rare bird species in our study. Similar to bees, of the 13 species classified rare, all were native. Of all bird species found in total, only four species were nonnative: Rock Pigeon (*Columba livia*), Eurasian Collared-Dove (*Streptopelia decaocto*), European Starling (*Sturnus vulgaris*), and *P. domesticus*. Therefore, native bird species may be disproportionately rare.

Does rarity beget rarity? Influences of rare plants on rare bee and bird species and vice versa

We found a positive association between the numbers of rare plants and bee species. We note that our positive associations are between the number of species that occupied gardens and not total abundances of rare birds and bees. Rare species are less abundant by definition, therefore the abundance of rare species may be less important as a metric here compared with studies that focus on total species richness. Our results indicate that the presence of a rare species, regardless of abundance, could signal unique environments that are attractive to other rare taxa or potentially directly benefit other rare taxa through species interactions. Bees have evolved close, mutualistic relationships with their plant partners (Michener, 2007) and may respond positively to gardener-curated plant assemblages. In addition to intentional plantings, many of the field-based rare plant species consisted of weeds and ornamentals (76.1%). These plants often exist in spaces between beds or along fence borders and are not disturbed by gardeners. Our results suggest that rare bees may benefit from the persistence of rare ornamental and weed species, although we do not know if this is an abundance-mediated or long-term effect. Therefore, in our study, rarity can beget rarity through the addition of rare plant species acting as host plants for rare bees. The result is surprising because few rare plants were native. However, future work is necessary to determine the specific relationships between rare plant-bee assemblages.

The presence of rare partners also provides resources for bees under disturbance conditions. Villanueva-Gutiérrez and Roubik (2016) found that, in drought years, some bee species forage for a greater percentage of locally rare pollen in their nests. Some plants also provide nectar and pollen resources during otherwise limited times (Dixon, 2009; Rathcke & Jules, 1993), and these plants can be important for bees with specific food requirements. Some of our rare bees were oligolectic and are expected to provide specialist pollination services in support of their known rare plant partners in our study, even if they are common outside of urban garden systems. For example, the rare bee, *Megachile apicalis* is a specialist partner of plants in the genus *Centaurea*, ornamental plants that are also rare in our system (Müller & Bansac, 2004). The rare generalist bees in our study could also support rare plants that happen to have fewer pollinators because of phenological, taste, or morphological mismatches with other bees found in the system.

In our study, rare bees and rare birds individually responded differently to local and landscape-scale garden characteristics. We found more rare bee species in gardens with more urban cover within 1 km, whereas there were fewer rare bird species in those gardens. Although the size of the garden was a significant driver for rare birds, it was not for bees (Table 3), and bees, but not birds, were driven by % canopy cover in the garden (Table 3). Even so, greater numbers of rare bee species

tend also to be associated with greater numbers of rare bird species and vice versa (Figure 2; Appendix S1: Figure S1). One possible reason for this is that other garden habitat characteristics may promote both rare bee and bird species. For example, rare birds and rare bees may both utilize resources in gardens that are atypical of the rest of the region, which has been associated with rarity and thin distributions in British breeding birds (Gregory & Gaston, 2000; Kean & Barlow, 2004). Furthermore, rare birds and rare bees may share dispersal patterns that result in local rarity in gardens. These relationships may be harder to observe. Bees and birds are highly mobile taxa with wide distributions, which may allow certain species to achieve the wide geographic ranges and low local abundances representative of the sparse type of rarity (Kean & Barlow, 2004).

What is rare in an urban gardening system?

It is important to note that what is rare in an urban system could be common elsewhere. For example, taro (*Colocasia esculenta*) was a rare plant in our study but is not of any conservation concern (Appendix S1: Table S3). Nonetheless, a rare species that is not of conservation concern at a larger geographic scale may still contribute disproportionately to ecosystem services if its functional role is less common locally. The large size of taro plants and specific culinary traditions that utilize them may dissuade some people from growing them in an urban garden, explaining their rarity. However, the gardener that does plant a taro is likely to have a large spatial footprint on the ecology of the garden. Planting taro and managing its growth may increase functional diversification of the garden, as more irrigation is needed to maintain the moist soils in which taro grows best, therefore resulting in a rare habitat that may attract other rare associated wildlife. Because taro is a relatively large plant (i.e., an average of 1–2 m tall and wide), if it has an impact on attracting bees or birds to the garden, the existence of even one in a garden can have a large impact on what other taxa are also present. Future studies could direct more focus on the ecosystem services provided by regionally or temporally rare species that may receive less attention because they are of least conservation concern. Several of the weedy species that were classified as rare may only be rare in the months we sampled. For example, in our system and region, henbit (*Lamium amplexicaule*), scarlet pimpernel (*Anagallis arvensis*), and chickweed (*Stellaria media*) are common early-spring weeds but were considered rare at the time of sampling in summer. These species could be increasing functional

diversity when they are less common in summer even if they do not when they are more common in spring.

Limitations and future study

There were limitations in the way that species were identified that may impact the number of rare species classified. As previously noted, weed species were likely not reported by gardeners, which we tried to supplement with field-based data. There were many plants that were difficult to identify (see Appendix S1: Table S3) beyond morphospecies or family levels. These unidentified species were often classified as rare. Future work could dedicate resources toward identifying these rare plants and understanding if they contribute significant ecosystem services. Cultivars were also difficult to determine, potentially minimizing the contribution of cultivar diversity to rarity in this study; only four of the rare plants identified were cultivars belonging to the same species of another cultivar (Table 2; Appendix S1: Tables S2 and S3). Future studies that target specific plant guilds where cultivars are more easily identifiable, may help clarify the contributions of cultivar diversity to rare species assemblages in urban gardens.

CONCLUSIONS

In this study, we begin to elucidate what rarity means and what drives rarity in urban gardens. Species that are rare in urban gardens are not necessarily of conservation concern but still contribute to the functional diversity of cities. We find that rare plants in urban gardens have important spillover effects on rare species in other taxa. Rare bees, birds, and plants were all positively associated. Intentional human management of urban gardens can therefore support rare species both directly and indirectly. We found that rare plants were most often planted by women gardeners, older individuals, and those who cultivated plants close to home. These results suggest a strong effect of human management on urban biodiversity and ecosystem function. In addition to encouraging women and local neighborhoods to grow in gardens, careful design of urban gardens to include rare plants may provide for increased rare bee species that in turn provide better pollination services across seasons and allow for longer crop production periods. This may require that garden managers encourage the planting of more rare species or allow for rare plants to grow in pathways and unmanaged areas. In general, urban gardens may include high numbers of species found at low frequency across urban landscapes. Therefore, urban

gardens may represent important locations for the preservation and support of rare species in cities. Future studies will help to address whether these rare organisms are persistent or transient residents in urban gardens.

CONFLICT OF INTEREST

The authors declare no financial or non-financial conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ong et al., 2022) are available in Dryad at https://doi.org/10.5061/dryad.47d7wm3gm.

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SUPPORTING INFORMATION

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