Land sharing between cultivated and wild plants: urban gardens as hotspots for plant diversity in cities

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Abstract

Plant communities in urban gardens consist of cultivated species, including ornamentals and food crops, and wild growing species. Yet it remains unclear what significance urban gardens have for the plant diversity in cities and how the diversity of cultivated and wild plants depends on the level of urbanization. We sampled plants growing within 18 community gardens in Berlin, Germany to investigate the species diversity of cultivated and wild plants. We tested species diversity in relation to local and landscape-scale imperviousness as a measure of urbanity, and we investigated the relationship between cultivated and wild plant species within the gardens. We found that numbers of wild and cultivated plant species in gardens are high – especially of wild plant species – independent of landscape-scale imperviousness. This suggests that all community gardens, regardless of their urban contexts, can be important habitats for plant diversity along with their role in urban food provision. However, the number of all species was negatively predicted by local garden scale imperviousness, suggesting an opportunity to reduce imperviousness and create more habitats for plants at the garden scale. Finally, we found a positive relationship between the number of cultivated and wild growing species, which emphasizes that community gardens present a unique urban ecosystem where land sharing between cultivated and wild flora can transpire. As the urban agriculture movement is flourishing worldwide with gardens continuously and spontaneously arising and dissipating due to urban densification, such botanical investigations can support the argument that gardens are places for the reconciliation of plant conservation and food production.

Keywords Berlin · Conservation · Novel ecosystems · Urban agriculture · Urbanization · Reconciliation ecology

Introduction

Rapid urbanization has led to the loss of green spaces in cities, with a majority of the world's population currently living and projected to live in cities by 2050 (UN-Habitat 2016). Consequently, urban gardens have become increasingly important for food production, recreation or social interaction (Čepić and Tomićević-Dubljević 2017; Lin and

Egerer 2020). Gardens thereby support a wide array of ecosystem functions, including food provision, habitat for biodiversity, carbon sequestration, climate mitigation and water retention (Lin et al. 2015), and are the focus of recent urban ecology research (Gaston et al. 2005; Guitart et al. 2012; Vergnes et al. 2013; Philpott and Bichier 2017; Clucas et al. 2018; Frey and Moretti 2019).

As part of urban green infrastructure, gardens contribute significantly to urban plant diversity (Davies et al. 2009; Goddard et al. 2010; Cameron et al. 2012). The composition of plant populations in cities is influenced by multiple urban drivers including human management, climate, pollution, land use change and biological invasions (Pyšek et al. 2010; Kowarik 2011; Lososová et al. 2012; Aronson et al. 2016; Piana et al. 2019; Swan et al. 2021). In contrast to rural regions, cities are characterized by high habitat heterogeneity including novel urban habitats with great potential for biodiversity (Kowarik 2011; Swan et al. 2021),

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encompassing parks (Fischer et al. 2016; Vojtk et al. 2020), cemeteries (Kowarik et al. 2016; Löki et al. 2019), urban woodlands (Trentanovi et al. 2013; Kowarik et al. 2019), wastelands (Bonthoux et al. 2014), railways (Westermann et al. 2011) and gardens (Thompson et al. 2003; Loram et al. 2008; Pergl et al. 2016; Frey and Moretti 2019). As a consequence, plant species richness in urban ecosystems can be higher than in non-urban ecosystems (Kühn et al. 2004; Knapp et al. 2009; Pyšek et al. 2010; Faeth et al. 2011; Kowarik 2011).

A high proportion of nonnative species and anthropogenic processes that drive plant dispersal, foster plant diversity in cities (Swan et al. 2021). Trade, traffic and horticulture seem to be the most prominent dispersal pathways (von der Lippe and Kowarik 2009; Kleunen et al. 2018). Ornamental plants play the largest role among introduced species, followed by plants for agricultural or forestry purposes (Kowarik 2005). For this reason, novel urban ecosystems such as community gardens designed for food production and ornamental purposes provide an interesting system to examine plant species diversity. In these agroecosystems, plant species assemble through gardeners' preferences (e.g., ornamental) and motivations to garden (e.g., food, nature connection) (Clarke and Jenerette 2015; Egerer et al. 2019b; Philpott et al. 2020), but also through both spontaneous and anthropogenic seed dispersal (von der Lippe and Kowarik 2009; Piana et al. 2019). Moreover, the flora of gardens is particularly influenced by the interaction of people's activities like planting, weeding (including using herbicides), watering, soil cultivation and fertilizing (Kendal et al. 2012; Padullés Cubino et al. 2018, 2020).

There is only a small number of comprehensive studies about the plant diversity in urban gardens (e.g. Thompson et al. 2003; Loram et al. 2008), and only a few analyze both cultivated and wild growing plants (e.g. Jaganmohan et al. 2012; Frey and Moretti 2019). Such assessments are needed to offer a fundamental ecological understanding of the taxonomic and functional diversity harbored in these systems that underlies ecosystem processes. Furthermore, such assessments can have important urban policy and planning outcomes for the management of urban greenspaces to enhance urban biodiversity (e.g., including community gardens as open spaces into public parks and places, conservation and integration of spontaneous vegetation in urban greenspaces) (Goddard et al. 2010; Lin and Egerer 2020). Finally, high plant diversity in urban gardens can have profound positive impacts on associated biodiversity, including arthropods (Shrewsbury et al. 2004; Faeth et al. 2005; Bang et al. 2012; Kaluza et al. 2018; Egerer et al. 2019a; Buchholz et al. 2020), birds (Daniels and Kirkpatrick 2006; Threlfall et al. 2017) and mammals (Van Helden et al. 2020).

Here, we assessed both the cultivated and spontaneous plant species diversity growing within 18 urban community

gardens across the metropolitan region of Berlin, Germany. In Berlin, community gardens are growing in popularity because they are not only source for food but also provide a wide range of ecosystem services including social interaction and environmental education (Guitart et al. 2012; Barthel and Isendahl 2013; Gregory et al. 2016). Community gardens are characterized by the cultivation of vegetable patches or raised beds on vacant lots, parking areas or rooftops by local residents. As horticultural spaces for the cultivation of crops and ornamental plants they also support space for spontaneously growing plants. Berlin historically had abundant greenspaces in most neighborhoods (Kowarik 2019), but the city is also rapidly densifying and green spaces are being lost (Kabisch and Haase 2014). In the Berlin context, community gardens are an increasingly valuable greenspace from a social-ecological perspective, but ecological research within these urban agroecosystems is lacking. We have little information about the plant species growing in these systems, which could inform how these systems differ from or share parallels with other greenspaces. To fill this gap, we systematically documented the cultivated and wild plant species (excluding grasses) within selected gardens to ask: (1) What is the species richness of all, cultivated (food crops, ornamentals) and wild growing (wild, weeds, spontaneous) plants in urban gardens? (2) How does plant species richness vary with local and landscape-scale urbanization (imperviousness)? (3) What is the relationship between cultivated and wild plant species richness?

Methods

Study sites

Our study system included 18 urban community gardens distributed across Berlin, Germany (Fig. 1). The gardens vary in age, size, number of participants and governance structure (Supplementary Information (SI) Appendix 1). Furthermore, the gardens vary in landscape surroundings and local management (Fig. 2). In some gardens the beds are individually managed (i.e., plant selection, irrigation, soil amending) by households in an allotment style, while in other gardens the beds are collectively managed by all participants. The gardens were a part of a larger study conducting research on wild pollinators. This research focuses on the largely herbaceous plant community in the gardens.

Data collection

Plant data

We visited the gardens three times from May to August 2020. Of the 18 gardens, four were only assessed twice due

Fig. 1 Distribution of 18 community gardens (yellow boxes) investigated in this study across an urbanization gradient in the city of Berlin, Germany. Gardens with endangered wild growing species (Seitz et al. 2018) are indicated with a red box

to logistical constraints. We established a 400 m² sampling plot, with a side length of 20 × 20-m in the center of each garden within which to concentrate our measurements. We altered the size of the sampling plot where necessary (i.e., where gardens were more narrow than they were wide, we created a 40 × 10-m plot). In this sampling plot, we randomly placed eight 1 × 1-m quadrats within which we identified all herbaceous plants (except grasses) to species level. The selection of the quadrats was performed using randomly determined distance values, measured along transects from the baseline of the sampling plot. We also documented small woody species within the plots including juvenile fruit trees and berry shrubs as part of the herb layer as many play a role in food production (e.g., *Ribes* and *Rubus*). Woody species

in the shrub or tree layer exceeding one meter in height were not considered. These 1 × 1-m plots were selected anew on each study day without overlap, which means a total of 16 or 24 plots were studied in each garden. We excluded the species identification of grasses because the study took place in the context of a pollinator study and grass species flowers are not relevant for pollinators. For plant identification and nomenclature, we used Jäger et al. (2016, 2017) and the *PlantNet* Handheld Application (see: <https://plantnet.org/en/>).

We identified the species status characterization, namely whether the plant species was: (i) cultivated (crop, ornamental) or (ii) wild (wild, weed, spontaneous vegetation). If species occurred as wild and cultivated, we

Fig. 2 Examples of four community gardens assessed in the study: one with high local imperviousness and low plant diversity (**a**; Wedding); one with low local imperviousness and high plant diversity (**b**; Tempelhof); one with high landscape imperviousness, low local

imperviousness and high plant diversity (**c**; Prenzlauer Berg); and one with low landscape imperviousness, low local imperviousness and low plant diversity (**d**; Hohenschönhausen). Photos: Monika Egerer

documented them in both status groups. In addition, we classified plants into native and nonnative species and split the latter into archaeophytic and neophytic species in Berlin. The differentiation of these status categories followed the mapping criteria of the floristic mapping of Berlin (Seitz et al. 2012). Cultivated species were intentionally sown or planted native or nonnative species. The classification as “cultivated” followed taxonomic criteria (taxa only known as cultivated species or varieties like some crops), morphological traits (e.g., for *Daucus carota*) or traces of cultivation (cultivation in rows or beds, promotion by weeding, component of typical “wildflower” seed mixtures). Wild growing species were species with exclusively spontaneous occurrences, that were not directly settled by humans (including spontaneous occurrences of cultivated species or escapes from cultivation which were not intentionally planted or sown). In addition, we documented all wild growing grasses in the plots as an own category, but without identification to species, except cultivated grass species such as *Zea mays*, due to their importance as crops. We summarized the total richness of plant species identified across all plots within each garden for each sampling round and across all sampling rounds. Where species were only identified to genus, we only counted those samples in the total plant species richness if there was not an observation of the same genus at the species level (i.e., we did not count *Brassica spec.* if, for example, *Brassica oleracea* was observed within that garden).

Local and landscape imperviousness data

To collect information on the level of urbanization within each site and within the surrounding landscape, we used imperviousness (i.e., sealed surface) as a representative measure of urbanization (von der Lippe et al. 2020). At the local habitat scale, within each 1 × 1-m garden plot, we assessed the percent imperviousness including concrete and rock. To measure landscape-scale imperviousness, we collected publicly available data on the surrounding landscape features of each garden from the Berlin Environmental Atlas (Senatsverwaltung für Stadtentwicklung und Umwelt 2016). Here we measured the proportion of imperviousness at a 2 × 2-m resolution within 500-m, 1-km and 2-km buffers using the Zonal statistics tool in QGIS software v. 2.18.0 (QGIS Development Team 2018).

Data analysis

To test whether local or landscape scale urbanization (imperviousness) predicts the characteristics of the plant community within gardens, we built models with the following response variables: (i) total plant species richness; (ii) cultivated plant species richness; (iii) wild plant species richness; and (iv) the ratio of wild to cultivated plant species. The species richness of all plant species documented in the garden for each sampling round was the response variable, and the percent of local imperviousness and the percent of

landscape imperviousness and their interaction were the predictor variables. Imperviousness was scaled using the *scale* function in R. Preliminary analyses revealed that 2-km provided the best model fit for landscape imperviousness based on Akaike's Information Criterion (AIC), where 2-km had a lower AIC value (< 2 AIC points) than the other models (Burnham and Anderson 2002). Thus, we used 2-km spatial scale predictor variable in all models. Garden site was included as a random effect. Generalized linear mixed effects models fit by maximum likelihood were fit with a Poisson family distribution for species richness analyses, and linear mixed effects models were fit with a gaussian distribution for ratio models. For all models, we evaluated model fit using AIC and an analysis of variance.

To test whether there is a relationship between the species richness of cultivated and wild plants, we used Pearson correlation tests using the *cor.test* function in R with each site observation per sampling round as a replicate. In gardens where a given species was classified as both a cultivated and a wild plant due to the context in which the plant was observed, we considered the most common class in which it was observed or its common state in the literature.

All statistical analyses were performed in R v. 3. 6. 0 (R Development Core Team 2016).

Results

Of 3,604 plant observations across all 18 gardens, we documented 404 taxa representing 255 genera (SI Appendix 2). Some plants were only identified to genus level (65 taxa). We recorded 194 cultivated taxa, 184 wild growing taxa (spontaneous taxa), and 26 taxa as wild and cultivated. The number of plant species per sampling round ranged between gardens, from 18 to 81 species observed within a garden (Table 1; SI Appendix 2). The average number of species documented in a sampling round across all gardens was 44.12 ± 14.14 , while the average total

number of species per garden was 83.44 ± 21.78 (Table 1). Gardens with highest total species numbers across all sampling periods were Spiel/Feld Marzahn (117; Marzahn, Berlin), Allmende-Kontor (115; Tempelhof, Berlin) and Kiezzgarten Fischerstraße (111; Rummelsburg, Berlin), while the garden with lowest species number was Inselgarten (41; Schöneberg, Berlin) (SI Appendix 1).

Cultivated plants represented 27.12% of all plant species observations. Wild plants represented a majority, with 64.62% of all observations. The most common species among crops were *Solanum lycopersicum* (tomato; 3.5% of all observations), *Beta vulgaris* (e.g., chard, beet), *Cucurbita pepo* (e.g., squash, zucchini, pumpkin) and *Fragaria x ananassa* (strawberry). Some species were only observed once across all observations (31.44% of all species observations). The most frequent (i.e., number of occurrences observed across all 1×1 -m plot) ornamental plant was *Calendula officinalis*, other ornamentals with high frequency were *Centaurea cyanus*, *Tagetes* spec., and *Helianthus annuus*. Some species were documented with both cultivated and wild growing (spontaneous) populations, for example, *Daucus carota* occurred as a cultivar (carrot) and as a wild form. 151 species were native (including archaeophytes), 208 species neophytes and 45 species determined only on genus level were not assigned to a status (Seitz et al. 2012, SI Appendix 2).

The most common species among wild plants were *Chenopodium album*, *Diplotaxis tenuifolia*, *Polygonum aviculare*, *Stellaria media*, *Taraxacum officinale*, and *Urtica dioica*. Among all species, we documented 19 species of conservation concern: four species of the Red List Germany (Metzing et al. 2018) and 17 species of the Red List Berlin (Seitz et al. 2018) (SI Appendix 2). We found 13 species of conservation concern were cultivated species, and six were wild growing species. Among the wild growing plants, we found two species threatened with extinction in Berlin (category 1): *Anthemis arvensis* and *Verbena officinalis*, both species of sandy and loamy fields. *Galium spurium*, a species classified as extinct in Berlin (category 0) was recorded in a raised bed in a rooftop community garden.

Table 1 Summary statistics of main variables collected in the gardens for this study, for each monthly observation within a garden (Min = minimum value; Max = maximum; SD = standard deviation)

	Min	Max	Mean	SD
Total plant species richness	18.00	81.00	44.12	14.14
Cultivated plant species richness	3.00	38.00	16.50	7.86
Wild plant species richness	10.00	51.00	27.62	9.78
Ratio of cultivated:wild plants	0.15	2.00	0.65	0.38
% Impervious @ 1 m²	0.00	72.00	17.10	25.16
% Impervious @ 500 m²	31.12	85.94	60.18	14.44
% Impervious @ 1000 m²	33.46	73.44	57.10	12.65
% Impervious @ 2000 m²	34.60	73.12	56.12	9.83

Total plant species richness in relation to urbanization at the landscape and local scale

Total plant species richness was negatively predicted by local scale imperviousness ($F=6.38$; $P=0.01$; Fig. 3; SI Appendix 3). However, plant species richness within gardens was not predicted by the landscape scale imperviousness surrounding gardens within 2 km ($F=1.52$; $P=0.27$), nor the interaction between local and landscape imperviousness ($F=0.49$; $P=0.27$) (SI Appendix 3).

Fig. 3 Relationships between species richness of all (a–b), cultivated (c–d), and wild plants (e–f) and urbanization at landscape- and local garden scale. Lines in b, d, and f represent relationships determined from generalized linear models fit with Poisson distribution. No regression line represents no relationship found in the statistical analysis (SI, Appendix 3)

Cultivated and wild plant species richness in relation to urbanization at the landscape and local scale

Landscape imperviousness did not predict cultivated or wild plant species richness (SI Appendix 3). Although local scale imperviousness did not predict cultivated plant species richness ($F = 3.57$; $P = 0.07$), local imperviousness did negatively predict wild plant species richness ($F = 3.35$; $P = 0.04$) (Fig. 3). No variables predicted the relationship

(ratio) of cultivated to wild plant species richness (SI Appendix 3).

Relationship between cultivated and wild plants

The ratio of wild to cultivated plant species richness varied across gardens (Fig. 4a). The abundance and species richness of cultivated and wild plants observed within gardens were positively correlated: the richness of cultivated plants

Fig. 4 The ratio of wild to cultivated plants varied across gardens (a); here a “1” represents an equal representation of wild to cultivated species within a garden. Less than 1 indicates more wild plants, while greater than 1 represents more cultivated species. The abundance and species richness of cultivated and wild plants observed within gardens were positively correlated: the cultivated richness of plants positively correlated with the richness of wild plants ($r \approx 0.29$; $p = 0.038$; b)

positively related to the richness of wild plants ($r = 0.29$; $p = 0.038$) (SI Appendix 4; Fig. 4b).

Discussion

Our work in one of Berlin’s novel urban ecosystem types – urban community gardens – demonstrates the high biodiversity of both cultivated and wild growing plants within this system, and illustrates an example for high plant diversity in cities (Kühn et al. 2004; Knapp et al. 2009; Kowarik 2011). We found that these gardens are rich in plant species, supporting a wide range of food and ornamental crops, but that wild growing plants represent the majority of all plant species. Indeed, six wild growing plant species we documented are actually endangered or extinct in Berlin (Seitz et al. 2018). This underlies the importance of community gardens for nature conservation within a production-focused system (Goddard et al. 2010; Borysiak et al. 2017; Cabral et al. 2017). We elaborate on three main findings of our work: (1) community gardens harbor both high cultivated plant diversity that supports urban food production and high wild plant diversity, potentially representing a high fraction of diversity within the urban landscape; (2) this plant diversity is independent of landscape-scale imperviousness, though local-scale imperviousness may reduce the potential for novel ecosystems to support wild plant diversity; and (3) cultivated and wild plant species coexist with potential for reconciling conservation-production trade-offs sensu “land sharing”.

High diversity of cultivated and wild growing plant species within urban gardens

In 18 community gardens we found 404 different taxa (excluding grasses), including 194 cultivated and 184 wild

growing species. The number of wild growing species corresponds to 7% of the total number of species found in Berlin (Seitz et al. 2012). Kronenberg and Kowarik (1989) recorded 400 (257 cultivated and 143 wild growing) species in five domestic gardens in Berlin. Biodiversity assessments in allotment gardens and community gardens in Leipzig, Germany, showed lower species numbers, with 290 (150 cultivated and 140 wild growing) species in six allotment gardens and 255 (98 cultivated and 157 wild growing) species in six community gardens (Cabral et al. 2017). Investigations of the spontaneous flora in allotment gardens in Poznan, Poland showed higher species numbers with 358 species in eleven gardens (Borysiak et al. 2017). Studies on plant diversity of domestic gardens in the UK showed also higher numbers of both cultivated and spontaneous growing plant species (1166 species in 61 gardens in Sheffield (Smith et al. 2006), 1051 species in 267 gardens in 5 different cities (Loram et al. 2008)). In contrary to these studies that investigated more gardens and/or recorded the whole flora using an inventory approach, we investigated only random samples and excluded grasses. Species numbers may be higher in domestic gardens than in community gardens, as they tend to have longer continuity of use while community garden participants or garden management may change each year. In addition, the management of community gardens focuses predominantly on the cultivation of crops, that are in some gardens provided by the garden administration for all participants.

Compared to other urban habitats in Berlin, total species richness of wild growing species in community gardens is lower than was found in inventory studies in tenant gardens in residential areas (Zerbe et al. 2003), but is comparable to urban woodland (165 species in *Robinia* stands, 213 species in *Betula* stands (Trentanovi et al. 2013)). The average total number of species per garden was approximately 84 species; comparing this with a study of the floristic composition

of different urban habitats in 32 European cities (Lososová et al. 2012), the species numbers in gardens were slightly lower than the average of all habitats, but equal to parks and boulevards. However, the comparison of species numbers with these studies of other urban habitats in Berlin and Europe is limited because study plots in European habitats were much larger (1 ha) than in our study.

The high proportion of wild growing plants underlines the potential of community gardens as habitat for wild growing species in cities. This is also in line with the investigations of plants in allotment and community gardens in Leipzig and Poznan (Borysiak et al. 2017; Cabral et al. 2017). Other studies about domestic gardens have shown that the alpha diversity of plant species within gardens can produce high gamma diversity across a city landscape (Loram et al. 2008). Our work in Berlin emphasizes this ecological pattern, and further underscores the food provision and botanical conservation potential of community gardens.

From a horticultural perspective, we found that gardens have many different cultivated food and flower crops involved in urban food production. The common crops grown in these gardens (e.g., *Solanum lycopersicum*, *Fragaria × ananassa*, *Cucurbita pepo*, *Beta vulgaris*) supports other studies in community gardens elsewhere (Philpott et al. 2020). Yet some interesting “novel” crops were also found, including *Glycine max* (soy bean) in one garden, and *Perilla frutescens* (shiso) in another garden. This could reflect gardener multicultural diversity (Lin and Egerer 2020; Philpott et al. 2020) or that gardeners are experimenting with “untraditional” crop plants in the German context. Also, historically important and “forgotten” crops (Krausch 1992) like *Amaranthus caudatus*, *Nicotiana tabacum* (tobacco) and *Ornithopus sativus* (serradella) or medicinal herbs like *Artemisia abrotanum*, *Silybum marianum* or *Leonurus cardiaca* were cultivated. Community gardens can thus contribute to the preservation of the genetic diversity of rare crops (Galluzzi et al. 2010; Barthel and Isendahl 2013; Taylor and Mione 2019). Though we did not estimate the harvest amount of fruit and vegetable production within these gardens, even small-scale, but highly intensive species-rich systems like gardens can contribute to healthy diets and reduce financial barriers to organic fruits and vegetables (Alaimo et al. 2008).

From a botanical conservation perspective, these gardens harbor a diverse assemblage of flora, several of which are of conservation concern in the region and represent a multifaceted natural history of garden flora. Among the wild growing species, we found six endangered species (Seitz et al. 2018). Three species (*Anthemis arvensis*, *Galium spurium*, *Lathyrus tuberosus*) are typical for agroecosystems and grow on sandy and loamy fields (Schneider et al. 1994; Jäger et al. 2017), and three species (*Barbarea vulgaris*, *Leonurus cardiaca*, *Verbena officinalis*) are species of ruderal areas and

roadsides in villages (Jäger et al. 2017), *Leonurus* and *Verbena* were historically used as medicinal plants (Krausch 2007). They have become rare in the intensive cultivated landscape and now find suitable habitats in extensively managed gardens. Although these species occurred only in one or two gardens and their populations were small, it demonstrates the potential of urban gardens as a space for rare and endangered species of agricultural and rural areas. While population survival of endangered plant species is challenging in many urban habitats, greenspaces in Berlin have been shown to harbor established populations of some endangered species of ruderal areas (Planchuelo et al. 2020). In community gardens, these plants could also benefit from organic cultivation and avoidance of herbicides, which was also documented in studies of organic and conventionally managed fields (Gabriel et al. 2006; Salonen et al. 2011; Rydberg and Milberg 2012; Albrecht et al. 2016). This also emphasizes the conservation opportunity in urban ecosystems for rare species outside their natural conservation area (Planchuelo et al. 2019).

Furthermore, gardens may expand the natural habitats of endangered species through intentional planting or accidental introduction. For example, we found *Galium spurium* in a raised bed in a rooftop community garden. This typical field plant was extinct in Berlin (Seitz et al. 2018), and the species could be introduced with substrate or planting material. Thus, even novel ecosystems like rooftop gardens can contribute to urban biodiversity (Orsini et al. 2014; Walters and Midden 2018) and be a surprising reservoir for endangered plant species.

Among the cultivated species there were 13 more species with conservation relevance, including arable weeds like *Agrostemma githago* and *Centaurea cyanus*. However, in most cases these species are presumably cultivars or their origin was unknown. Even though the Red List status usually refers to wild populations or regional provenances, these examples show the potential of gardens as habitats for rare and threatened species. In these cases, the use of regional provenances can lead to the conservation or reintroduction of rare species with benefits for biodiversity conservation (Fischer et al. 2013; Lang et al. 2016, 2021; Albrecht et al. 2016).

Gardens are diverse regardless of landscape-scale imperviousness, though local scale imperviousness may reduce potential for high diversity

The plant diversity harbored and cultivated within these community gardens can be high regardless of where these gardens are located in the urban landscape, emphasizing that landscape-scale imperviousness does not necessarily determine local alpha diversity. This also underscores the potential for gardens to be valuable for plant diversity, plant

species conservation, and urban food production, regardless of their position in the city landscape. However, at the local scale, imperviousness within gardens negatively predicts local plant species richness. Perhaps this negative correlation is of no surprise: higher sealing reduces habitats for plants at the local level (Scalenghe and Ajmone-Marsan 2009; Yan et al. 2019). In gardens with low imperviousness habitat diversity is higher because there are not only beds for growing crops, but also grassland, margins and ruderal areas of predominantly extensive management (Fig. 2c, d). Yet, instead we propose that highly sealed gardens are a space for management intervention. Imperviousness at the local scale could be reduced – especially with unsealing measures, or by increasing the number of raised beds or other forms of vegetated interventions – to dampen the negative relationship and heighten habitats especially for wild growing plants. Reduced sealing also has a positive effect on water conservation, soil moisture, heating effects (Scalenghe and Ajmone-Marsan 2009; Lin et al. 2018a), and on other trophic levels of biodiversity (Geslin et al. 2016; Rocha and Fellowes 2018; Levé et al. 2019; Egerer et al. 2019a).

Our findings also have policy implications: gardens that include habitats analogues to (semi)natural systems in cities can support biodiversity conservation. In Berlin, this includes community gardens with or within fields and grasslands, which had some of the highest plant richness values across all gardens and contained many of the Red List species. These systems cannot be replaced with novel container gardens that arise on rooftops or within unused parking lots. These sealed surfaces require more effort to increase and maintain plant species richness, especially for wild plants. While such novel garden systems are often very socially valuable (Gregory et al. 2016), cities need to implement policies that prevent development and protect gardens that exist outside of sealed areas to best conserve the remaining species diversity that it has.

Cultivated and wild plants can coexist – and potentially synergize – in urban gardens

We found evidence for synergies among cultivated and wild plants in gardens, with species abundance and richness of cultivated plants (food crops, ornamentals) positively correlated with wild plant species richness in gardens. This challenges traditional narratives that position food production at odds with biodiversity conservation (Phalan et al. 2011; Gabriel et al. 2013). Rather than posing wild plant species abundance and richness at odds with production, our results reconcile production-conservation goals and illuminate potential synergies among food production, biodiversity, and potential ecological functions within urban community gardens. These are unique systems where we can reconsider and reformulate contemporary paradigms of ‘land

sharing’ versus ‘land sparing’ (Lin and Fuller 2013; Collas et al. 2017). Our study provides an important contribution to the literature by showing that in urban community gardens, the principle of land sharing is implemented through the simultaneous cultivation of crops and the conservation of wild plants. The social context of these gardens may here be decisive. Though we did not investigate motivations to garden or the socio-cultural context of gardeners, if urban food production is less essential here than in other regions of the world, wild species may not be immediately managed as weeds, and rather allowed space to grow alongside cultivated neighbors. Surveys about the motivation of gardeners in urban gardens generally showed that there is also interest in contact with nature (Armstrong 2000; Breuste and Artmann 2014; Pourias et al. 2016), which could be an opportunity for the acceptance and integration for wild growing plants.

Limitations and future directions

Our work is limited in that our random sampling may not be totally comprehensive of all plant species within the gardens. However, the standard assessment means that we are able to provide comparative assessments between gardens, and an assessment within a given standardized area. Future investigations that have more time and resources can expand this to study plants within the entire gardens, and also how plant diversity may be related to other factors such as garden size, which could relate to the species pool of a garden and thereby be an important factor driving spontaneous and anthropogenic seed dispersal. In addition, we did not determine the cultivars for crops. This motivates future studies to explore the diversity of different cultivars within common crops like *Beta vulgaris*, *Cucurbita pepo*, *Solanum lycopersicum*, and *Lactuca sativa*. Such work on cultivars could also contribute to informing how the diversity of crops relates to the conservation of e.g., wild pollinators and pollination function or biological pest control in these gardens, specifically in relation to urban food production.

Conclusion

A popular debate in the scientific and planning community is whether or not land sharing or land sparing is the best solution to conserve biodiversity and maintain ecosystem functions that support society (Fischer et al. 2014; Grass et al. 2019). Do we intensify agricultural production within agricultural landscapes to set aside other land for biodiversity? Do we densify our cities, removing remnant forests and grassland, to spare land outside city boundaries for nature conservation? Such conflicts plague discourse and decisions in urban areas on how to provision green spaces and densify urban neighborhoods (Lin and Fuller 2013; Stott et al.

2015). As many cities lose green spaces for plant diversity and conservation, an open question is how to balance their ‘natural’ history with the contemporary pressure to seal the soils that are its seedbank.

Urban community gardens have risen as a popular social and ecological movement to reclaim some vegetated habitats within the densifying environment. Community gardens are a nexus of urban food production, urban greening, human-nature connection and public health – and can also be refugia for diverse wild growing plant communities (Cabral et al. 2017; Lin et al. 2018b; Lin and Egerer 2020). Our work here contributes to our understanding of the growing importance of plant diversity conservation within these urban ecosystems. The plant diversity of gardens has wide implications for animal biodiversity, species interactions, and ecosystem functions, for example, the protection of wild pollinators and pollination services (Makinson et al. 2016; Baldock et al. 2019; Tasker et al. 2019; Egerer et al. 2019a). This potential for conservation is particularly interesting as community gardens are primarily established for food production (Corrigan 2011; Gregory et al. 2016) and recreational reasons (Breuste and Artmann 2014), and suggests that the possibility for species conservation can be further heightened by raising awareness for biodiversity management through the conservation of wild growing plants. In Berlin, there are already initiatives and projects to involve citizen scientists into the propagation and cultivation of threatened plant species in gardens (Fišer et al. 2021), which should be accompanied by conservation authorities and Botanical Gardens (Godefroid et al. 2011; Lauterbach et al. 2019). Thus, community gardens can present a system for reconciliation ecology: anthropogenic habitats that are modified to harbor a wide variety of species (Rosenzweig 2003). Gardens are where we may best conserve species where people live, work and play. In sum, regardless of their built context, gardens across a city can support a wide range of plant species, where both human needs and nature’s biological diversity can coexist.

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Authors' contributions B.S., M.E. and S.B. conceived of the study. B.S., J.H., L.N., J.W., L.W., and M.E. carried out the data collection (field surveys). B.S. and M.E. analyzed the data. B.S. and M.E. drafted the manuscript with contributions from all authors.

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Code availability Code available upon request.

Declarations

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