The Gardening Bug and Gardens for Bugs: Urban Pollinator Gardening, Social Contagion, and Conservation

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ABSTRACT

As cities around the world grow, conservationists have become increasingly interested in ways to create habitat for animals in cities and also connect an increasingly urban-dwelling public with nature. Pollinator gardening, the practice of flower gardening to provide resources for insect pollinators, has become one of the more popular such urban conservation practices among both ecologists and the public. Despite the great promise of pollinator gardens, a great deal is unknown about their roles in the lives of insects and humans. In this dissertation, I study pollinator gardens to characterize their conceptual origins, spatial distribution, contagious properties, and ecological consequences for insects.

I establish that pollinator gardening is a concept with its roots in a diffuse collaboration between many participants, including both ecologists and laypeople, and discuss the implications of this for conservation. I quantify pollinator gardening by creating a large data set of the locations of diverse flower gardens in the Boston metropolitan area, using imagery from Google Street View in combination with field surveys. I find flower gardens are rare, but more common in neighborhoods with small lot sizes, suggesting opportunities for urban conservation in dense urban areas. Furthermore, I test for social contagion in flower gardening, the process by which ideas and behaviors naturally spread through networks of people. I find strong evidence for contagion of flower gardening between nearby neighbors, in the form of highly localized clusters of flower gardens along streets. I explore the possible implications of this clustering from the perspective of insect ecology using simulations, as well as a field experiment with monarch butterflies and aphids. I find that contagion increases connectivity in urban landscapes, and this may have effects on insect habitat use. In sum, I find that front yard flower gardening is still uncommon, but is likely socially contagious, and that this pattern has implications for

conservation and ecology. By adopting a multidisciplinary approach in order to understand both human social behavior and how these behaviors translate into effects on the urban landscape, I advance our understanding of pollinator gardens and urban ecology more broadly.

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INTRODUCTION

Pollinator gardening, which aims to provide habitat for insect pollinators in residential settings, is a participatory conservation practice that is rapidly growing in popularity and has also increasingly attracted the attention of urban ecologists. These gardens are thought to be effective ways to engage members of the public and moreover appear to receive relatively high rates of use by insects. Recent concerns about widespread insect population declines and the severe consequences that could result from such declines have made pollinator gardens even more interesting for conservationists. Pollinator gardens therefore seem to be an idea whose time has come, enjoying a rare combination of public popularity and conservation urgency. But from an ecological perspective, much remains unknown about pollinator gardens, including basic questions about how they come to be and how they function as habitat. In this dissertation, I explore how pollinator gardens work by mapping where pollinator gardens are located on the landscape, testing whether pollinator gardening appears to be socially contagious (spreading naturally through human interactions), and measuring some of the ecological impacts of pollinator gardening and contagion on insects.

In **Chapter 1**, I introduce pollinator gardening as a socio-ecological phenomenon by exploring its multifaceted definition. This broad and flexible definition stems from the fact that pollinator gardening emerged from an unplanned collaboration between conservationists and gardeners. Grassroots, participatory conservation practices of this kind will generally contain considerable heterogeneity. Using the conservation literature, I survey some of the challenges confronting pollinator gardening as a result of this broad definition, including the risks of miscommunication and the spread of ecologically poor practices. However, I subsequently identify a set of benefits of conceptual flexibility that are particular to participatory conservation;

specifically, these benefits derive from increased participation and satisfaction for more flexible practices. Grassroots conservation efforts require widespread participation from the public to achieve their goals, and I suggest that for pollinator gardening, the benefits to conceptual flexibility are likely to outweigh the costs. To cope with doing research on such a broadly defined concept, I also suggest a framework for identifying narrower, operational definitions when required.

In **Chapter 2**, I produce an estimate of the prevalence of pollinator gardening and test two possible drivers of gardening and garden diversity, income and lot sizes. I use Google Street View to map the locations of diverse front yard flower gardens (our proxy for pollinator gardens per se) for a set of 11 cities in Greater Boston. I show that front yard flower gardening is rare in our area, but flower gardens are nonetheless key drivers of citywide biodiversity. I find that these flower gardens are more common in neighborhoods with higher incomes, consistent with the widely reported 'luxury effect' for urban biodiversity. Unexpectedly, I observe an equally strong effect of lot sizes, with more flower gardening in smaller lot size neighborhoods. These results point to an underappreciated role of higher-density urban neighborhoods for pollinator conservation, and imply a possible biodiversity cost associated with large-lot neighborhoods.

In **Chapter 3**, I test for the presence of social contagion in front yard flower gardening. Using our maps of flower gardening produced with Google Street View, I measure how the presence of a flower garden affects the probability of nearby neighbors having flower gardens. After accounting for background variation in flower garden prevalence, there are strong effects of nearby neighbors gardening, with neighbors of houses with flower gardens having triple the probability of flower gardening themselves. This effect is significant out to 15 neighbors away, but it decays rapidly with each additional neighbor away; the small spatial scale of the peak effect and rapid rate of decay with distance are both consistent with social contagion of flower gardening between neighbors. Social contagion in this conservation practice has ecological implications because it accelerates the rate of habitat creation and makes the habitat patches more clustered than random. I use a simulation approach to quantify how the distribution of flower gardens in this landscape would differ in the absence of social contagion.

In **Chapter 4**, in order to understand how contagion-driven garden clustering could affect insects, I use a field experiment to assess responses to resource densities in two garden-resident arthropods that are hosted by milkweed, the milkweed aphid (*A. nerii*) and the monarch butterfly (*D. plexippus*). Basic ecological theories predict that insects can respond to resource density by increasing or decreasing their rate of habitat use, with the responses depending on their life history and dispersal traits. I find that aphids colonize milkweed plants more rapidly in neighborhoods with higher background milkweed densities, as theory predicts based on their passive wind-dispersed, clonal life history. In contrast, monarch butterflies exhibited higher oviposition rates in neighborhoods with lower milkweed densities and higher flower gardening prevalence. This suggests that flower garden-rich neighborhoods may be more attractive to monarchs, perhaps thanks to greater nectar availability in these neighborhoods; as a result, clustering of flower gardens caused by social contagion could be ecologically relevant for monarchs in cities.

In **Chapter 5**, I synthesize the socio-ecological perspectives developed throughout the preceding chapters in order to make the case for pollinator gardens as a biodiversity solution. I do this with an overview of the ecological evidence about pollinator gardens as habitat, as well a discussion about the nature of pollinator gardening as a participatory conservation activity and the possible importance of social contagion. I provide a set of baseline recommendations for gardeners who want to support insect populations, as well as a set of priorities for researchers who want to improve our understanding of the ecological functioning of pollinator gardens in the future.

By using both ecological approaches and an understanding of the social roles of gardening, I am able to arrive at a more complete picture of gardens as a venue for pollinator conservation, and to better characterize how they function. I conclude by discussing the importance of these findings in the context of problems facing urban conservation, and the role basic ecology can play in resolving these.

Chapter 1 - Defining the pollinator garden: is conceptual flexibility a bug or a feature?

Abstract

Participatory conservation invites members of the public to directly engage in conservation actions, expanding habitat creation and improving connection with nature among participants. While these practices are exciting for conservationists, they have several qualities distinguishing them from traditional conservation. One of these is that the definition of these practices tends to be broad and variable, shaped by the participation of many individuals. We explore this issue in the context of pollinator gardening, a popular, loosely defined practice that has recently gained attention from conservationists and ecologists. We characterize some of the conservation risks of maintaining a broad definition, including impaired communication among stakeholders and the risk of spreading ineffective practices. However, we argue there are also underrecognized benefits to definitional flexibility that are specific to participatory conservation; these derive from the fact that many participants must be recruited in order to have substantial ecological effects. Allowing definitions to remain broad encourages adoption of these practices by more people, accommodates more participants' needs, and also allows researchers to better track the realities of a heterogeneous and dynamic movement. We also suggest a framework for researchers to cope with broad definitions while maintaining rigor.

Introduction

Conservation involving grassroots public participation is a promising avenue for habitat creation and outreach. Inherently, activities emerging from grassroots movements tend to be loosely defined. We explore this issue using pollinator gardening, an increasingly popular conservation practice. Should ecologists encourage strict guidelines for pollinator gardens to maximize their conservation benefits? For example, a broad definition of a "pollinator garden" that includes non-native plants might increase the number of flower gardens (as opposed to lawns) but might also reduce the use of native plants. Here, we discuss costs and benefits of broadly inclusive versus ecologically strict definitions of a pollinator garden.

In recent years, various new conservation approaches have gained traction that involve voluntary participation by larger numbers of laypeople directly in conservation activities. These approaches are thought to improve conservation outcomes by giving stakeholders more agency and increasing buy-in; these more bottom-up approaches have been characterized using various concepts including participatory conservation (Matarrita-Cascante et al. 2019), grassroots conservation (McDuff 2001), and civic ecology (Krasny et al. 2014, 2015). In this essay we will typically refer to participatory conservation, specifically thinking of those activities that are carried out by individuals on their own lands.

One recently popular participatory conservation activity is pollinator gardening, which encompasses a set of practices generally focused on providing nectar, pollen, and other resources for pollinators (often insects)(Majewska and Altizer 2020). These practices originated from the confluence of the gardening community, which had a preexisting tradition of noticing and appreciating flower-visitors (e.g. butterfly or hummingbird gardens), with the modern conservation movement, which has become increasingly concerned with apparent insect declines and the possibility of collapse in pollination services (Potts et al. 2010, Wagner 2020, Van Klink et al. 2023). Interest in pollinator gardening is booming thanks to mounting evidence of their high value as habitat (Majewska et al. 2018), alongside benefits experienced by gardeners, e.g. improving connection with nature and human health outcomes (Raymond et al. 2019). Yet the definition of pollinator gardening — planting gardens 'for pollinators' — typically remains broad, even among researchers of the topic; in a sense, the term could encompass anything that self-identified pollinator gardeners are doing. At minimum, the concept entails providing diverse sources of pollen and nectar for flower visitors to consume, but can also variously emphasize locally native plantings, nesting resources, reductions in grass mowing, and many other management practices like reduced chemical application or water usage (e.g. Hall et al. 2017, Majewska and Altizer 2020, Baldock 2020). Some authors (e.g. Aronson et al. 2017, Turo and Gardiner 2019), additionally emphasize the constraint that pollinator habitat needs to be compatible with local social and aesthetic norms, lest it be rejected by residents; others focus only on ecological impacts. In sum, the pollinator gardening concept has so far remained relatively flexible, with different researchers and advocates (de)emphasizing various elements from this broader set of gardening practices, depending on their priorities or the focus of their work.

Disadvantages of a flexible definition of pollinator gardening

Conceptual heterogeneity within the pollinator gardening concept carries risks, as documented by the conservation literature. First, the definition of a conservation practice closely relates to its scope and goals; broad definitions imply broad (or even unspecified) goals. This can create challenges for developing effective practices and could result in failure to recognize tradeoffs between different goals. For instance, Dearborn and Kark (2010) identified a range of goals for urban conservation, ranging from rare species conservation to achieving human health benefits, each of which could lead to a different set of possibly conflicting best practices.

Second, human dimensions, and particularly relationships among stakeholders, are the most commonly reported contributor to failed conservation efforts (Catalano et al. 2019). A broad and heterogeneous definition could harm these relationships by impairing communication with potential pollinator gardeners by making messaging more complex and varied, leading to greater risk of overwhelming and confusing some participants (Knapp et al. 2020). It could also make it difficult to understand how expectations about pollinator gardening outcomes may differ between potential gardeners and advocates/researchers, which can lead to dissatisfaction for conservation volunteers (Propst et al. 2003).

Last, if a conservation concept is too flexible, over time it could drift into losing its original intent, or even becoming functionally meaningless. Similar concerns have been raised in related fields, for instance about nascent semantic drift in the term "ecological restoration", linked to underlying ideological disagreements about restoration's goals and their achievability (Woodworth 2017). In pollinator gardening, this problem could occur if the term pollinator garden began to be consistently applied to plantings with little or no ecological benefits for pollinators. These risks may also be elevated for participatory, grassroots practices like gardening, because it is not feasible to control which practices spread and become popular; as a result, conceptual flexibility could open the door to the eventual inclusion of practices with poor conservation value.

Given these disadvantages, it might be natural to assume that in order to achieve its conservation potential, pollinator gardening should be more narrowly and rigorously defined by researchers and advocates. However, because pollinator gardening relies on broad participation from the public to achieve meaningful conservation benefits, we argue that there are also compelling reasons *not* to make the concept of pollinator gardening narrow or rigid.

Advantages of a flexible definition of pollinator gardening

First, by being adaptable, pollinator gardening can be more inclusive and appeal to a wider variety of participants, each of whom bring their own vision, constraints, and knowledge. Pollinator gardening's ability to attract large numbers of voluntary, novice participants is in many ways its greatest strength. This is one source of its rapid spread, and thus one of the key factors underlying its conservation potential. Flexibility leads to broader appeal; for instance, previous work has also found that offering environmental activities with a range of required effort levels can attract different groups of volunteers and better accommodate their needs (van Heezik et al. 2020, Behrens and Colombelli-Négrel 2024). Gardens are also emotionally-rich, personal spaces, with gardeners having a wide array of perceptions and priorities for their gardens (Freeman et al. 2012), meaning that preferences for different conservation activities will likely vary. Additionally, because meaningful habitat creation through gardening involves many gardens rather than just one (Goddard et al. 2010, Belaire et al. 2014), accommodating some ecologically 'suboptimal', idiosyncratic management decisions within individual yards in order to increase overall uptake may be worthwhile.

Second, a flexible definition allows the pollinator gardening movement to evolve and adapt, incorporating regionally-appealing elements and also adding or subtracting elements over time. For example, over the past decade, as priorities of the pollinator gardening movement have shifted to include conserving the entire life cycle and not just the conspicuous adult life stages, advice for homeowners to “leave the leaves” (advice to not remove fall leaves to allow insect development at the ground surface) and create “soft landings” (diverse plantings at the base of a tree with arthropod habitat in mind) to benefit overwintering insects has become mainstream (e.g., Brewster n.d., Xerces Society n.d.). Because there is little top-down control over how the public interprets these guidelines, gardeners are free to adopt new practices as researchers learn from experience.

Third, an inclusive definition helps researchers understand gardens as they are and as they become, rather than gardens as we constrain them to be. By not enforcing a misleadingly rigid definition, as researchers we can appropriately recognize the dynamics that underly participatory conservation: a collaboration with a broad group of participants, and a movement that naturally shifts over time in composition and emphasis. This allows for research and guidance to not only adapt as new information emerges, but also to learn from gardeners about their motivations and constraints in a dialogue, which is a more effective way to influence gardening practices (van Heezik et al. 2012). This approach is also similar to some of the principles of coproduction from the broader conservation literature (Beier et al. 2017), which advocates for close collaboration between researchers and the people actually engaged in on-the-ground management (here, the gardeners), coupled with an adaptive approach that changes guidance over time with new knowledge and in response to practical constraints, in order to identify and reach shared goals (cf. civic ecology, Krasny et al. 2014).

Finally, a broad definition might actually improve communication and understanding. Even if researchers come up with a precise definition of an ideal pollinator garden, this definition may not exactly align with pollinator gardens as defined by gardeners in the general public. When there is such a conceptual mismatch between scientists and the agents carrying out actions, miscommunication with and discouragement of volunteers is more likely (Propst et al. 2003). For pollinator gardening, lack of general knowledge about pollinators could exacerbate this; for instance, although public interest in "saving the bees" has increased dramatically in recent years, a majority of the North American public continues to have little awareness of native bees and instead a relatively high awareness of the introduced and agriculturally managed European honey bee (Wilson et al. 2017, Hall and Martins 2020). While spreading awareness of these distinctions is a good long-term conservation goal for pollinator gardens, in the meantime (at least from a marketing perspective) pollinator gardening might benefit most from leveraging connections with the insects the public already recognizes, and subsequently building on these relationships to convey more nuanced information.

Researching capacious conservation concepts

If, as we propose, pollinator gardening benefits from remaining a flexible, accommodating concept, researchers of pollinator gardening still need to achieve specificity and rigor in their work. We suggest achieving this by situationally adopting narrower, operational definitions based on which facets of the pollinator gardening concept a particular project is concerned with. The approach we suggest bears similarity to the concept of boundary objects (Leigh Star and Griesemer 1989), which describe scientific concepts produced from multiple intersecting social groups, which are inherently broad and adaptable, yet have a sufficiently constant conceptual core to remain coherent. In each instance, for a particular actor, the broader cloud of ideas or concepts has an explicit and narrower meaning, i.e. "[boundary objects] are weakly structured in common use, and become strongly structure in individual use" (Leigh Star and Griesemer 1989 p. 393). In the case of pollinator gardening, existing research varies in how explicitly and how specifically operational definitions are provided; for example one recent study defined a pollinator garden as human-managed habitats aimed at increasing the number of nesting sites and floral resources available (Watson et al. 2022). Another (Majewska et al. 2018) defined them as gardens containing plants attractive to [insect] pollinators, referring specifically to pollen and nectar, but not nesting habitat for bees or larval food for butterflies. Some others (Johnson et al. 2017, Baker and Potter 2020, Silvert et al. 2023) use the phrase “pollinator garden” but do not provide an operational definition.

This essay was inspired by a workshop at which we, a set of 12 researchers and practitioners working on pollinator garden ecology, struggled to find a consensus definition of pollinator gardening. We debated how different types of plantings and practices fit into the context of the pollinator gardening movement, and during the process considered different definitions as existing along different conceptual axes (Fig. 1). The most popular conceptual space for pollinator gardening in our group included axes for aesthetic design, diversity of plant species, and intention to support flower-visiting insects (Figure 1A). These axes were chosen for the context of studying a range of garden types with value for insects, plants, and people, and follow from one possible operational definition of pollinator gardening: a space that is intentionally designed and cultivated with flower-visiting insects in mind, emphasizing intentionality to support insects through plant selection and maintenance practices (Figure 1A).

However, another definition of a pollinator garden might be any cultivated space that includes flowers used by flower-visiting insects, excluding ornamental cultivated plants like petunias that provide insects with no pollen or nectar, but including nearly any other garden with flowering plants. Some definitions might reduce the emphasis on intentionality for pollinators and focus on ecological value (Figure 1B), broadening the definition to include weedy lots and remnant habitat patches, and emphasizing insect-oriented management such as pesticide use and providing habitat throughout species' life cycles. In other cases, the most useful definition might be one that places emphasis on human dimensions, focusing on the gardeners' relationship with the garden, their constraints, and their intentions, as opposed to their actual ecological impacts.

In describing these two examples, we don't want to limit the dimensions of the (hyper) cube that defines pollinator gardening. Our goal is to embrace the flexibility and diversity of these practices, while employing rigorous and contextually-relevant definitions when needed for research. A similar approach has recently been advocated for by researchers of public parks, who provided an 'inventory' of various dimensions of park quality from which researchers from various disciplines could select elements to focus on (Lee et al. 2024). These frameworks provide ways to cope with studying malleable concepts from an interdisciplinary perspective, by maintaining definitional clarity and rigor while still retaining and recognizing the flexibility present in successful participatory conservation.

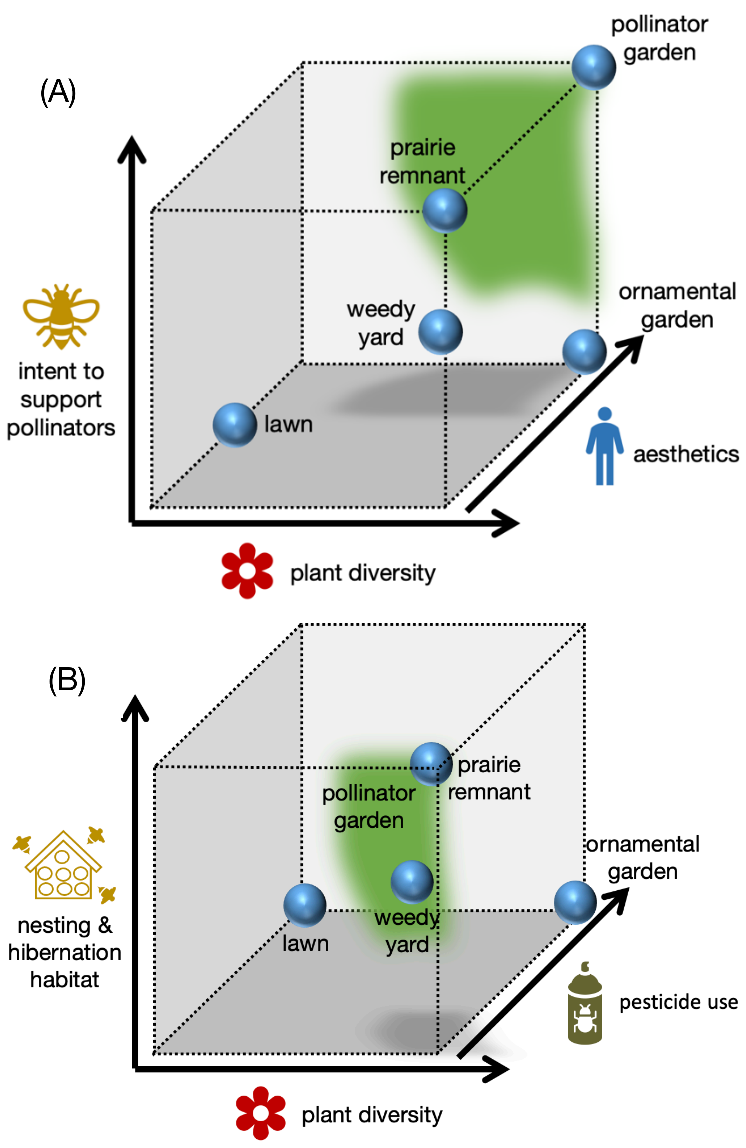


Fig. 1.1: Conceptual diagrams showing two example operational definitions of pollinator gardens, with axes that vary depending on priorities of the researchers or conservationists. In each definition space, the green cloud indicates types of habitat that have increased value for pollinators (and/or people). Blue spheres indicate where different kinds of yard or planting might fall in each definition. (A) Our working group's most popular definition, with flowering plant diversity, intent to support pollinators, and aesthetic intentionality. Here, the 'ideal' pollinator garden would maximize all three axes. (B) An alternative operational definition with increased focus on ecological value and outcomes. Here, the 'ideal' pollinator garden would maximize plant diversity and nesting habitat and minimize pesticide inputs.

Conclusions

Effective conservation is increasingly recognized as fundamentally linked to study of human behavior (Schultz 2011, Bennett et al. 2017b). This is because many conservation practices require changes to current behaviors by members of the public, to accomplish goals ranging from habitat restoration to reducing emissions. This recognition has allowed a deeper understanding of why some conservation measures have the capacity to spread rapidly and others do not (Bennett et al. 2017a, Mascia and Mills 2018).

Human behavior is especially salient for participatory conservation practices like pollinator gardening. Participatory conservation practices evolve in a collaborative process with the public, so 'human dimensions' arise not only in studying the adoption of these conservation practices, but also their creation. Participatory conservation also explicitly relies on action from many, mostly small landholders, requiring more participants to adopt new behaviors than traditional conservation, but also fostering engagement with nature in more people (Garfinkel et al. 2024). As with traditional conservation problems, ecologists still have a key role to play in participatory conservation, by quantifying the efficacy of existing practices and identifying new ones. However, if we attempt to define these practices too narrowly, we may constrain their popularity and growth.

Chapter 2 - Pollinator gardening is constrained by income but not lot size in urban front yards

(in revision at Landscape & Urban Planning)

Abstract

Flower gardens can create valuable habitat for urban pollinators, but little is known about the existing spatial pattern of gardens on the landscape or factors associated with the decision to plant a flower garden. We mapped the distribution of front yard flower gardens compared to four other front yard landscaping types (lawn, shrubs, non-vegetated, and weeds) across >86,000 addresses in Greater Boston, MA, USA using Google Street View. We complemented these data with on-the-ground surveys at a stratified random subset of ~500 yards. We predicted that census tracts with higher incomes would have higher flower garden frequencies and that these gardens would have higher species richness, and that census tracts with larger lots would also have higher flower garden frequencies and species richness. Yards identified as flower gardens using Google Street View contained around double the cultivated floral species richness of lawns and more than any other yard type. However, flower gardens were infrequent in front yards, and were a substantial front yard cover type in only ~2% of yards in our region. Flower garden frequency and cultivated species richness increased with census tract income, both consistent with the luxury effect hypothesis. However, higher-income lots also had more lawns and fewer spontaneous (weedy) species. Surprisingly, flower gardens had higher frequencies in census tracts with smaller lots. In our region, flower species diversity appears to be constrained by income or education but not lot size, pointing to the potential role of small urban lots as a target for pollinator habitat.

Introduction

In recent years, pollinator gardens have become increasingly popular among both ecologists and the public, buoyed by a series of studies providing evidence of their value as habitat for insect pollinators (reviewed by Majewska and Altizer 2020). Pollinator gardens are a subset of flower gardens, which generally can support a diverse and abundant community of pollinators even in urbanized environments (Hall et al. 2017). Because the term pollinator garden is poorly defined in the ecological literature (Murphy et al. *in prep*), in this paper we include all diverse flowering herbaceous plantings under the umbrella of "flower garden", including pollinator gardens, ornamental gardens and vegetable gardens. This decision is ecologically justifiable since the factor most consistently linked to urban pollinator diversity is flower diversity (Quistberg et al. 2016, Majewska and Altizer 2020, Wenzel et al. 2020), presumably because each pollinator species visits a different subset of flower species, meaning that gardens with more flower species constitute habitat for more different pollinator visitors. For urban bees, resources available on a local scale are better predictors of abundance and species richness than resources at the larger, landscape scale (Quistberg et al. 2016), which suggests that flower gardens are still visited even within otherwise inhospitable areas (cf. Hall et al. 2017, Majewska and Altizer 2020). Using these floral resources, some urban-dwelling pollinators have similar or even higher reproductive success compared to nearby agricultural areas (Samuelson et al. 2018). As a result, flower gardening is a behavior that many conservation groups are interested in encouraging (e.g. Goddard et al. 2010, Derby Lewis et al. 2019).

In order to better understand the motivations behind flower gardening and other ecologically beneficial forms of landscaping in yards, several studies have interviewed residents about their beliefs and goals. This work has identified various personal attitudes linked to these behaviors. For instance, the belief that native plants belong in the city is one of the few significant predictors of having native landscaping (Wheeler et al. 2022). Similarly, engagement with pollinator conservation in particular is linked to personal beliefs that individual actions can make a difference for conservation (Knapp et al. 2020). However, personal attitudes do not always translate into actual landscaping. For instance, native landscaping was not any more common among homeowners who reported prioritizing a 'natural' yard (Padullés Cubino et al. 2020) and non-lawn landscaping options were just as unpopular among self-described environmentally-concerned individuals compared to others (Feagan and Ripmeester 1999). This discrepancy reflects a general gap between preferences and existing landscaping, which suggests that yard owners experience barriers to achieving their ideal landscaping (Larsen and Harlan 2006, Padullés Cubino et al. 2020).

In contrast to our knowledge about motivations of people already engaged in flower gardening or native landscaping, less is known about spatial patterns of pollinator or flower gardening across the general population. The lawn, currently the most popular landscaping type in the United States, is associated with success, safety, beauty, and neatness in American culture (Robbins 2007, Cook et al. 2012). Lawns are also often perceived as an indicator of community participation, conscientiousness, and courtesy towards neighbors (Feagan and Ripmeester 1999, Blaine et al. 2012). In the U.S., turfgrass covers an area the size of the state of Georgia, and is arguably the largest irrigated crop in the U.S. (Milesi et al. 2005). Broadly speaking, when making landscaping decisions, U.S. homeowners tend to prioritize what they believe to be a neat or beautiful aesthetic with the minimum amount of input in money or time (Cook et al. 2012, Blaine et al. 2012, Padullés Cubino et al. 2020), sometimes in combination with pressures to conform with neighborhood norms (Nassauer et al. 2009). These millions of lawns — in addition to their many other consequences (e.g. intensive watering and chemical application regimes, Robbins 2007) — are likely poor in flower cover and diversity because the ideal lawn is weed-free and has high grass coverage (Nielson and Smith 2005, Fuentes 2021, Burr et al. 2021).

Therefore, the most important driver of variation in pollinator habitat quality between yards, at least in the United States, might be whether a yard has a flower garden at all.

In this paper, we evaluate the distribution of flower gardens in comparison to other landscaping choices, including lawns, shrubs, non-vegetated surface, and weeds. We quantified landscaping types using street-level imagery provided by Google Street View, which we complemented with on-the-ground surveys. Using the surveys, we estimated floral species richness across each yard type. Front yards are a proxy for overall landscaping choices (cf. Minor et al. 2023), although people make different landscaping choices about front and back yards (Locke et al. 2018, Avolio et al. 2020). One strength of the front-yard approach is that studying front yards requires only measuring factors visible from the public right of way. Therefore, it has the benefit of not relying on obtaining permissions from landowners (see Burr et al. 2018 and Minor et al. 2023 for similar approaches). In contrast, voluntary study participant pools (e.g., for surveys of back yards) are often biased in composition because volunteers tend to identify as more interested in nature and gardening than the general public (Chamberlain et al. 2004).

Specifically, we investigated the spatial distribution of front yard types and the floral species richness of each yard type in relation to two leading predictors, income and lot size. These and other household- and parcel-level features are thought to be more important drivers of actual landscaping than personal ideals or attitudes of homeowners (Cook et al. 2012), though little is known about how they affect flower gardening or pollinator habitat in particular. Income has received substantial attention as a driver of urban biodiversity and landscaping through the 'luxury effect' (Hope et al. 2003), in which diversity is generally higher in wealthy areas across many regions and taxa (Kinzig et al. 2005, Leong et al. 2016, Baldock et al. 2019; but see Leong et al. 2018 and Chamberlain et al. 2020 on variation in the luxury effect across systems). For flower gardening, the luxury effect suggests wealthy neighborhoods would have more flower gardens and possibly more species within flower gardens. Larger lots tend to have more use types, e.g. lawns, cultivated borders, and unmown grass (Loram et al. 2008) and have been found to have higher species diversity in many studies (e.g. , van Heezik et al. 2013), though there are several counterexamples (e.g. Albuquerque et al. 2005, Young et al. 2019, Yahner 2001). For flower gardening, these relationships imply that larger lots may also have more space for flower gardening and possibly more flowering plant diversity within larger gardens.

We characterized how these two factors jointly drive the presence of pollinator resources by measuring variation in front yard flower gardening across a range of incomes and lot densities in 11 cities in Greater Boston, MA, USA, using Google Street View. These cities spanned a twofold variation in income and threefold variation in lot sizes and yielded a data set of ~86,000 addresses. We surveyed a stratified random subset of ~500 of these addresses in person to test our expectation that flower gardens (as identified via Google Street View imagery) would have the most diverse flowering plant communities compared to other yard types. We then measured the effects of income and lot size on floral diversity at two scales. First, we tested their effects on the frequency of different yard types, including flower gardens, between neighborhoods. Second, we tested their effects on species richness within individual flower gardens and the other yard types. Urban floral diversity includes both cultivated flower species and spontaneous forbs (i.e., weeds; see, e.g., Minor et al 2023). Therefore, we separately analyzed patterns of species richness and diversity for cultivated and spontaneous flower species to better isolate the primarily human decision of cultivating plants from the presence of weeds, which reflects both ecological processes (plant dispersal and growth) and human decisions (weed control).

We predicted that income would positively predict floral diversity at both scales, meaning that flower gardens would be more common in higher income neighborhoods and that individual gardens would have more species in higher income neighborhoods. We also predicted that larger lot size neighborhoods would be associated with higher frequency of flower gardening, and that within yards, larger lots would have higher floral diversity. In addition to these *a priori* hypotheses, we conducted an exploratory analysis of yard type frequencies including three additional predictor variables sometimes hypothesized to influence landscaping decisions (education levels, homeownership rates, and race; e.g., Minor et al. 2023). By investigating spatial variation in flower gardening, we explore how neighborhood characteristics translate into landscape-scale patterns of pollinator habitat. We discuss the implications of these patterns for encouraging pollinator and flower gardening in home yards.

Methods

Study Site Selection

We identified a set of 11 cities in the Boston, MA, U.S. area that independently vary in income and lot size. In our region, as in many in the U.S. (Brueckner et al. 1999), these two factors are generally positively correlated, but for our selected cities this correlation was intentionally weak (Fig. A1, Pearson's $r = 0.37$, $df = 9$, $p = 0.27$ and see Appendix B). While we focused our analysis on smaller scale variation at the census tract level, we used cities as a convenient way to select a wide range of neighborhoods in such a way that these two factors of interest would be uncorrelated, which also made later ground surveys more feasible. We focused on the census tract scale as opposed to finer spatial grains because, first, American Community Survey data at the block group level for our area had very high margins of error. Second, we were interested in quantifying variation in a yard type we suspected was uncommon, flower gardens; flower gardens were rare enough that we could not reliably estimate the frequency of gardening at the block group level.

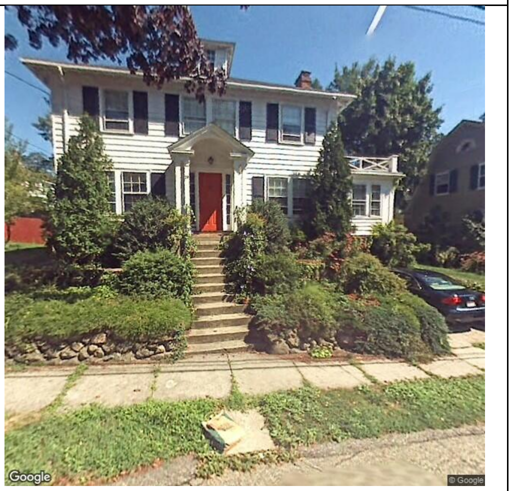
Our study area includes urban and suburban areas within 25 km of Boston, a city of 653,833 (U.S. Census Bureau, 2020), which is the center of the Boston-Cambridge-Newton metropolitan statistical area (2020 population = 4,941,632). Boston itself was excluded from the study because its substantially larger size would have limited the amount of data collection possible in other cities. Initially, we selected tracts in 10 cities in the Greater Boston Area (Fig. 1b, west of Boston: Belmont, Cambridge, and Waltham; north of Boston: Medford, Saugus, Stoneham, Woburn, and Lynn; south of Boston: Milton and Quincy). We later added an 11th city (Somerville), after the data became available through a separate project (Murphy, Dooley, and Crone, *in prep*). As a result, during in-person site visits to estimate floral diversity (described below), we visited yards only in the 10 original cities, not including Somerville.

For all 11 focal cities, we used Massachusetts tax assessors' data (provided by MassGIS) to create a list of all addresses of 1-, 2-, and 3-family residences, plus small apartment buildings of 8 or fewer units. Together, these housing types comprise the majority of all residential properties in our region (83% of all residential addresses). We excluded other types of housing (e.g. large apartments) because they probably operate under different management regimes, given that they often do not have conventional yards and are not generally managed by individual residents.

Yard Type Scoring

We used Google Street View to assess the vegetation of the front yards of houses in the 11 cities. Google Street View provides 360-degree camera imagery at street level for public roads, and past work (Burr et al. 2018) suggests it is sufficiently detailed to make broad categorizations about vegetation types with relevance to pollinators. Yards were scored as being in one of five categories: lawn, shrubby, non-vegetated, weedy, or flower garden (see extended descriptions in Table 1). We initially chose these categories because, during informal pilot evaluations of scoring, it was easier to identify flower gardens (our main interest) by having multiple options of non-garden types. Flower gardens were defined as diverse yards with several species of flowering herbaceous plants; they included both flower gardens and other types of gardens, such as ornamental and vegetable gardens. These categories were based on the primary cover type visible in the image; the Street View API automatically attempts to pan and zoom camera coverage so that the called address is in the center of the image (example images are shown in Table 1). As a result, the primary yard type was determined based only on the portion of the yard directly in front of the house. For corner lots or for imagery that included portions of side yards, we restricted our scoring to be based only on the front yard, as determined by the face of the house with an apparent front door on it, in order to ensure consistency across different lot shapes. For images where <75% of the total front yard area was visible (e.g. due to a parked car blocking coverage), the image was categorized as un-scorable and not included in subsequent analysis.

Table 1: Extended descriptions of each of the five yard categories used during Google Street View Image scoring.

Yard Category	**Description**	**Example Image**
Lawn	turfgrass lawn, typically exotic, e.g. Kentucky bluegrass *(Poa pratensis*), fescue (*Festuca*), or other cultivated Poaceae, often with a thinner border of shrubs or hedging, e.g. of privet (*Ligustrum*) or yew (*Taxus*) (scored based on plurality)	
Shrubby	shrubs, typically both flowering (e.g. rhododendron and hydrangea) and not (e.g. yew, *Taxus*), often with ornamental trees (e.g. dogwood (*Cornus*), and/or tall grasses (e.g. *Miscanthus*); lawn areas are often also present at margins (scored based on plurality)	
Non-vegetated	covered with mulch, concrete, asphalt, artificial turf, or bare soil; lacking grass or other plants; often some stray weeds in concrete cracks or container plants along margins (scored based on plurality)	

Weedy	most often lightly-managed lawns, typified by taller grass with mixed herbaceous species distributed throughout, e.g. red clover (*Trifolium pratense)* (scored based on ≥25% of visible front yard space)	
Flower garden	all types of diverse, herbaceous flowering planting, including vegetable gardens, container gardens, and pollinator gardens (scored based on ≥25% of visible front yard space)	

We were particularly interested in flower gardens because of their rarity (see *Results*), unique morphology in yards, and probable high contribution to floral diversity. Because we were mostly interested in flowers, yards were scored as flower gardens if ≥25% herbaceous flowering plants (even if they were ≥25% weedy or ≥50% some other type), then, as weedy yards if they were ≥25% weedy (even if they were ≥50% some other yard type), then one of the other yard categories based on the plurality of the yard, if neither flower garden nor weedy yard criteria were met. Scorers were instructed to also consider that non-garden lot types frequently still have perennial, low-maintenance ornamental flowering plants (e.g. daylilies or rhododendrons) or a few potted annual plants (e.g. *Impatiens* or *Petunia*), which are not sufficient to be classed as a flower garden in our pollinator-centric definition. However, for less clear-cut cases, to avoid missing possible flower gardens, scorers were instructed to err on the side of scoring borderline addresses as gardens; subsequently one of us (A.M.) scored all of the tentatively scored flower gardens and weedy yards a second time to ensure consistency in this assignment process.

In 2021, using the Google Street View API (Google Maps API, n.d.) and the list of addresses (N = 101,266), we downloaded 100,919 images and were able to score 86,429 of them (86%), the remainder of which generally had inadequate or missing imagery. Images were sorted in random order and then manually scored by a single scorer. Scorers used ImageAnt (Stucky, n.d.), an image scoring software, for convenience when inputting their data. Manual scoring using this protocol generally took under 2 seconds per address (median = 1.14 seconds), though more challenging images could take substantially longer (e.g. 5% of images took >6.5 seconds). Images were given to scorers in randomized batches of 10,000 and scoring occurred over two college semesters, meaning that individual sessions were usually short (typically not more than an hour). These scored addresses were then geocoded using the Google Geocoding API. For additional information on scoring and repeatability see Appendix C.

Google Street View coverage is periodically updated with repeated photo coverage and survey schedules vary across routes, meaning that the imagery is from various times of year and also from different years (though all imagery is from 2007 or later and the majority is from 2018-2020). The public Google Street View API does not currently support specifying a time range for imagery, so it was not possible to specify a year or a seasonal range for imagery in our API request. In an effort to address this, similarly to Burr et al. (2018), we instructed scorers to record images apparently not taken during the growing season (e.g. with visible snow or trees without leaves) as un-scorable. These non-growing season images make up a portion of the 14% of all images that were not scored; the rest are mostly addresses that the API could not resolve because no imagery of the street exists. To our knowledge, the public Street View API also does not support returning the date of the coverage provided, so we are not able to report the frequency distribution of coverage dates for our dataset. Based on personal observation and the relatively low rate of un-scorable imagery, a substantial majority of available coverage at the time we downloaded the imagery was taken during the growing season, when we expect landscaping to be most visible.

Floral Diversity Surveys

For a stratified random subset of scored addresses (N = 562), we performed in-person surveys of front yard floral diversity. Surveyed sites were stratified across both front yard types and cities, with 12 sites selected in each of the 5 yard types across the 10 initial cities; in some cities, there were <12 weedy lots detected at the time of surveying, so in these cases we surveyed all the known weedy lots. One of us (A.M.) visited these sites once per month during June, July, and August 2021, the peak flowering season in our region. These monthly visits occurred approximately every 4 weeks for each site. We repeatedly visited the same sites instead of adding more sites because floral communities change over time and we wanted to capture yard diversity over the course of the season. Some of the sites (N = 43; 8% of the total) were removed from subsequent analysis because they were not visited in all of the 3 months or because their addresses were misidentified in the field. This led to the following number of yards in the floral survey data, by yard type: 114 lawn, 122 shrubby, 108 non-vegetated, 114 flower garden, and 61 weedy. During these surveys, we followed the same definition of a front yard described above:

the space in front of the house on the face of the house that had a front door, though naturally our scope of vision in person was wider than the panned and zoomed Google Street View coverage.

We recorded all currently flowering plant species at the time of our visit and took voucher photographs of each of the flowering morphospecies present in each yard. A species was considered in bloom in the yard if one flowering unit was open and appeared capable of producing nectar or pollen. We did not record plant species that were not in bloom or are entirely wind-pollinated because of our interest in how flowering landscapes drive pollinator diversity (and for ease of identification). Species were categorized as being either cultivated or spontaneous, where cultivated species generally occur as intentional plantings by humans and spontaneous species generally do not. In cases where a specimen was apparently growing as a weed, but is a commonly cultivated species in our area (e.g. common milkweed, *Asclepias syriaca*), we categorized the species as cultivated. For species that were historically cultivated but today predominantly occur as feral or invasive weeds in our area (e.g. creeping bellflower, *Campanula rapunculoides*), we categorized the species as spontaneous.

For the majority of morphospecies (77%) we were able to identify the flowering plant to the species or species complex level using online gardening resources for the cultivated species (www.gardenia.net and plant brochures from retailers Proven Winners and Prairie Moon Nursery) and a field guide for spontaneous species (Del Tredici 2020). Another 17% of morphospecies were identified to the genus level (particularly for plant genera used in the horticultural trade where hybrids and cultivars are abundant). The remaining 6% of morphospecies were not identifiable based on photographs and were sorted into unique labels based on appearance. We provide a list of the 30 most common morphospecies observed and their frequency in the supplementary materials (Table A1). We henceforth use the terms "species" and "species richness" to describe these taxonomic groups for convenience.

Data Sources, Statistical Analysis, and Software

All statistical analyses were performed in R (v4.1.2)(R Core Team 2021). We used the tidyverse package (v1.3.1)(Wickham et al. 2019) for data cleaning, with the included ggplot package (v3.4.1) as well as the patchwork package (v1.1.1)(Pedersen 2022) for graphing. We made maps with QGIS (v.3.22.14)(QGIS Association, 2022). Significance of predictors was assessed with likelihood-ratio tests implemented with the Anova function in the car package (v3.1.1)(Fox and Weisberg 2019). We used MassGIS data for mapping focal city boundaries (Bureau of Geographic Information (MassGIS), Commonwealth of Massachusetts, Executive Office of Technology and Security Services). Roads were mapped using TIGER/Line shapefiles (U.S. Census Bureau, 2019). We used the tidycensus package (v1.1.2)(Walker and Herman 2022) to compile income and demographic data from the American Community Survey for the five-year period 2015-2019 (U.S. Census Bureau; subsequent survey years were affected by the COVID-19 pandemic and were not used). We also obtained lot size information from MassGIS, which compiles data from city tax assessors' offices and provides them in geocoded formats. Both income and lot size were gathered as medians for the tract-level analyses. Lot sizes were on a per-lot basis for floral richness analyses. Lot size variation could in principle be distinct from front yard size variation; to test how well lot sizes corresponded with front yard sizes, we used data for the Boston, MA metro area provided in Locke et al. (2022), which used GIS and remote sensing to obtain estimates of front and back yard sizes as well as lot sizes. In their data, the correlation between estimated front yard size and lot size was strong (Pearson's correlation test on log areas, $r = 0.85$, $t = 976$, $df = 360844$, $p < 0.0001$).

Our Google Street View data set included points in 145 census tracts (mean scored lots per tract = 594.4, range = 29 – 1885). Per-tract median lot sizes were highly skewed and one tract was an outlier with median lot size 8.8 SD above the mean; given that there were no observations of tracts in the range of 3.6–8.8 SD, we decided to remove this tract from all further analyses. This exclusion had negligible effects on results and model performance (Fig. A2). We also excluded a single very large yard from the ground-truthing floral survey data for the same reasons, and with the same negligible outcome on the richness analyses.

Using the Google Street View data, we tested for the effect of lot size and income on per-tract frequency of each of the five yard types, using a two-step process: First, frequency distributions of yard types were compared using multinomial logit models with fixed effects of lot size, income and their interaction, and random effects of census tract and city to account for spatial autocorrelation, implemented with the mclogit package (v7.3.17)(Elff 2022). All predictors were centered at 0 and scaled. Given significant results in this omnibus multinomial analysis (see *Results*), we implemented binomial GLMMs predicting the proportion of lots in each lot class (in turn), again with fixed effects of lot size, income, and the lot size × income interaction and random effects of city and census tract, fit with the lme4 package (v1.1.34)(Bates et al. 2015).

For our exploratory analysis with additional predictor variables, we obtained race, education, and renter status data from the American Community Survey (2015-19) and used the same modeling protocol described above (omnibus multinomial test and follow-up binomial GLMMs predicting the frequency of each yard category). Similar to our analysis of income and lot size only, we analyzed yard type frequency as a function of the following fixed effects: city, income, lot size, race (% white), education (% of 25+ year olds with bachelor's degree or higher), and renter rate (% renter-occupied). All predictors were centered and scaled at the census tract level. We assessed VIF with vif function from the car package (v3.1.2) for this larger model (cf. Appendix B) and found VIFs were high enough that we could not reliably estimate their separate effects (income VIF = 8.52, lot size VIF = 2.87, % renters VIF = 4.17, % white VIF = 4.04, % bachelor's degrees VIF = 6.64), so this *post hoc* analysis should be interpreted with caution. We did not test for interactions in this analysis because it was exploratory and because of the large number of parameters that would result from such a model.

Using the front-yard floral surveys, we analyzed alpha diversity (the number of species per yard) and gamma diversity (the total number of species per yard type)(cf. Minor et al. 2023 for a similar approach with front yard plant diversity). All analyses were conducted separately for cultivated and spontaneous species diversity. To estimate alpha diversity (mean species richness per yard) across yard types, we used negative binomial GLMs with fixed effects of yard type, implemented with the MASS package (v7.3.55)(Venables and Ripley 2002), suitable for our overdispersed count data. To compare gamma diversity across yard types (total species richness per yard category, standardized for sample size) we used the estimateD function in the iNEXT package with q = 0 (v3.0.0)(Chao et al. 2014, Hsieh et al. 2016). We also used iNEXT for drawing rarefaction/extrapolation curves. For comparing alpha and gamma diversity across yard types, we report and graph 83.4% conf. intervals, because non-overlapping 83.4% intervals are significantly different at the 95% confidence level (Payton et al. 2003).

Finally, similarly to the tract-level analysis, we tested whether income and lot size affected both cultivated and spontaneous species richness of flowers within yards (alpha diversity), using negative binomial GLMs. In this analysis, we used census tract income to represent the income for each lot we visited during flowering species richness surveys because the Census Bureau does not report per-household income for privacy reasons. Lot sizes for this species richness analysis were obtained from MassGIS tax assessors' records and are on a per-lot basis. The distribution of the number of yards surveyed in person per tract in this analysis was: 1 lot = 24% of tracts, 2–5 lots = 46% of tracts, 6+ lots = 30% of tracts.

Results

Study area

In our 11 study cities, per-tract household incomes varied from \$56,409–\$136,520 (mean = \$93,233) and lot sizes ranged from 308 m^2–1001 m^2 (mean = 515 m^2). Lot density ranged from 228 lots/km^2–925 lots/km^2 . Renting population ranged from 10.4%–65.9% (mean = 40.2%), white population ranged from 47.3%–90.3% (mean = 73.7%), and college-educated population (% bachelor's degree or higher) ranged from 17.6%–78.0% (mean = 51.8%)(Table A2, all per city means of tract medians).

Yard type

Of 86,429 lots scored using Google Street View (GSV), the most common front yard type was lawn (58.2%), followed by shrubby (27.3%), non-vegetated (11.8%), flower garden (2.3%), and weedy (0.4%). Income and lot size were significant predictors of variation in lot type frequencies across tracts (omnibus multinomial model, income $\chi^2 = 14.7$, df = 4, $p < 0.01$, lot size $\chi^2 = 30.1$, df = 4, $p < 0.0001$). The income × lot size interaction was marginally significant (multinomial model, income × lot size $\chi^2 = 7.5$, df = 4, $p = 0.1$).

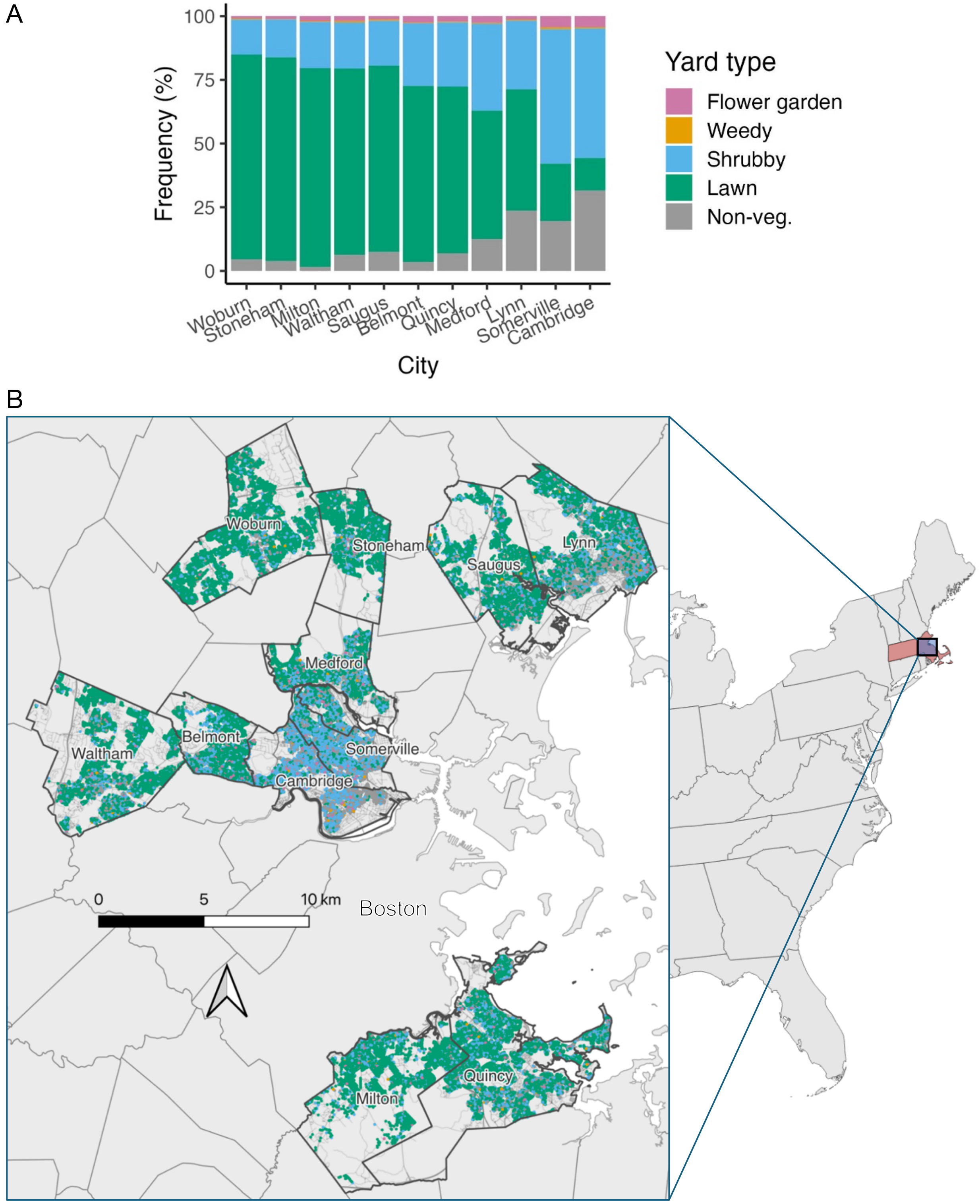


Fig. 1: (a) Frequencies of yard types across cities. The x axis is ordered by decreasing frequency of lawn, the most abundant cover type. (b) Map of the eastern U.S. and the 11 study cities with points for GSV scored sites, colored by lot class according the same legend as in the bar chart. Points overlap due to the scale. Data sources: MassGIS, U.S. Census Bureau, Google Street View.

Census tracts with higher incomes had more lawns and flower gardens (lawns $\beta = 0.17$, $\chi^2 = 15.9$, df = 1, $p < 0.001$; flower gardens $\beta = 0.24$, $\chi^2 = 15.0$, df = 1, $p < 0.001$) and fewer non-vegetated lots (non-vegetated $\beta = -0.41$, $\chi^2 = 40.3$, df = 1, $p < 0.0001$)(all binomial GLMMs, Figs. 2 & A3, Table 2). Census tracts with higher incomes also had marginally more shrubby lots (shrubby $\beta = 0.07$, $\chi^2 = 3.9$, df = 1, $p = 0.05$). Weedy lot frequency was not significantly related to tract income (weedy $\beta = -0.13$, $\chi^2 = 1.9$, df = 1, $p = 0.17$)(Figs. 2e & A3, Table 2). Census tracts with smaller lot sizes had fewer lawns ($\beta = 0.81$, $\chi^2 = 43.8$, df = 1, $p < 0.0001$) and more flower gardens, weedy yards, and non-vegetated yards (Figs. 2 & A3, Table 2, flower garden $\beta = -0.4$, $\chi^2 = 16.6$, df = 1, $p < 0.0001$; weedy $\beta = -0.27$, $\chi^2 = 6.7$, df = 1, $p < 0.01$; non-vegetated $\beta = -1.16$, $\chi^2 = 48.6$, df = 1, $p < 0.0001$). Census tracts with smaller lot sizes also had marginally more shrubby lots (shrubby $\beta = -0.12$, $\chi^2 = 3.7$, df = 1, $p = 0.06$). The income × lot size interaction was significant and negative for lawns and shrubby lots (lawns $\beta = -0.28$, $\chi^2 = 8.3$, df = 1, $p < 0.01$; shrubby $\beta = -0.25$, $\chi^2 = 4.7$, df = 1, $p < 0.05$) and significant and positive for non-vegetated lots ($\beta = 0.43$, $\chi^2 = 9.2$, df = 1, $p < 0.01$)(Fig. 2a,c, Table 2). For other lot types, the income × lot size interaction was not statistically significant (Table 2).

In our exploratory analysis of yard type frequencies as a function of additional demographic predictors, the omnibus multinomial test yielded significant effects of lot size, education (% bachelor's or higher), and renters (% renting)(lot size $\chi^2 = 38.1$, df = 4, $p < 0.0001$; education $\chi^2 = 33.7$, df = 4, $p < 0.0001$; renters $\chi^2 = 18.4$, df = 4, $p < 0.01$)(Table A3). In this omnibus test, income and race (% white) were not significant predictors (income $\chi^2 = 0.4$, df = 1, $p = 0.98$; % white $\chi^2 = 4.89$, df = 4, $p = 0.3$)(Table A3). In *post hoc* univariate models with all five predictors, flower garden frequency was higher in tracts with smaller lot sizes ($\beta = -0.43$, χ^2

= 27.5, df = 1, $p < 0.0001$) and higher rates of postsecondary education ($\beta = -0.43$, $\chi^2 = 27.5$, df = 1, $p < 0.0001$)(Table A3).

Table 2: Summary of binomial GLMM results (also see Fig. 2), predicting frequency of each lot type in response to lot size × income, with random effects of city and census tract. Statistics are for likelihood ratio tests. Predictors are both centered at zero and scaled, and are per-tract medians.

Yard Type	Variable	Slope	Chisq	Df	P
Flower garden	**Income**	**0.24**	**15**	**1**	**<0.001**
Flower garden	**Lot size**	**-0.4**	**16.6**	**1**	**<0.0001**
Flower garden	Lot size:Income	-0.13	1.7	1	0.2
Lawn	**Income**	**0.17**	**15.9**	**1**	**<0.001**
Lawn	**Lot size**	**0.81**	**43.8**	**1**	**<0.0001**
Lawn	**Lot size:Income**	**-0.28**	**8.3**	**1**	**<0.01**
Nonveg.	**Income**	**-0.41**	**40.3**	**1**	**<0.0001**
Nonveg.	**Lot size**	**-1.16**	**48.6**	**1**	**<0.0001**
Nonveg.	**Lot size:Income**	**0.43**	**9.2**	**1**	**<0.01**
Shrubby	Income	0.07	3.9	1	0.05
Shrubby	Lot size	-0.12	3.7	1	0.06
Shrubby	**Lot size:Income**	**-0.25**	**4.7**	**1**	**0.03**
Weedy	Income	-0.13	1.9	1	0.17
Weedy	**Lot size**	**-0.27**	**6.7**	**1**	**<0.01**
Weedy	Lot size:Income	-0.19	1.4	1	0.24

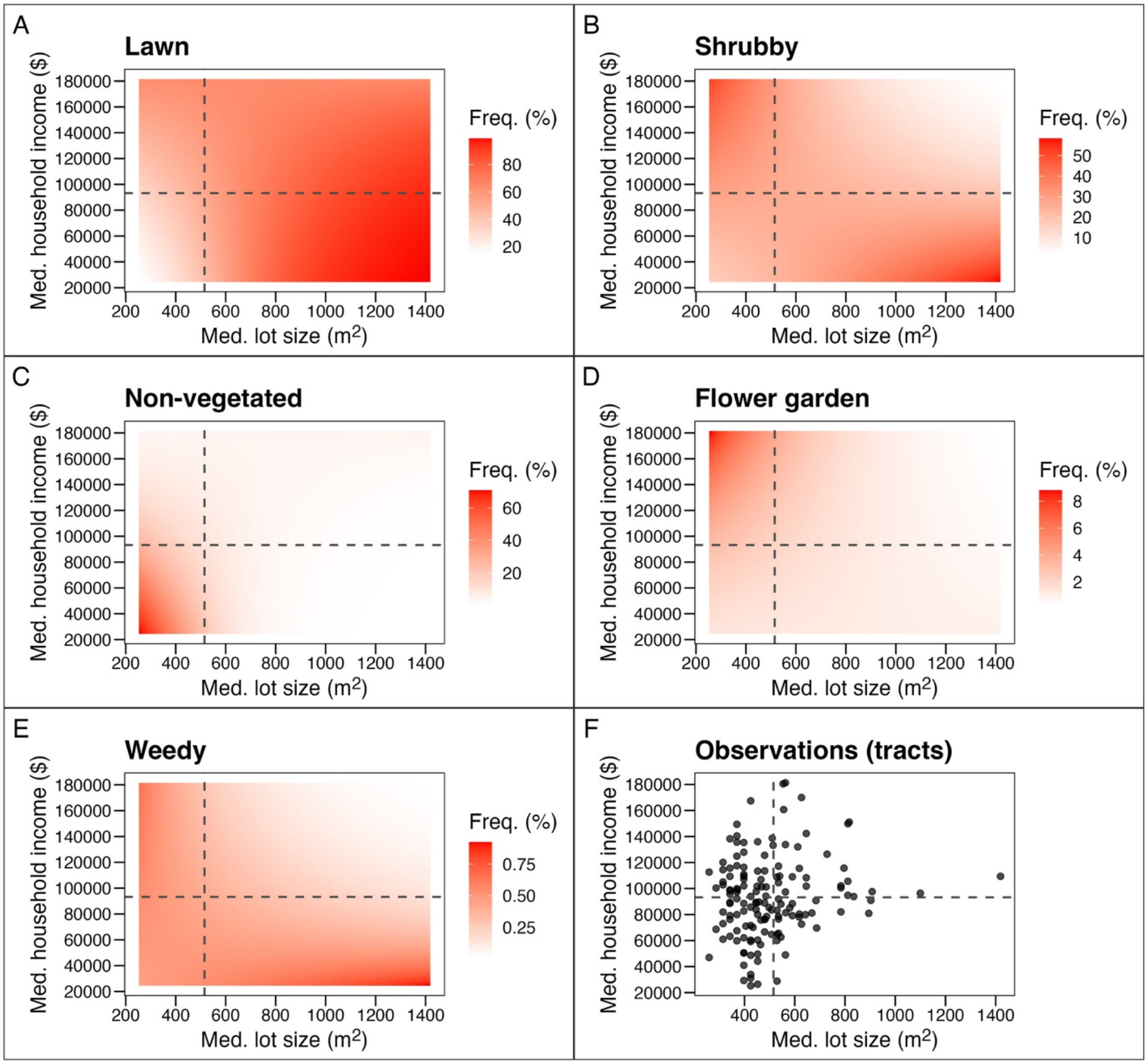


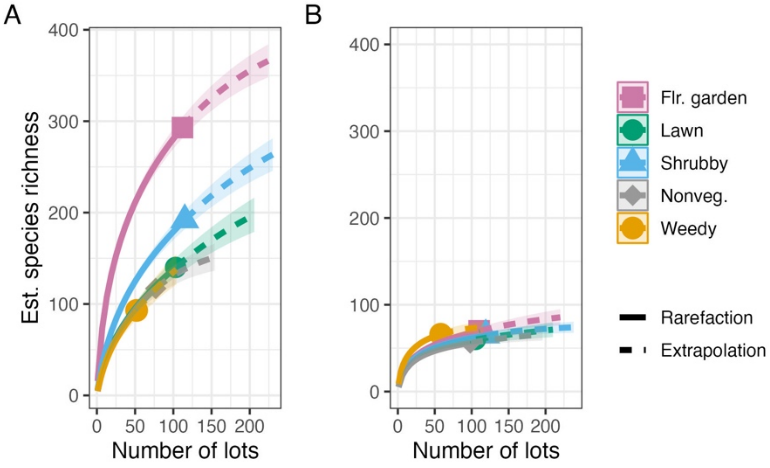
Fig. 2: The joint effects of per-tract income and lot size on the predicted frequency of each of the five yard types based on binomial GLMMs with random effects of city and census tract. The graphs are arranged in decreasing abundance of each yard type (A = Lawn, B = Shrubby, C = Non-vegetated, D = Flower garden, E = Weedy). The dashed lines indicate the mean for income and lot size across all tracts. Red color intensity indicates higher predicted frequencies; note the scale differences in the legends provided. Panel F shows the distribution of observed tracts (N = 144); predictions for areas not represented by data should be interpreted with caution. Univariate relationships for these same models are shown in Figs. A3 and A4.

In the exploratory analysis, lawn frequency was higher in tracts with larger lot sizes ($\beta = 0.62$, $\chi^2 = 43.1$, df = 1, $p < 0.0001$) and fewer renters ($\beta = -0.28$, $\chi^2 = 14.5$, df = 1, $p < 0.0001$)(Table A3). Shrubby yard frequency was higher in tracts with higher rates of postsecondary education ($\beta = 0.46$, $\chi^2 = 12.2$, df = 1, $p < 0.001$)(Table A3). Non-vegetated yard frequency was higher in tracts with smaller lot sizes ($\beta = -0.91$, $\chi^2 = 46.5$, df = 1, $p < 0.0001$), more renters ($\beta = 0.5$, $\chi^2 = 17.4$, df = 1, $p < 0.0001$), and lower rates of postsecondary education ($\beta = -0.66$, $\chi^2 = 17.4$, df = 1, $p < 0.0001$)(Table A3). Weedy yard frequency was higher in tracts with smaller lots ($\beta = -0.29$, $\chi^2 = 4.63$, df = 1, $p < 0.05$) and marginally higher in tracts with more renters ($\beta = 0.26$, $\chi^2 = 3.9$, df = 1, $p = 0.05$)(Table A3). All other lot type frequency relationships were not statistically significant.

Species diversity - patterns

Across the 519 lots we visited in person, we recorded 461 flowering species blooming over the course of the season. Of these species, 80.0% (369 species) were classified as cultivated and 20.0% (92 species) as spontaneous. The rarefaction curve appeared to reach saturation for the spontaneous floral community, but not the cultivated community (Fig. 3).

Fig. 3: Species rarefaction curves for (a) cultivated and (b) spontaneous flower communities across the five management classes. The solid line is the rarefaction curve, the solid point indicates the actual N lots sampled in each class and the dashed line is an extrapolation to 2x sample size. Error bars indicate 83.4% confidence intervals around estimates to facilitate comparisons between groups: non-overlapping error bars indicate significant differences between groups at the 95% confidence level.



Gamma diversity also varied across yard types (rarefied/extrapolated species richness standardized by sample size, Fig. 4a). The cultivated floral community was more diverse than the spontaneous community across all 5 yard categories. Gamma diversity of cultivated flowers was highest in flower gardens (est. richness = 284.9 [83.4% CI = 268.9–300.9]), followed by shrubby yards (est. richness = 182.6 [83.4% CI = 167.7–197.6]), and then the other three categories, which did not significantly differ from each other (lawns est. richness = 140.7 [83.4% CI = 124.7–156.7], weedy yards est. richness = 137.8 [83.4% CI = 116.8–158.9], and non-vegetated yards est. richness = 133.1 [83.4% CI = 118.8–147.4])(Fig. 4a). Gamma diversity of spontaneous flowers was highest in weedy yards (est. richness = 74.2 [83.4% CI = 67.4–80.1), though this did not significantly differ from flower gardens or shrubby yards (flower gardens est. richness = 71.2 [83.4% CI = 65.7–76.7], shrubby est. richness = 64.6 [83.4% CI = 59.9–69.3]), but was significantly higher than lawns and non-vegetated lots (lawns est. richness = 61.4 [83.4% CI = 56.7–66.2], non-vegetated est. richness = 58.4 [83.4% CI = 53.1–63.8])(Fig. 4a).

Alpha diversity varied among yard types (negative binomial GLM, cultivated species richness $\chi^2 = 227$, df = 4, $p < 0.0001$, spontaneous species richness $\chi^2 = 39$, df = 4, $p < 0.0001$)(Fig. 4b). Cultivated alpha diversity was highest in flower gardens ($\alpha_{cult} = 15.4$ sps./yard [83.4% CI = 13.8–17.2]), followed by shrubby yards ($\alpha_{cult} = 6.2$ sps./yard [83.4% CI = 5.5–6.9]), then lawns and weedy yards, which did not significantly differ ($\alpha_{cult} = 4.8$ sps./yard [83.4% CI = 4.3–5.5] and $\alpha_{cult} = 4.1$ sps./yard [83.4% CI = 3.4–4.8] respectively), and then non-vegetated yards ($\alpha_{cult} = 3.2$ sps./yard [83.4% CI = 2.8–3.6])(Fig. 4b). Spontaneous alpha diversity was highest in weedy yards ($\alpha_{spont} = 8.2$ sps./yard [83.4% CI = 7.4–9.2]), followed by shrubby, lawn, and flower gardens, which did not significantly differ from each other ($\alpha_{spont} = 5.4$–5.7 sps./yard [overall range of 83.4% CIs = 5.0–6.2])(Fig. 4b). Non-vegetated yards had significantly lower spontaneous alpha diversity than all other groups (α_{spont} = 4.4 sps./yard [83.4% CI = 4.0–4.9])(Fig. 4b).

Species diversity - drivers

Full models for flower richness at the lot scale showed convergence and singularity errors, so we reduced models by first assessing random effects and then removing nonsignificant interactions (Zuur et al. 2009). For cultivated species richness, there was no support for random effects of tract or city (ΔAIC = 2 and variance estimates of ~0; cf. Arnold 2010). For cultivated species richness, we sequentially removed non-significant interactions including the three-way lot type × income × lot size interaction, as well as two-way interactions between lot type × income and lot type × lot size (Table A4). As a result, the final model for cultivated flower richness included fixed effects of income × lot size + lot type (Table A4). For spontaneous species richness, the best-performing model included a random effect of census tract (ΔAIC = 2.5 compared to a model of the same structure with no random effects). For

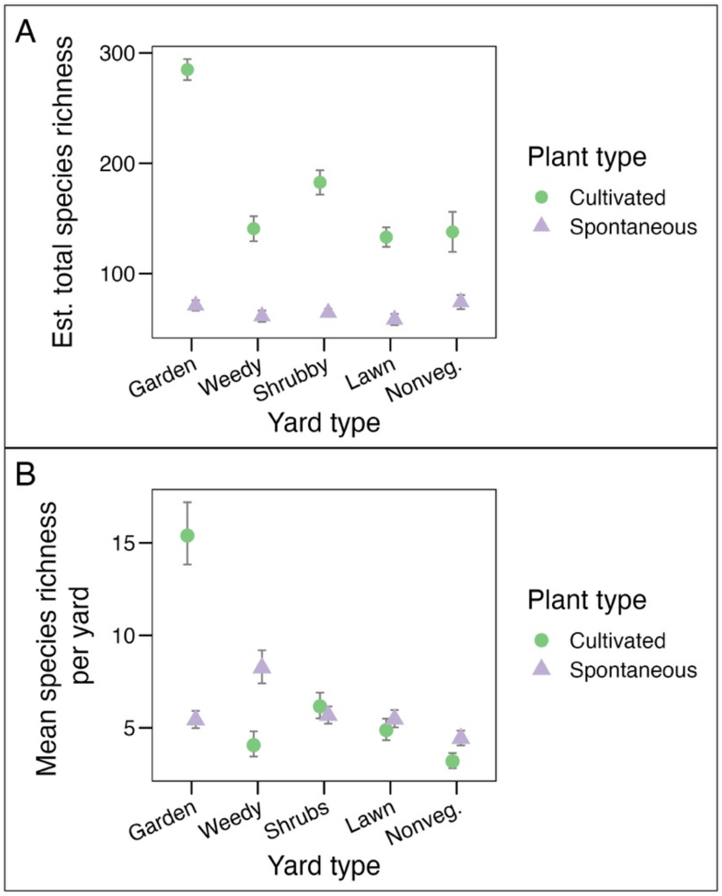


Fig. 4: (a) Floral gamma diversity across yard categories and plant type, estimated with rarefaction/extrapolation to standardized sample sizes. (b) Floral alpha diversity across yard categories, measured as the estimated average species richness per yard from a negative binomial GLM. Both sets of error bars are 83.4% confidence intervals around estimates to facilitate comparisons between groups: non-overlapping error bars indicate significant differences between groups at the 95% confidence level.

spontaneous species richness, all interaction terms were sequentially removed as none were significant (Table A4), yielding a final model for spontaneous flower richness including fixed effects of income + lot size + lot type.

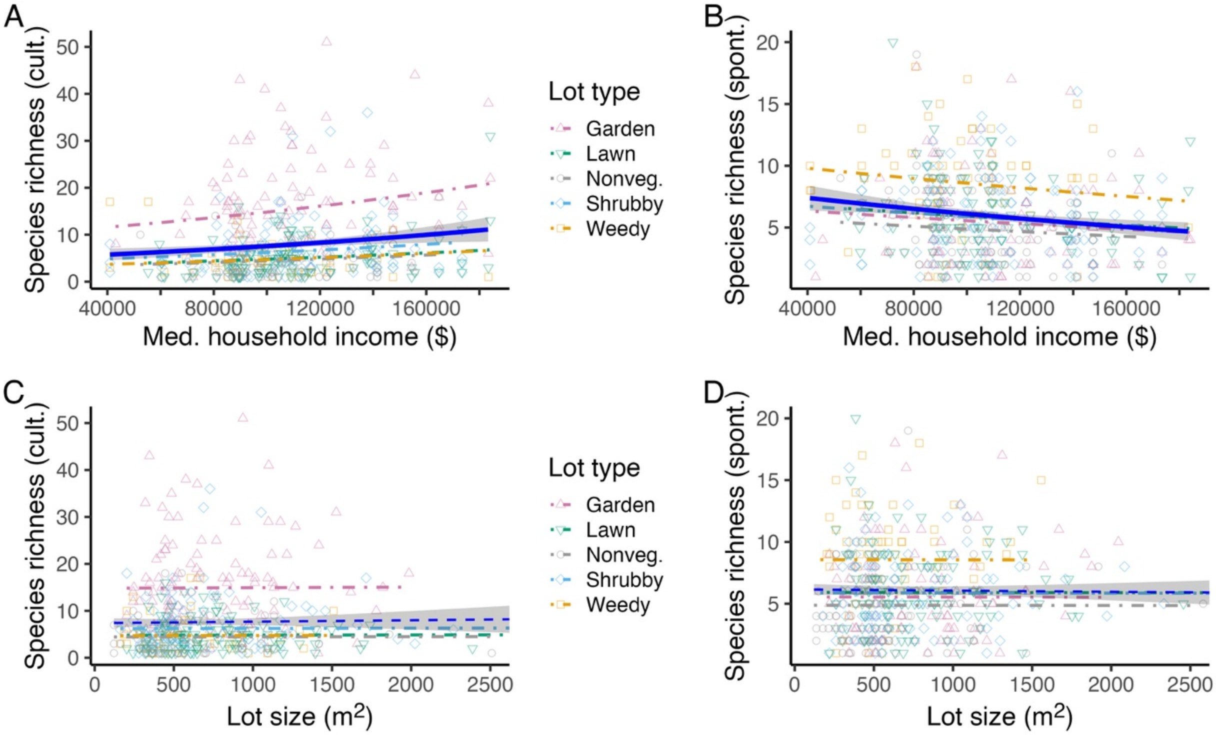


Fig. 5: Effects of income and lot size on cultivated (a, c) and spontaneous (b, d) floral species richness (alpha diversity). Raw data (individual yards) are shown as points with color/shape showing lot type. Fitted lines are the result of a negative binomial GLM predicting species richness with fixed effects of income × lot size + lot type. The fitted dotted lines are the predictions for each lot type and the blue lines are the overall mean response across lot types with 95% conf. intervals. Household income is at the census tract level and lot sizes are at the per-lot level. In (c) and (d) the x-axis was truncated at 2500 m^2, so 6 points with larger lot sizes are not shown in this visualization. Thick blue lines indicate a significant overall relationship for (a) and (b), and thin dashed blue lines indicate a non-significant relationship for (c) and (d).

In relation to lot size and income, cultivated floral richness varied across yard types (negative binomial GLM, $\chi^2 = 208.6$, df = 4, $p < 0.0001$)(Table A4). Front yards in higher income tracts had higher cultivated species richness (Fig. 5a & Table A4, negative binomial GLM, $\beta = 0.12$, $\chi^2 = 9.1$, df = 1, $p < 0.01$). The species richness-income relationship did not vary by lot type for either cultivated or spontaneous flowers (see model selection results above). Lot size was not significantly related to cultivated floral species richness (Fig. 5c & Table A4, $\beta = 0.01$, $\chi^2 = 1.3$, df = 1, $p = 0.25$). The income × lot size interaction was significant and positive for cultivated species richness (Table A4, $\beta = 4.5$, $\chi^2 = 4.5$, df = 1, $p < 0.05$). Spontaneous floral richness also varied across lot types (Table A4, negative binomial GLM, $\chi^2 = 39.1$, df = 4, $p < 0.0001$). Front yards in higher income tracts had lower spontaneous species richness (Fig. 5b & Table A4, $\beta = -0.08$, $\chi^2 = 7.9$, df = 1, $p < 0.01$). Lot size was also not significantly related to spontaneous floral species richness (Fig. 5d & Table A4, $\beta = -0.01$, $\chi^2 = 0.04$, df = 1, $p = 0.8$).

Discussion

Flower gardens were key drivers of front yard floral diversity, with garden lots harboring more than double the total cultivated species richness of lawn lots. Income had a positive relationship with flower gardening and with per-yard cultivated floral richness, and together these relationships imply higher flower species diversity in wealthier neighborhoods, consistent with the luxury effect hypothesis (Hope et al. 2003, Leong et al. 2018, Chamberlain et al. 2020). Unexpectedly, flower gardens were not more common in neighborhoods with larger lot sizes; instead, census tracts with smaller lots had higher flower garden frequencies. This relationship contrasts with the general expectation that larger lots would support more land uses (Smith et al. 2005, Loram et al. 2008), including more flower gardens. Flower gardens were also the only yard type that had more cultivated than spontaneous species per yard (i.e. $\alpha_{cult} > \alpha_{spont}$, Fig. 4b). As a result, in spite of the fact that flower gardens are a rare front yard type in our region at just ~2% of all yards, they likely play an outsized role in driving floral diversity across the area. For reference, ~43% of land cover in the Boston area is residential (Ossola et al. 2019b), and 25% of all cultivated flower species were only ever observed in flower gardens (93 species), as compared to 4% for lawns (15 species).

Our Google Street View classification approach appeared to capture meaningful differences in front yard landscaping and thus in floral resources. These results affirm past work that has used Google Street View to characterize landscaping decisions without species-level ground truthing (e.g., Burr et al. 2018). We observed more cultivated flower species in yards scored as flower gardens, affirming that remote scorers were able to detect meaningful differences in flower diversity using Street View images. In addition, we saw concordance with expectations across other categories. For instance, yards scored as "weedy" based on Google Street View images had more spontaneous than cultivated species per yard. The only other yard category with more spontaneous than cultivated species was non-vegetated yards, suggesting that we were able to discriminate these from more intentionally cultivated flower gardens, lawns, and shrubs. At the same time, our ability to "ground truth" categories from our data was also limited to assessments of flowering plant species diversity, because flower gardens were the focus of our study design. In hindsight, it would also have been informative to estimate % cover of different land use types (e.g., ornamental flower garden, vegetable garden, turf grass, shrubs, trees, and impervious surface) during our ground visits to assess the land uses associated with each yard type.

In our study, income was linked to variation in front yard types, in ways that partly support the luxury effect hypothesis. The two more florally diverse yard types, flower gardens and shrubby yards, were more common in higher income neighborhoods. Flower gardens could be more common in wealthy neighborhoods for a variety of reasons: the people who live in these neighborhoods may have different priorities for their yards (Padullés Cubino et al. 2020), simply have stronger preferences for this landscaping type (Larsen and Harlan 2006) and/or be better able to afford costly flower gardens, even if they are broadly desirable (Blanchette et al. 2021). Another hypothesis is that the income-diversity relationship actually reflects higher education levels; income and education level were strongly correlated in our data (r = 0.71 for tract-level income and education). Similar to our results, Minor et al (2023) found stronger associations of plant species diversity with education than income in Chicago. However (as those authors noted), it is difficult to assess the relative importance of each of these factors when they are so tightly correlated. Flower gardening may be an indicator of membership or status within certain social groups, which are defined by both income and education status, as well as other features (c.f. ecology of prestige, Grove et al. 2014). Another pattern in our data that contradicts the luxury effect hypothesis is that the frequency of lawns also increased with income.

Contrary to our expectations of a positive species-area relationship, census tracts with smaller lots had elevated frequencies of florally diverse yard types (flower gardens and shrubs). This was linked to reduced frequency of lawns, the most abundant yard type, in tracts with smaller lots. Our study cities cover substantial variation in lot sizes, from 320 m^2 (0.08 acre) median lot size in the dense cities of Somerville/Cambridge up to ~800 m^2 (0.2 acre) for more suburban Stoneham/Woburn. Lot size in general seems to have underappreciated and complicated impacts on yard landscaping decisions. Although the previously-reported empirical pattern is generally more species and yard types in larger lots (Delahay et al. 2023), some studies have found similar diversity patterns to ours, e.g. Yahner (2001) reported greater butterfly species richness in residential neighborhoods with smaller lots. In other studies, larger lots have been linked to features suggestive of lower flower diversity: more tree cover (Bigsby et al. 2014, Ossola et al. 2019a), more grass cover due to increased lawn landscaping (Wheeler et al. 2020), and more monoculture lawns in particular (Fuentes 2021). One surprising implication of this result is that minimum lot size policies, now widespread in the U.S. (Boudreaux 2016), may actually impose a constraint on city-wide biodiversity because the larger lots they produce are more likely to be lawns. In a complementary way, this negative relationship suggests that urban neighborhoods with small lots are a promising target for outreach programs aimed to increase pollinator gardening.

One interesting possible explanation for the negative relationship between lot sizes and flower gardening frequency is that individual landscaping decisions occur in a social context (Cook et al. 2012). Landscaping can be socially contagious, meaning that nearby homeowners tend to make similar landscaping decisions to each other (Nassauer et al. 2009, Hunter and Brown 2012). As a rare and highly visible behavior, front yard flower gardening is a good candidate for undergoing social contagion. At least one previous study has suggested that the number of neighbors with visual adjacency (i.e. those visible from the focal house) could mediate contagion; in their case, the authors reported that an increased number of visually adjacent neighbors gardening on the road verge increased the probability of verge gardening (Hunter and Brown 2012). In a remote-sensed study of Boston area landscaping (Locke et al. 2022, Ossola 2019a&b), turf grass cover, but not tree cover, was more spatially autocorrelated in front than back yards, again suggesting the importance of visual adjacency for spatial contagion. If flower gardening is contagious, it may be that the effects of contagion are stronger in neighborhoods with smaller lots, contributing to the higher gardening rates we observed in these neighborhoods.

After accounting for fixed effects of lot type, species richness within lots was not clearly associated with lot size or income. In relation to income, cultivated floral richness increased but spontaneous floral richness decreased (Fig. 5). Spontaneous flowers may have important roles in provisioning resources for some pollinators (e.g. clovers for certain solitary bees, MacIvor et al. 2014), which makes trends in their richness important for understanding yards as pollinator habitat. Similar to this pattern, weedy flower species richness in front yards decreased with income in Chicago (Lowenstein and Minor 2016) and lawn plant species diversity was lower in higher income areas across several cities (Wheeler et al. 2017). Overall, these trends have been interpreted as suggesting that wealthier yard owners are less constrained in their ability to both add cultivated plants and remove weeds (Lowenstein and Minor 2016, Wheeler et al. 2017, Blanchette et al. 2021). Lot size, in contrast with income, appears not to be a strong constraint for yard floral richness in our region. Neither spontaneous nor cultivated flower species richness increased with lot size within yards of a given type (Fig. 5), which is especially surprising for spontaneous species.

Limitations and ways forward

In designing our study, we decided to survey a large number of yards at a relatively coarse level of detail in order to measure a rare yard type (flower gardens) across a wide range of neighborhoods and decouple variation in lot sizes from income, overcoming a major barrier to estimating their separate effects (Leong et al. 2018). However, other demographic features included in our *post hoc* analysis were still correlated with income and with each other, and more work is needed to understand their separate roles. Future work could attempt to expand our approach of stratifying sampling across existing variation of more of these variables, or could apply statistical techniques like structural equation models, which can allow researchers to separate the effects of correlated variables (e.g. Garfinkel et al. 2024). Another factor worthy of future study is the role of Homeowners' Associations (HOAs), which are uncommon in our area — because nearly all development occurred before 1950, predating the advent of modern HOAs (McCabe 2011) — but which can constrain gardening when present (Silvert et al. 2023).

There are also tradeoffs between study breadth (our goal) and depth. Our yard surveys were simply species lists of blooming plants, which were efficient to gather without permission, but were less detailed than, for instance, flower counts by species would have been (e.g., Kurylo et al. 2020). Our Google Street View data were also gathered with a relatively coarse, five-category scale. Street View is not yet appropriate for more detailed measurements, e.g. percent of yard with each cover type, because not all of the yard is visible in all images and because the image resolution is too low. Another limitation of Street View data is that it only surveys front yards, and back yards can systematically differ in management and biodiversity (Locke et al. 2018). For example, ground studies have shown that front yards may have a larger proportion of flower gardens (Avolio et al. 2020) and back yards may tend to have more food plants (Vila-Ruiz et al. 2014) and greater vegetation complexity and food availability for birds (Belaire et al. 2016). A previous study in the Boston area using remote-sensed data also reported more tree cover in back than front yards (Ossola et al. 2019b). One promising direction for Street View — for questions amenable to simple categorization schemes like ours — is AI image classification, which could increase throughput dramatically; similar approaches have recently been used for automatically classifying subjective perceptions of Street View images (Ogawa et al. 2024), but have not yet been applied to flower gardening or pollinator research.

Conclusions

In closing, we document disproportionately large contributions of front yard flower gardening to urban flower diversity. We found that patterns of front yard types, and thus floral diversity, varied at two scales, both in the frequency of flower gardens on the landscape and in terms of species richness within those flower gardens. From a pollinator conservation perspective, these patterns suggest that pollinator habitat quality in front yards might be determined mainly by landscaping typologies — e.g. decisions to have a flower garden or to leave the weeds. Another possible implication for pollinator conservation is that outreach programs could be targeted at either scale, i.e., either encouraging people to plant a flower garden, or encouraging people with flower gardens to plant more or different species.

Our study also showed that Google Street View is a viable way to map yard type distributions over large areas with ecologically meaningful categories. In the context of promoting pollinator gardening, it would surely be interesting to explore the distribution of flower gardens in other metropolitan areas, especially those with less dense populations and larger lot sizes, other climate conditions, especially more arid climates, and in regions outside the United States. Future work could seek to further understand what factors drive the creation of flower gardens and enhance our general understanding of the sometimes-surprising ways in which constraints such as lot size and income might affect urban biodiversity.

Chapter 3 - Flower gardening is socially contagious

Abstract

Conservation in residential yards faces key problems in the form of recruitment (finding enough volunteers for these small patches to be impactful) and coordination (making habitat patches nearby enough to each other so that they are connected by movement). One factor — often hypothesized but rarely explicitly tested — which could ameliorate these challenges is social contagion, which describes a persistent, passive process in which individuals tend behave more similarly to those with whom they interact the most. Nearby neighbors may interact more and thus spread ecologically beneficial practices, such as pollinator gardening. We test for the presence of social contagion in front yard flower gardening and find that next door neighbors to flower gardens are nearly three times as likely to have flower gardens themselves. This strong effect decays rapidly with each successive neighbor away, consistent with a contagion process. Using a simulation approach, we show that contagion leads to flower gardens being ~7–10% closer together compared to random; although modest in absolute terms, this effect causes substantially more gardens to be within 50m of each other, altering structural connectivity for pollinators.

Introduction

Ecologists and conservationists increasingly recognize the value of urban residential lands for conservation, as these properties comprise a substantial portion of all urban lands (e.g. 36–47% in the U.K., Loram et al. 2008) and they can be managed effectively for conservation, yielding benefits ranging from reduced carbon emissions to increased yard biodiversity and improved resident connections with nature (Lerman et al. 2023). Yet a pair of related problems confront any efforts to carry out conservation in front and back yards (the areas around private homes). First, residential conservation suffers from a 'multiple stakeholder' problem, i.e. the fact that many individuals must be convinced to carry out changes in their land management in order to yield significant conservation benefits, with each stakeholder having different aims and priorities (Aronson et al. 2017). Second, these efforts also face a coordination problem, which stems from a mismatch in scale: while yards are managed independently by members of the public, most animal populations cannot be sustained within a single yard and instead must depend on resources from multiple, nearby properties that are managed as habitat (Goddard et al. 2010, Aronson et al. 2017). As a result, true habitat quality in an urban area depends not only on one yard manager, but on groups of nearby yards functioning together (Belaire et al. 2014).

Concerns about patch size and connectivity in urban landscapes stem from an implicit assumption that urban residents manage their land independently. While this is clearly true to some extent, many aspects of human behavior are socially contagious, meaning that individuals behave more similarly to those they interact with more (e.g. Burt 1987, Centola and Macy 2007, Blanchet 2013). In this context, the term spatial contagion has been used to describe spatial clustering of yard features/management (Kirkpatrick et al. 2009, Hunter and Brown 2012, Locke et al. 2022), presumably through increased interactions among neighbors (Martini et al. 2014). Spatial contagion could lead to spatial clustering of wildlife-friendly practices in yards, and higher connectivity of wildlife habitat, even in the absence of external coordination. In addition, contagion is one way to change behavior of multiple stakeholders at once. Even though social pressures often discourage new, wildlife-friendly landscaping, there is surprisingly strong willingness to change adopt wildlife-friendly landscaping types, provided that sufficient numbers of neighbors do so as well (Nassauer et al. 2009). Contagion has been discussed in various reviews of urban conservation (e.g. Goddard et al. 2010), but the strength and nature of contagion has rarely been explicitly tested and its ecological implications have not yet been fully quantified.

Although direct tests are lacking, various lines of evidence show that landscaping types tend to be spatially clustered, meaning that neighbors tend to maintain similar landscaping to each other. These spatial autocorrelations in landscaping are often suggested to be partially driven by social contagion. In Montreal, vegetation structure was similar between nearby neighbors along the same side of the street (Zmyslony and Gagnon 1998); gardens in the road verge were spatially clustered in Ann Arbor (Hunter and Brown 2012); tree cover was similar between nearby neighbors in Boston (Locke et al. 2022); and yard plant diversity was autocorrelated along streets in Chicago (Minor et al. 2023). The interactions underlying hypothesized contagion are typically defined broadly, meaning they could be conscious or unconscious and include both direct verbal communication as well as encounters like simply observing the neighbor's yard, among others. In the case of yard management, interactions are likely to occur more frequently between nearby neighbors.

Here, we develop a test for contagion of an urban conservation practice using the signature of fine-grained spatial clustering, and discuss the ecological impacts of this spatial structure. Our research was motivated by growing interest in pollinator gardening, the practice of planting diverse flowers to provide nectar and pollen for pollinators. This practice has attracted much attention from conservationists and ecologists in recent years because of its high potential ecological value: gardens in these urban areas can host pollinator biodiversity and population growth rates that are comparable or even higher than surrounding non-urban areas (Hall et al. 2017, Majewska and Altizer 2020). Yet like any yard-level intervention, pollinator gardening's conservation potential is likely constrained by both the multiple stakeholder and coordination problems. For instance, many invertebrate pollinators common in urban gardens tend to travel relatively short distances on a typical foraging trip, e.g. on the order of 100–300 meters for solitary bees (Zurbuchen et al. 2010, though longer journeys are possible). Therefore, the prevalence and scale of spatial contagion is likely to be ecologically relevant, because highly local clustering benefits species with smaller foraging and dispersal ranges the most.

Specifically, we focused on spatial contagion of flower gardening in front yards. In addition to its ecological relevance, front-yard flower gardening is a strong candidate for contagion. Flower gardening is a highly visible activity, as neighbors cannot help but see the garden once it is created, and particularly once it is blooming. One previous study has identified spatial clustering consistent with contagion in gardening in road verges at local spatial scales (~100m), with the authors suggesting that visual adjacency was a key factor driving contagion (Hunter and Brown 2012). Flower gardens also have broad visual appeal and are well-liked, with diverse flower gardens like pollinator gardens yielding even more positive responses (e.g. Lindemann-Matthies and Marty 2013). Front yards are a convenient study system because they can be surveyed comprehensively, without permission of residents (which comes with other biases, Chamberlain et al. 2004). Homeowners also consistently report that the influence of their neighbors is a primary motivator of landscaping decisions (Goddard et al. 2013), with many reporting feelings of obligation to uphold perceived community standards (and home values)(Blaine et al. 2012, Harris et al. 2013), making front yards particularly susceptible to social influence.

In order to test for contagion in flower gardening, we quantified clustering in flower gardens and partitioned this clustering across scales, from the citywide scale to the highly local, neighbor scale. This allowed us to assess how much of the existing distribution of gardens could be explained by contagion, compared with other larger scale factors (including demography). One key challenge in detecting contagion is the presence of confounding demographic drivers, because demographically similar people tend to live near each other (i.e. neighborhoods vary in racial makeup, typical income, etc.). These demographic factors are often also linked to yard landscaping, e.g. income, race, and education have been previously been found to affect yard biodiversity (Hope et al. 2003, Leong et al. 2018, Minor et al. 2023). We knew that clustering of flower gardens at the city and neighborhood levels would be due at least in part to these factors (Murphy and Crone *in review*). We hypothesized that, after accounting for similarity at these scales, there would still be additional, localized clustering along individual streets, the latter of which would be a sign that flower gardening is socially contagious. To estimate contagion strength, we gathered a large data set of the locations of flower gardens across >86,000 addresses in 11 cities in the Boston, MA, USA metropolitan area, (Murphy & Crone, in review). We first estimated the spatial scale of contagion after accounting for differences among cities and neighborhoods. Then, we quantified the contributions of city, neighborhood, and local contagion to overall clustering of gardens on the landscape using simulations. We contextualize this variation in relation to the spatial scale of pollinator movement, and discuss the ways contagion might be harnessed to promote pollinator gardening and pollinator conservation.

Materials & Methods

Study Area and Mapping Flower Gardens

Our study area comprises 11 cities in the Greater Boston area. The housing stock in these cities ranges from Victorian rowhouses in the high-density areas bordering the central city of Boston to mid-20th century, low-to-moderate-density suburbs 10–20 km away from the urban core. We selected these cities to capture a range of demographic characteristics and housing densities over a small area (Murphy & Crone, in review). In the metro Boston area, ~43% of all land cover is residential (Ossola et al. 2019b).

We identified the locations of front yard flower gardens in 11 cities in the Greater Boston area using Google Street View (described in Murphy & Crone, in review). In brief, we downloaded imagery using the public Google Street View API in 2021. The imagery provided is street-level and the API attempts to pan and zoom the 360-degree camera coverage to center the front of the called address. To obtain a list of addresses in our study area, we used Massachusetts tax assessors' records provided by MassGIS. We limited the survey to one-, two-, and three-family homes plus small apartment buildings of 8 or fewer units, comprising 83% of all residential addresses in our area. The final scored data set included 86,429 scored addresses out of the 101,266 in the study area (14% of images were unscorable). We visited a stratified random sample of ~110 yards of each category (i.e. ~110 gardens and ~440 other yards), in order to ground-truth the Street View assessments. 86% of addresses scored as flower gardens on Google Street View were confirmed to have flower gardens when visited in person and addresses scored as flower gardens on Google Street View had more than 2 times greater total floral species richness than other landscaping types.

Clustering/Contagion Analysis

In order to test whether flower gardens were more spatially clustered than expected by chance, we used a mixed modeling approach based on estimating the probability of occurrence for flower gardens. Specifically, we estimated the probability that a yard is a flower garden as a function of whether a neighbor N houses away was a flower garden or not. In other words, for N

= 1, the model tested whether a house whose next-door neighbor had a flower garden was more likely to have a flower garden. We used binomial generalized linear mixed models (GLMMs) because these allowed us to use random effects to account for background variation in flower garden frequency between cities and neighborhoods. We compared the neighborhoods around two sets of data: all the observed flower garden addresses (N = 1940) and a random selection of non-garden addresses (N = 1940). We included three random effects in these models: city, census tract, and census block group, and a fixed categorical effect of focal yard type, i.e. is the house N neighbors away a garden or a random non-garden. These models therefore estimate the probability of the Nth neighbor away having a flower garden, while allowing for cities/tracts/block groups to vary in their background flower gardening frequencies (see Fig. 1 and Appendix: supplemental analysis). In summary, our final models tested the probability that houses in a neighborhood had flower gardens, with a fixed effect of neighborhood center type (garden or non-garden), and random effects of city, census tract, and census block group. We repeated the analysis for neighborhoods of radii from 1–30 neighbors nearest the center.

We calculated the effect size of a neighbor having a garden as the difference between the estimated probability of having a flower garden in a neighborhood of size N centered around a flower garden vs. a random non-garden. For example, for a given neighborhood size, if the predicted probability of a yard being a flower garden was 0.02 (2%) for the neighborhood around a random non-garden and was 0.04 (4%) for neighbors around a random garden, the effect size would then be 0.04 - 0.02 = 0.02, and the odds ratio would be 0.04/0.02 = 2, indicating that in this hypothetical, gardens would be twice as frequent around gardens compared to non-gardens. Conversely, if there were no evidence contagion, then this odds ratio would be approximately 1, i.e. no different from random. We estimated 95% confidence intervals around these effect sizes using the delta method to account for the SE for each of the gardening probability estimates that we had subtracted from each other.

Our primary analysis defined neighborhoods using a fixed number of nearest neighbors. However, our communities differed in lot sizes (from a median of 162 m^2 in the census tract with the smallest lot sizes to 1862 m^2 in the tract with largest lot sizes; Murphy and Crone *in review*). Therefore, we also tested for the influence of lot sizes on the strength of contagion. To do this, we calculated the median log lot size (m^2) based on public tax assessor's geospatial data (MassGIS) for the 30 neighbors around each focal garden or non-garden. We then binned each of the focal neighborhoods into one of 5 lot size bins, where 1 = smallest lots and 5 = largest lots. We selected bin ranges that produce consistent sample sizes across each bin (all the focal yards were pooled and then binned so, total N = 1940 gardens + 1940 non-gardens, yielding 776 addresses in each of the 5 lot size bins). We used 5 bins to ensure sufficient sample size in each bin, as model performance declined with smaller sample sizes. We then calculated the effect size of neighbors gardening across the range of 1–30 neighbors, as before, on each of the lot size bins separately. We fit a simple linear model of the form log(effect size) ~ log(nth neighbor) to these estimates across neighborhood sizes, with the aim of representing contagion strength in each of the lot size bins. From these simple fits, we calculated the intercept value (the theoretical maximum contagion strength closest to the focal house) and the slope of the curve (the rate of decline in contagion strength with each additional neighbor away from the focal house).

Configuration of flower gardens across scales

To understand the importance of spatial contagion, we compared the distribution of flower gardens would be from each other if they had been distributed randomly vs. if they were clustered at several larger scales vs. the observed distribution. This allowed us to assess how much of the overall distribution of flower gardens throughout the study area was due to clustering at each spatial scale, and thus how much of the distribution could be attributed to clustering at highly local scales, consistent with contagion, as opposed to larger-scale demographic factors (see Appendix: supplemental analysis). For this analysis, we created four simulated data sets. First, we simulated a random distribution of gardens by re-assigning every address in the data to a random yard type pulled from the observed data, without replacement. This essentially reshuffled the 1,940 observed gardens to be in new, random addresses. Note that we refer to this as the "Random" simulation, because the locations of the gardens are randomly reassigned to new addresses; the spatial distribution of these gardens is not completely random on the landscape because houses are only located in some areas and not others (e.g. houses do not occur in parks, or wetlands, or industrial zones). However, this random simulation is the appropriate reference model for our purposes (cf. Hobson et al. 2021). The other simulations we created repeated this same process except with reshuffling the locations of the gardens constrained within each city, within each census tract, or within each census block group. We compared 83.4% confidence intervals to assess statistical significance differences between simulations/observed data, because when these intervals do not overlap, the groups differ at the 95% confidence level (Payton et al. 2003).

We quantified clustering across scales using the Clark-Evans index (Clark and Evans 1954), R, which ranges from 0 to ~2.1 and is a measure of clustering in which a value of 1 indicates a random distribution of points. A perfectly clustered population (i.e. all points have the same location) would have R = 0, while a maximally dispersed population would have R = ~2.1. The lower the R value, the more clustered the distribution, and values significantly less than 1 indicate significant clustering compared to a random distribution. A value significantly greater than 1 indicates significant ordering (dispersion). To account for bias due to the edges of the observation window we used the 'guard' correction in the R function 'clarkevans' in the spatstat package (Baddeley et al. 2015).

We also calculated two distance-related metrics. First, we calculated the average distance between gardens in each of the simulated cases and in our observed data. Here, the average distance between gardens in the random simulation would simply reflect the average distance between scored addresses in the dataset and we expect contagion to lead to significant clustering and thus decreases in the average distance. Second, we calculated the percent of flower gardens that were nearby to other gardens in each scenario. The definition of "nearby" is necessarily somewhat arbitrary; we picked 50m for both ecological and social reasons. Ecologically, we were interested in how contagion might be changing the connectivity of urban gardens from the perspective of insect pollinators, which commonly visit and move between gardens yet have a relatively limited typical foraging distance (e.g. Zurbuchen et al. 2010). Socially, we expected the strength of contagion to be strongest between very nearby neighbors; this was supported by past work suggesting that while contagion was sometimes detectable out to distances of 500 or more meters, it was strongest in one study within 91m (Hunter and Brown 2012) and in another within 4 neighbors, a broadly similar distance (Zmyslony and Gagnon 1998).

Software

We performed all spatial and statistical analyses using R (v4.1.2)(R Core Team 2021). For graphing, we used the ggplot package (v3.4.1) with the patchwork (v1.1.1)(Pedersen 2022) and cowplot (v1.1.1)(Wilke 2020) packages for layouts. We used the sf (v1.0.14)(Pebesma and

Bivand 2023) and ggspatial (v1.1.9)(Dunnington 2023) packages for mapping. We used sf for spatial data handling, nngeo for calculating nearest neighbors (v0.4.7), and spatstat (v3.0.8) (Baddeley et al. 2015) for calculating Clark Evans index and distance metrics. We used the tidyverse package (v1.3.1)(Wickham et al. 2019) for data handling, and the cut_number function in dplyr for binning. We used the lme4 package (v1.1.34)(Bates et al. 2015) to construct binomial generalized linear mixed models. We compiled census and GIS data from the U.S. Census Bureau (U.S. Census Bureau, 2019) and MassGIS (Bureau of Geographic Information (MassGIS), Commonwealth of Massachusetts, Executive Office of Technology and Security Services). We used the tidycensus package (v1.1.2)(Walker and Herman 2022) for downloading Census geospatial files. We used MassGIS tax assessors' data to obtain lot size information and property valuations.

Results

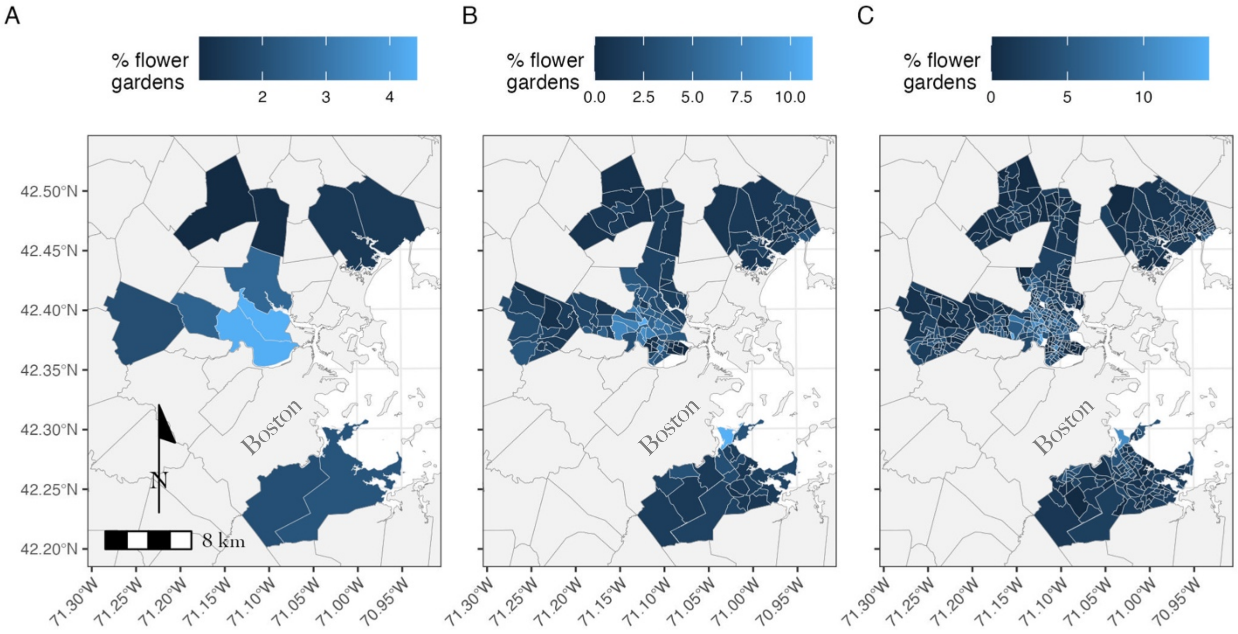


Fig. 1: Maps of the frequency of flower gardens as a % of all surveyed front yards, summarized at the (a) city level (n = 11), (b) census tract level (n = 145), and (c) census block group level (n = 505).

We scored 86,256 front yards using Google Street View. Of these, 1,940 (2.2%) were scored as flower gardens. These flower gardens were located across the 11 study cities, in 145 census tracts and 505 census block groups (mean scored addresses per city = 7841.5, mean scored addresses per tract = 594.6, mean scored addresses per block group = 170.7). Frequency of flower gardening ranged from 1.0–4.4% (mean = 2.3%) at the city level, 0–11.1% (mean = 2.6%) at the census tract level, and 0–14.3% (mean = 2.6%) at the census block group level (Fig. 1).

The neighborhoods surrounding flower gardens had higher rates of flower gardening than neighborhoods surrounding non-gardens, after accounting for background variation in gardening frequency (binomial GLMM, $\chi^2 = 49.1$, df = 1, $p < 0.0001$, Fig. 2). Houses whose nearest scored neighbor had a flower garden had an estimated flower gardening frequency of 6.1% compared to an estimated frequency of 2.1% among nearest neighbors of random non-gardens (binomial GLMM, Table 1, Fig. 2). This difference declined with distance from the gardening neighbor, with houses 5 neighbors away from a garden having an estimated gardening frequency of 4.2% compared to 2.0% for random non-gardens (Table 1). However, flower gardening frequency remained significantly elevated up to 15 neighbors away from a flower garden (Table 1, Fig. 2), after which the effect size became non-significant and continued declining towards 0.

In our exploratory analysis of one possible mediator of contagion, lot sizes, we did not observe consistent impacts of lot size on contagion (Fig. S2). The range of lot size values represented by our binning procedure was: bin 1 = 121–366 m^2, bin 2 = 366–457m^2, bin 3 = 457–552 m^2, bin 4 = 552–713 m^2, and bin 5 = 714–4172 m^2. The intercept of the contagion curve (i.e. the theoretical peak amount of contagion, nearest to the focal house) was highest in the largest yards (bin 5: intercept = 0.082 [95% conf. int. = 0.06–0.11]), followed by the smallest yards (bin 1: intercept = 0.061 [95% conf. int. = 0.49–0.075]), followed by the yards in bins 4, 2, and 3. (intercepts = 0.049 [95% conf. int. = 0.043–0.56], 0.034 [95% conf. int. = 0.025–0.048], and 0.033 [95% conf. int. = 0.026–0.042] respectively). The rate of decline in contagion strength with N neighbors away was significantly steeper in the largest lot neighborhoods (bin 5: slope = -1.12 [95% conf. int = -1.22 – -1.02]) compared to the other four bins (for bins 1–4, slopes = -0.648 [95% conf. int. = -0.73 – -0.57], -0.609 [95% conf. int. = -0.73 – -0.48], -0.555 [95% conf. int. = -0.64 – -0.47], and -0.546 [95% conf. int. = -0.60 – -0.50], respectively).

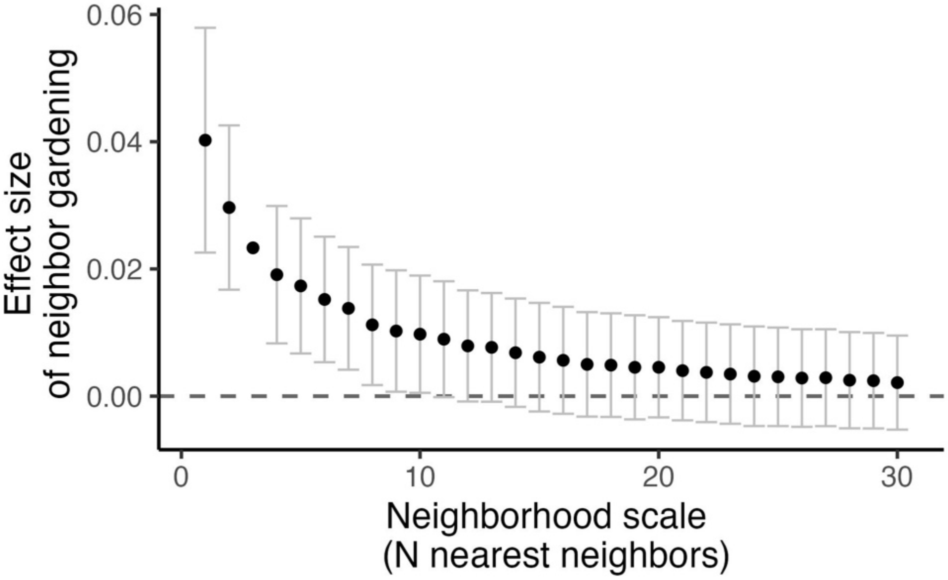


Fig. 2: The effect of a neighbor gardening on the prevalence of flower gardening, as a function of how far away the neighbor is. Effect size is calculated using a binomial GLM estimating the probability of being a flower garden with a fixed effect of the neighbor being either a garden or a random non-garden. Positive values for effect size indicate elevated prevalence of gardens within the set of N neighbors away from a flower garden. Error bars show 95% confidence intervals, calculated using the delta method. Confidence intervals could not be estimated for one neighborhood size (N = 3) because of model convergence failure.

Table 1: Summaries of the binomial mixed model outputs used for making Fig. 2, here showing the estimates for scales N = 1, 2, 5, 15, and 30. The effect size is calculated as the difference in garden frequency between neighborhoods of size N centered around either a flower garden vs. centered around a random non-flower garden. The odds ratio gives the 'relative risk' increase in gardening rates when the neighborhood of size N is centered on a garden and is given by the ratio of $R_{garden}/R_{non\text{-}garden}$ where R is the frequencies of flower gardens in each case; a ratio of 1 would indicate no contagion, a ratio of 2 would indicate a doubling in garden prevalence, etc.

	Flower garden frequency			
N Neighbors	**Around a Garden**	**Around a Non-garden**	**Effect size of neighbor gardening** [95% conf. int.]	**Odds ratio** (gardens *x* times more frequent)
1	6.10%	2.07%	4.0% [2.3–5.8%]	2.9
2	4.96%	2.00%	3.0% [1.7–4.3%]	2.5
5	3.53%	1.79%	1.7% [0.7–2.8%]	2
15	2.43%	1.82%	0.6% [-0.2–1.5%]	1.3
30	2.00%	1.79%	0.2% [-0.5–1.0%]	1.1

For randomized data sets at all neighborhood scales (city, census tract and census block group), the Clark-Evans aggregation index (R) was higher (i.e. less clustered) than for the observed flower garden distribution (Fig. 3). The random garden distribution (mean R = 0.71 [95% conf. int. = 0.69–0.73]) was not significantly different from the random by cities distribution (mean R = 0.68 [95% conf. int = 0.66–0.71]). The random by census tract and census block group simulations were both significantly more clustered than the random simulation (by census tract, mean R = 0.67 [95% conf. int. = 0.65–0.69]; by block group, mean R = 0.66 [95% conf. int. = 0.64–0.68]) and did not significantly differ from each other. The observed garden distribution was more clustered than all scales of simulated random distribution (R = 0.61).

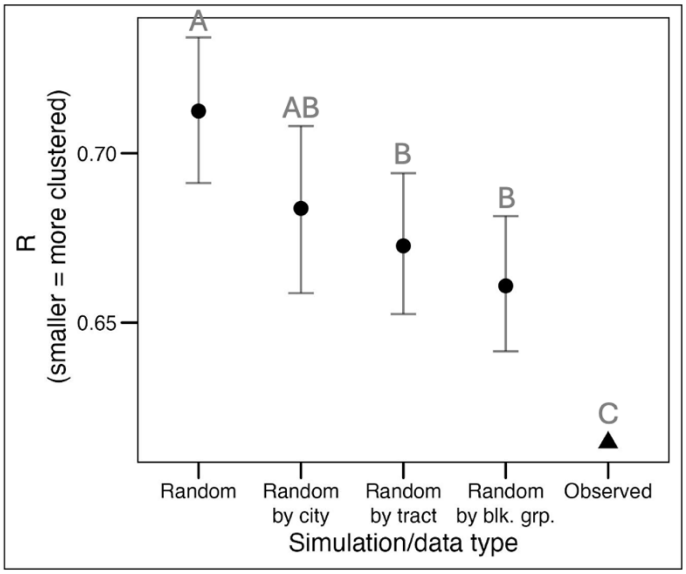


Fig. 3: Clark-Evans aggregation index (R) for flower garden spatial distributions for each of the simulated data sets compared to the observed distribution. For random simulations, the gardens were reshuffled among all addresses; for random by city, gardens within each city were reshuffled; etc. The R value for the observed locations of flower gardens is shown as a triangle and the simulated scenarios are shown as filled circles with 95% confidence intervals from 100 runs of the simulation. The grey letters indicate significant differences between simulations/data.

For the average distance to the nearest flower garden (Fig. 4a), gardens were farthest apart in the random simulations (mean distance = 138m [95% conf. int. = 133–142m]), followed by random by city, which did not significantly differ from the random simulations (mean distance = 132m [95% conf. int. = 127–137m]). Random by tract and by census block group produced gardens that were significantly closer together than random simulations, but not these did not differ significantly from random by city (for random by tract, mean distance = 130m [95% conf. int. = 126–134m]; for random by block group, mean distance = 128m [95% conf. int. = 124–132m]). The observed mean distance to nearest garden was significantly closer than all the simulated cases, with mean distance = 119m [95% conf. int. = 113–124m].

For the percent of gardens near to another garden (within 50 m by our definition)(Fig. 4b), the random simulation produced significantly fewer compared to the other cases (random simulations, % nearby other gardens = 14.3% [95% conf. int. = 11.8%–16.8%]). All of the next three smaller clustering scale simulations yielded significantly higher frequencies of nearby gardens, though they did not significantly differ from each other (random by city % nearby other gardens = 19.1% [95% conf. int. = 17.4–20.9%]; census tract % = 20.9% [95% conf. int. = 19.2–

23.2%]; block group % = 21.8% [95% conf. int. = 19.7–23.6%]). The observed frequency of gardens being nearby other gardens was significantly higher than all four simulated cases (observed % nearby other gardens = 30.7% [95% conf. int. = 28.7–32.8%]).

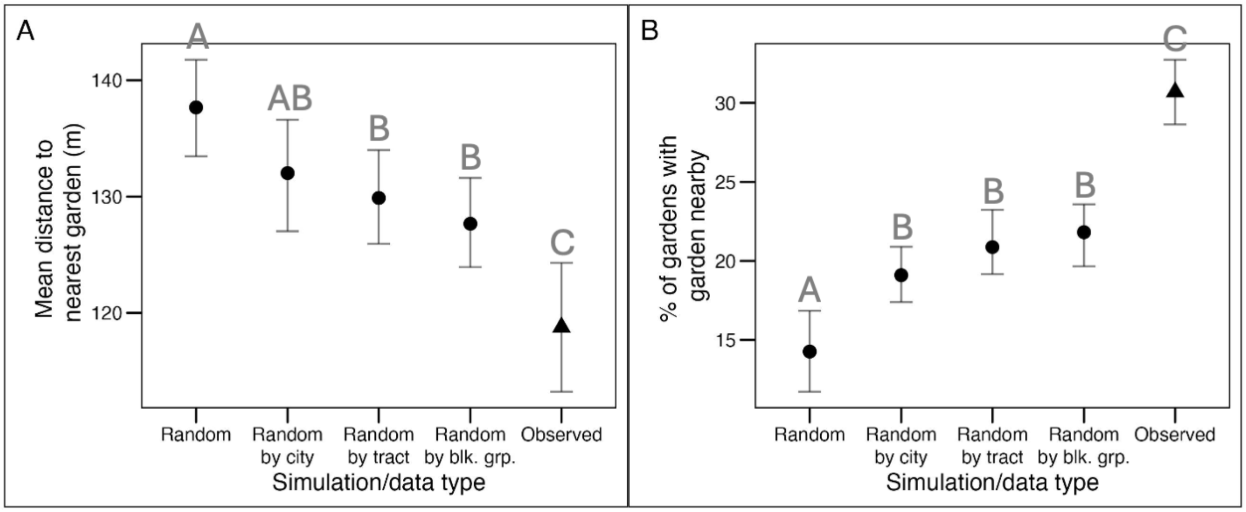


Fig. 4: (a) The average distance to the nearest garden (meters) across the simulations and the observed flower garden distributions. The distance is calculated as the crow flies, to the nearest known neighboring flower garden. *(b)* The percent of all flower gardens that are within 50 meters of another flower garden ("nearby" another flower garden). For both (a) and (b), in the random simulations, the gardens were reshuffled amongst all addresses; for random by city, gardens within each city were reshuffled; etc. For both (a) and (b), the values for the observed locations of flower gardens is shown as a triangle and for the simulated scenarios are shown as filled circles, each with 95% confidence intervals. The grey letters indicate significant differences between simulations/data.

Discussion

We provide evidence for social contagion of urban flower gardening by identifying strong, highly localized increases in the presence of flower gardens in yards that are nearby other flower gardens. Crucially, this effect is present after accounting for background variation in the frequency of flower gardening across neighborhoods. Demographics could conceivably be confounding because they also play a role in flower gardening and other yard landscaping choices, e.g. household income and education levels are related to yard plant biodiversity (Minor et al. 2023). The steep decline of the contagion effect (Fig. 2) and the small, 15-house size of the area of influence both provide good evidence for this process being driven by contagion. As noted by (Hunter and Brown 2012), clusters that are this small in size are unlikely to be strongly driven by demographic factors (see also Appendix: supplemental analysis). Regardless of the specific mechanisms underlying this process of contagion, the self-organizing and fine-grained clustered pattern it produces has important ecological implications, through increasing the rate of urban pollinator habitat creation and passively improving habitat connectivity, thereby combating both the multiple stakeholder and coordination problems in urban conservation.

Our finding of contagion in flower gardening is consistent with several lines of evidence suggesting that yard landscaping practices are frequently observed and discussed by neighbors. Interactions with friends and neighbors can in fact be among the most important drivers of garden decisions (Goddard et al. 2013), and yard management practices have the capacity to spread through neighborhoods through casual conversations between neighbors (Martini et al. 2014). Several previous studies have also identified patterns of clustering in yard landscaping elements at a similar scale to ours: Zmyslony and Gagnon (1998) found that along the same side of a street, vegetation elements were more similar between nearest neighbors (and up to 4 neighbors away) and Hunter and Brown (2012) reported that road verge gardening was most clustered within 91 m of existing road verge gardens. In contrast, some other, similar studies have not found evidence of contagion in yard landscaping, e.g. in Tasmania there was little evidence of clustering of yard types and in fact there was some evidence of increased dissimilarity between neighbors (Kirkpatrick et al. 2009); similarly, the same Montreal study that found vegetation similarity on the same side of the street (Zmyslony and Gagnon 1998) found that neighbors on opposite sides of the street were actually significantly dissimilar to each other. One possible cause of these varied results is differences in the type of landscaping being measured: for instance, our work and Hunter and Brown's (2012) both focused specifically on gardens with flowering plants on the front side of houses, which are highly visible, relatively rare, and well-liked for aesthetic reasons; these features might contribute to particularly strong contagion, compared to contagion in other landscaping features like hedge design, etc. Future work could attempt to untangle which landscaping practices can be contagious and why.

Social contagion of flower gardening suggests that this practice has the capacity to passively spread through neighborhoods, even in the absence of explicit interventions by conservationists. Being socially contagious helps overcome both the multiple stakeholder and coordination problems facing urban conservation, i.e. the issues stemming from the fact that individual urban land holdings tend to be very small in size relative to the area requirements for sustaining entire populations and communities of organisms. This has repeatedly been pointed to as a barrier to the conservation efficacy of these measures (Goddard et al. 2010, Aronson et al. 2017). Previous authors have even suggested deliberately encouraging contagion as one possible route to overcoming these barriers, via increasing recruitment of new landholders (Goddard et al. 2013, Locke et al. 2022, Minor et al. 2023). The possible utility of contagion for conservation also points to a variety of future directions for research, for instance, exploring what factors may influence the rate of contagion, either at the parcel level or the neighborhood level, or even strategies for how to most effectively "seed" neighborhoods with gardens in order to create maximum contagion (Hunter and Brown 2012).

In an effort to begin addressing these questions, we tested for whether contagion was stronger in small lot size neighborhoods, with the reasoning that increased rates of visual/social contact with neighbors as a result of denser housing would make contagion stronger. However, we found no such trend, and instead observed contagion across all lot size bins, with the largest lot size neighborhoods in fact having the highest peak contagion strength (Fig. S2). Locke et al. (2022), similarly to us, expected stronger autocorrelation in tree canopy for smaller lot neighborhoods and similarly found the reverse pattern, in which larger lot block groups actually had stronger autocorrelation in yard tree canopy. It is possible that while fewer neighbors are visible for owners of large lots, there are other countervailing factors in play for large lot neighborhoods that could favor contagion. For instance, attitudes about landscaping norms might vary across neighborhood types in ways that encourage adoption of new landscaping like gardens, e.g. Visscher et al. (2014) found that exurban residents on larger lots tended to have proportionally less lawn and reported less concern over neighborhood norms compared to smaller lot residents (note, however, that these lots were exurban and were generally much larger than those in our study). The role of personal conceptions of the neighborhood, how this varies across residential contexts, and the resulting differences in social interactions are also key areas for future contagion research.

Beyond altering the rate of creation of flower gardens, contagion has impacts on the spatial arrangement of habitat on the urban landscape. Specifically, we observed an increase in structural connectivity, as our simulations indicated that flower gardens are ~10% (13 meters) closer together on average compared to a random distribution, and ~7% (9 meters) closer together compared to a random distribution within block groups. However, it remains an open question how biologically relevant this effect is, i.e. whether functional connectivity is also greater because of this level of spatial clustering. This gap in our understanding of functional connectivity in urban settings is a previously-reported limitation (LaPoint et al. 2015).

There are, however, some reasons to predict that pollinators could be affected by changes in structural connectivity of this magnitude. For instance, common urban pollinators like solitary bees have generally small maximum foraging ranges on the order of 100–200m (Zurbuchen et al. 2010), though they are capable of rarer long distance movements. As a result, while the average distance between gardens changed by only ≤10%, we estimated a doubling in the proportion of gardens that are nearby other gardens compared to a random arrangement, where we defined "nearby" as 50m. This definition was arbitrary, but was intended to capture how a typical bee foraging trip would be affected by contagion-driven structuring of flower garden habitat. A useful line of future work would be to explicitly measure functional (rather than structural) connectivity, through direct studies of movement or genetics in pollinators (LaPoint et al. 2015), to understand whether contagion has meaningful effects on flower visitors to urban gardens.

However, the social dynamics that lead to contagion are not necessarily always a boon for conservation. Pressures from neighbors also can operate to reduce the likelihood that an individual landholder will start a garden when on a street where there are not currently flower gardens. In this way, florally depauperate neighborhoods, which are of lower habitat quality for pollinators, may experience pressure to continue staying florally depauperate (Goddard et al. 2013). This process of pressure from neighbors to conform to the status quo is relatively well documented (e.g. Nassauer et al. 2009), and in a sense reflects a converse outcome from the same drivers as contagion of flower gardening; in other words, mimicry between neighbors of *non*-wildlife-friendly practices can also occur, via pressures to maintain landscaping like turfgrass monocultures (cf. the ecology of prestige concept, Grove et al. 2014). Contagion, as a result, may be initially slow to act, as the pioneer gardens that are first in their neighborhood lack the 'support' of neighbors. An interesting area of future research would be attempting to understand what factors characterize individuals who are early adopters of novel landscaping practices, as these are the seeds around which garden clusters can form.

Conclusion

Social contagion is a passive, bottom-up process that appears to make flower gardening a more effective conservation measure. Similar phenomena are likely to occur in other environmentally-friendly behaviors in cities. In recent years, conservationists increasingly recognize the important role of human behavior and decision-making in determining the success of conservation efforts (Schultz 2011, Bennett et al. 2017a). This is probably even more important for conservation activities on urban residential lands, where many individuals must take action to have a significant collective effect. Social contagion theory offers a promising way forward for understanding the interplay between social networks, landowner decision-making, and the ecological patterns produced as a result. In addition to the implications for the two key urban conservation challenges discussed here — landholder recruitment and coordination — contagious conservation measures also offer unique opportunities to research how self-advertising, self-organizing practices can be encouraged and guided for maximum societal and ecological benefit. While previous work discussing urban conservation in residential yards has sometimes discussed the potential for bottom-up factors like contagion to lead to self-organization, the practical focus has generally remained on top-down levers for marketing and coordinating conservation practices, perhaps because the next steps in those approaches are better-understood. However, recent work on encouraging clean energy transitions has begun probing not only the theory but the practice of using contagion for environmental causes (Boele et al. 2023). In the future, these kinds of interdisciplinary perspectives will be key for understanding and maximizing the spread of new, environmentally-friendly behaviors in cities.

Chapter 4 - Resource availability affects host use by two specialist herbivores in an urban landscape

Abstract

Pollinator gardens and other urban conservation practices on residential lands aim to create small patches of connected, nearby habitats to support urban-dwelling animals. Pollinator gardens are created more often in some neighborhoods than others, leading to patchiness in resource availability. Additionally, the urban landscape contains patchy sources of weeds outside of gardens. Urban insects thus are confronted with a heterogeneous resource landscape, which ecological theories predict can lead to variation in per-capita resource use, with insect herbivores using plants in resource-rich areas either more or less heavily. We tested these predictions in two milkweed-hosted insects, the monarch butterfly (*Danaus plexippus*) and the milkweed aphid (*A. nerii*), with pots of milkweed in urban parks embedded in neighborhoods that varied in milkweed and garden presence (measured via indexes). We found that aphid colony establishment occurred faster in neighborhoods with higher milkweed indexes and that monarch butterfly oviposition rates were higher in neighborhoods with higher flower garden indexes and lower milkweed indexes, both partially consistent with theory. These patterns suggest that urban insects may alter rates of habitat use in response to host and garden availability, and also suggest possible ecological consequences of collective yard landscaping decisions made by people.

Introduction

Urban areas are increasingly being targeted for conservation with the addition of pollinator gardens and other flower patches, which provide food for a diverse set of insects in the form of nectar, pollen, and host plants (Hall et al. 2017, Majewska and Altizer 2020). These gardens do not exist in isolation; instead, habitat quality for urban animals is determined by resource abundance across multiple nearby yards or gardens, because individual urban patches are generally too small to support populations on their own (Belaire et al. 2014). As a result, habitat quality for urban pollinators can be better described by resource densities across areas of dozens of yards, e.g., the number of flower gardens in a neighborhood. Although the presence of diverse insect communities within these urban flower gardens is well established (e.g. Quistberg et al. 2016, Wenzel et al. 2020), much remains unknown about how insects in gardens use these habitats, including basic relationships between habitat use and availability. Flower garden frequency and plant diversity vary across urban neighborhoods (Hunter and Brown 2012, Minor et al. 2023, Murphy & Crone in review), which creates variation in the density of resources for insect pollinators and herbivores. In natural settings, many studies have found that rates of habitat use vary with resource density, meaning that areas with high resource densities receive significantly more or less use by animals (e.g. area-restricted search, Dorfman et al. 2022). The analogous, unanswered question for urban gardens is: how does insect habitat use respond to the neighborhood availability of hosts and flower gardens?

There are two relevant and contrasting bodies of theory relating herbivore densities to plant densities, which predict either increasing or decreasing rates of per-capita plant use with increasing plant density. First, the resource concentration hypothesis (Root 1973) predicts (among other things) that areas with denser resources will contain higher per-plant herbivore densities (herbivore loads) because these patches are more rapidly colonized and reproduced on. Empirical evidence for resource concentration has mostly come from outbreaking agricultural pests, e.g. nymphs of tarnished plant bugs (Rhainds and English-Loeb 2003) and larvae of diamondback moths (Merwin et al. 2020). In contrast, the resource dilution hypothesis (sometimes called the resource diffusion hypothesis) predicts that herbivore densities are instead negatively related to plant densities (Yamamura 1999, Otway et al. 2005) because even as patches with more plants support a greater absolute number of herbivores, the plant density eventually increases beyond the capacity of consumers to increase rates of consumption/reproduction; in other words, consumers become satiated and herbivore loads per-plant are diluted. Field evidence for dilution is much more widespread than for concentration, and a wide variety of insects exhibit negative relationships between plant and consumer densities, including pollinators visiting flowers (Heinrich 1979, Schmid et al. 2016, Wenninger et al. 2016) and various butterflies on their larval host plants (Root and Kareiva 1984, Yamamura 1999, Hasenbank and Hartley 2015). In this study, we evaluated these contrasting predictions by comparing host plant use by monarch butterflies and milkweed aphids across a gradient of urban neighborhoods that varied in the availability of flower gardens and background milkweed hosts.

Butterflies are among the taxa attracting the most attention from urban conservationists, thanks to their broad appeal with the public and frequent occurrence in gardens, where they lay eggs on host plants and consume nectar. The monarch butterfly has received particular attention in North America; spurred by widely reported steep population declines (Brower et al. 2012, Thogmartin 2024), various groups (e.g. Thogmartin et al. 2017, Derby Lewis et al. 2019, Johnston et al. 2019) have advocated for the planting of urban flower gardens that include nectar and milkweed (genus *Asclepias*), the latter of which are monarchs' sole native host plants. While monarchs remain relatively abundant in many urban areas, their patterns of habitat use in gardens are not well understood. In addition, because monarchs and other butterflies require both larval hosts and adult nectar plants (which fuel flight and reproduction), predicting patterns of habitat use is more complex; in general, these two resource requirements can moderate each other or conflict when nectar and hosts do not overlap (Murphy 1983, Janz 2005).

First, with respect to host plant density, monarchs (and other butterflies) are thought to exhibit resource dilution, such that there are lower per-plant larval loads on denser patches of milkweed hosts. For instance, in observational studies, isolated stems of milkweed typically receive more eggs per stem (Zalucki and Suzuki 1987, Pitman et al. 2018). Additionally, juvenile monarch survival may be higher on isolated host stems (Zalucki and Kitching 1982), which would favor dilution rather than concentration. This pattern of host use is also consistent with field observations of monarch butterfly movement, which reveal both an aptitude for locating isolated, low-density hosts (Zalucki et al. 2016, Fisher and Bradbury 2021) and a tendency towards flying over many suitable hosts in between oviposition events (Borkin 1982). In contrast, with respect to nectar plant density, butterflies generally slow their movement and take tighter turns to stay near patches of nectar plant, leading to higher adult densities near areas with more nectar plants (Root and Kareiva 1984, Murphy et al. 1984), which could be partially consistent with resource concentration in relation to nectar plants. For monarchs in particular, field observations suggest that females spend substantially more time nectaring than ovipositing (James 2016) and have higher oviposition rates in landscapes with both high nectar diversity and moderate host density (Kral-O'Brien et al. 2020). In an experimental garden, adult monarch density was also positively linked to floral abundance (Majewska et al. 2018), consistent with the idea that adults spend more time near denser nectar resources.

The milkweed/oleander aphid (*Aphis nerii*) is another common resident of flower gardens that feeds on milkweed, and is not of conservation concern but is instead a pest species. *A. nerii,* though also a milkweed specialist, exhibits a contrasting life history with monarchs, involving a largely passive, wind-driven dispersal stage, contact-based host location, and subsequent clonal reproduction (Kring 1972, Harrison and Mondor 2011). In both theory and data, host finding traits have been found to be important determinants of host-herbivore relationships; thanks to their relatively constrained patch finding abilities, aphid immigration rates into a patch are predicted to be more strongly related to patch area when compared to more active searchers like butterflies (Andersson et al. 2013). However, in relation to host plant density, even these prototypical pests generally exhibit dilution in field studies, with aphids being spread out over more hosts in higher density patches (Yamamura 1999, Andersson et al. 2013). Neighborhoods with higher milkweed densities have greater habitat area, perhaps supporting higher aphid densities, and thus potentially higher rates of colony establishment on new milkweed stems. This would reflect agreement with one prediction of theories of insect-plant density, in a way that might contrast with butterflies, who may immigrate to isolated patches more readily.

In order to understand how rates of host use vary with urban neighborhood context, we placed identical containers of milkweed in 20 public parks and monitored the milkweed in these containers for monarch butterfly eggs and for milkweed aphid (*A. nerii*) colony establishment. We created an index of milkweed and garden availability across neighborhoods using ground surveys for milkweed in yards and Google Street View-derived estimates of flower garden frequency. For monarchs, we tested whether per-stem oviposition rates were related to the interaction of local milkweed index × flower garden index, where milkweed index is a proxy for host density and flower garden index is a proxy for nectar density. We predicted that there would be a dilution effect for host plants, in which our potted stems would receive fewer eggs per stem in neighborhoods with a higher background host index. We predicted that per-stem monarch oviposition rates could be higher in high flower-garden neighborhoods if gardens are attractive because they are nectar-rich; conversely, oviposition could be lower if adult monarchs spend more time nectaring in these neighborhoods and consequently less time ovipositing. For the aphids, we predicted that aphid colony establishment would occur faster in neighborhoods with a higher milkweed index, consistent with predictions about contact-searcher immigration from insect-plant density theory. Flower gardens were not included in modeling aphid host use because unlike the monarchs, we did not have clear expectations about flower gardens being associated with aphid presence.

Materials & Methods

Study species

Monarch butterflies are large, charismatic butterflies native to North America. They are known for their long annual migration cycle (Brower et al. 2012, Gustafsson et al. 2015). Monarchs are larval specialists on milkweed plants of the genus *Asclepias*, of which in our region (Massachusetts) common milkweed (*Asclepias syriaca*) is the most abundant wild species, while two additional species are common and are also cultivated (*Asclepias tuberosa* [butterfly weed] and *Asclepias incarnata* [swamp milkweed]). As adults, monarchs are generalist visitors of a variety of plants for nectar, from which they obtain sugar to power flight and reproduction (Brower et al. 2006). They are strong fliers, and during breeding generations they are thought to travel on the order of 10 km over the course of a 2–3 week adult lifespan (Zalucki 1983), laying 300–400 eggs singly on milkweed (Oberhauser 2004). Though the population in Eastern North America has substantially declined in recent decades (Brower et al. 2012), they are relatively common in urban areas around Boston, MA, U.S.

Milkweed aphids (*A. nerii*) feed on various plants in the Apocyanaceae (dogbane/milkweed family)(Stoetzel 1990). Highly invasive, *A. nerii* seems to reproduce exclusively parthenogenetically — males have never been reported in the field — and as a result has extremely low genetic diversity, with much of the United States apparently populated with a few "superclones" per year (Harrison and Mondor 2011). As *A. nerii* cannot overwinter in our study region, it recolonizes every year in spring/early summer with small population sizes and rapidly grows in abundance and range during the summer months (Harrison and Mondor 2011). Dispersal is poorly understood, but *A. nerii* colonies periodically produce winged migratory morphs during times of crowding or reduced host quality (Groeters and Dingle 1989) and long-distance movements appear possible, if rare (Loxdale et al. 1993).

Site selection & potted milkweed set up

We placed pots of milkweed in 20 urban parks in Somerville and Medford, MA, near Boston. These cities are relatively dense but have various small public parks distributed throughout the primarily residential landscape. These parks were useful for our purposes because with cooperation from the municipal governments we were able to choose from a large menu of possible neighborhoods with varying host and nectar plant backgrounds. We intentionally selected a set of parks that were in neighborhoods with varying levels of gardening, and after preliminary surveys, found that they also varied substantially in milkweed presence in front yards.

For the pots of milkweed, at each site we placed a single 30-gallon fabric containers (Grassroots Living Soil Fabric Pot, Sacramento, CA, USA). In each container we initially planted four 1-gallon butterfly weed (*Asclepias tuberosa*; Stonepost Nursery, Raymond, NH, USA) and four 2-gallon swamp milkweed (*Asclepias incarnata*; Van Berkum Nursery, Deerfield, NH, USA). We used Miracle-Gro Potting Mix (Miracle-Gro Lawn Products Inc, Marysville, Ohio, USA) to fill the fabric containers. We watered the pots with large plastic jugs whenever the top few cm of soil became dry.

Although we planted both *A. tuberosa* and *A. incarnata*, only *A. incarnata* grew substantially and we observed high mortality of *A. tuberosa* across sites, probably due to soil moisture conditions or other factors in the pots that were unsuitable for its growth. In any case, *A. incarnata* received 98% of monarch eggs. As a result, we discarded all monarch egg/larva observations on *A. tuberosa* and all subsequent monarch analysis was only on eggs laid on *A. incarnata*. *A. nerii* did colonize and use *A. tuberosa,* in spite of its poor performance, so both host species were included in the aphid analysis. *A. incarnata* performed well in all pots, growing to >1 m in height over the course of the study, from an initial height of ~30 cm.

Resource context indexes

In order to measure the resource contexts around each site, we created indexes of host and flower garden availability. For the milkweed index, we surveyed the surrounding neighborhoods within a radius of 125m of the pot, a distance chosen to balance time constraints with coverage and also in light of published estimates of monarch perceptual range for host plant of around 125m (Fisher and Bradbury 2021). Given that we were working in a dense urban setting and obtaining cooperation from hundreds of landowners was impractical, we were only able to survey areas visible from the public right of way, including front yards, road verges, and within the parks themselves. We searched all visible space of all lots that intersected the 125m buffer. We performed these milkweed surveys twice, once in June and once in July. Since the majority of eggs were laid in July-August (Fig. S2) we used the milkweed counts for July only in our analysis of monarch oviposition.

For the garden index, we quantified the frequency of flower gardens in front yards using a data set we created during a separate project (Murphy & Crone, in review). Briefly, these data consist of manually scored Google Street View imagery for cities in the Greater Boston Area (including our focal cities of Somerville and Medford). We used this street-level imagery of front yards to score residential addresses as being gardens or other yard types. The garden category included all diverse herbaceous plantings, including vegetable gardens, pollinator gardens, and other flowering plantings. Each yard was assigned a single score based on the presence of a flower garden (≥25% of front yard in imagery) or, if no garden was present, the plurality of whatever landscaping type was present. As part of that project we also visited a stratified random subset of the addresses scored via Street View and found that the garden-scored addresses had substantially elevated floral diversity, so we concluded that this data set effectively captured the presence or absence of gardens in front yards at scale and that garden presence was linked to elevated nectar availability, making it a suitable proxy for garden and nectar density for the present study. We defined neighborhood gardening frequency as the percent of front yards that had flower gardens within a given buffer distance, following the same rule of counting all lots that intersected the buffer. The maximum possible neighborhood size for these data is the municipal boundaries of Medford and Somerville, though in practice we only explored neighborhood sizes of 1–500m to avoid excessive overlap between park neighborhoods.

Fig. 1a-d: (a) Pot of milkweed on day of first planting, with informational sign. (b) Female monarch visiting one of our study pots. (c) A monarch egg in one of the pots. (d) A monarch caterpillar and aphids (*A. nerii*) feeding on swamp milkweed in one of the study pots. Photos: Atticus Murphy & Karen Dooley.

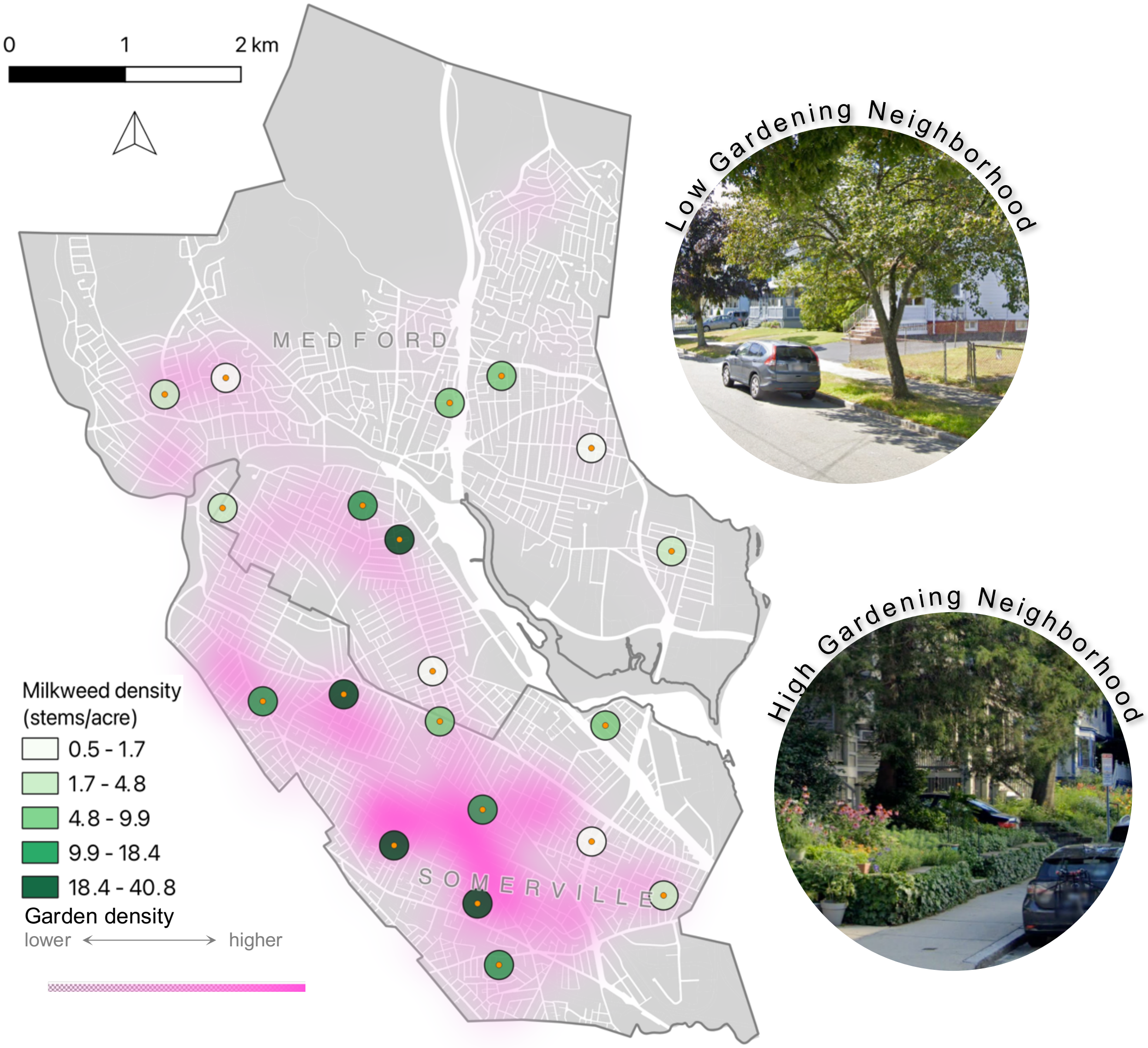


Fig. 2: Map of the 20 study sites at which we placed pots of milkweed. Each site is marked with an orange dot and is a municipal park, ten in Somerville, MA and ten in Medford, MA. The shade of green in the 125m radius circle around each site indicates the neighborhood milkweed density (stems/acre) in the 125m radius survey area around each park. Pink color intensity indicates front yard flower garden density as a heatmap derived from our Google Street View data set (interpolated using kernel density estimation in QGIS with radius = 13mm). Milkweed density colors were set using 'Equal Count' breaks in QGIS. Map data sources: MassGIS, Google Street View.

Aphid and monarch surveys

We surveyed each pot every 3 or 4 days throughout the survey period June 23–August 19. This survey period was timed to capture the beginning of rapid monarch population growth in our region in mid or late June, and to continue until southward migration was about to begin; it also roughly coincides with the peak of milkweed aphid abundance in our area (pers. obs.). Survey schedules were rotated so that each site received the same number of total surveys and the same number of 3-day and 4-day gaps between surveys. Each pot was surveyed by a team of three, and the plants were haphazardly divided between surveyors.

During each survey, we also recorded the number of aphids (*A. nerii*) present on milkweed in our pots. We recorded to the nearest 5 for ≤50, the nearest 10 for ≤100, and the nearest 100 for colonies >100. We defined aphid colony establishment as occurring on the day that ≥50 individuals of *A. nerii* were observed at a site. We chose to analyze time to colony establishment rather than date of first sighting both in order to account for observer error at small colony sizes (i.e. observers were likely to miss single individuals but unlikely to miss larger groups) and because small groups sighted on the plants often vanished after one or two surveys, due to either mortality or emigration. We used time to establishment as opposed to total or average abundance over the season because over the longer term, within-pot dynamics likely dominate in importance over neighborhood context.

We turned over every leaf on each milkweed plant and searched for monarch eggs/larvae, as well as searching both opened and unopened flowers. Monarchs laid eggs on essentially all surfaces of the plant, though the underside of leaves and the interior of flower clusters seemed the most frequent locations. Our every 3 or 4 day survey schedule reflected a balance of minimizing double counting while maximizing survey frequency, as during this gap between surveys, nonviable eggs became clear/dark or disappeared whereas fertilized eggs generally hatch by 4 days (Oberhauser 2004). Thus, we can assume that in general the eggs in our data were each counted once and represent a potentially viable larva.

Neighborhood size selection

With our resource context measurements, we obtained milkweed and garden indexes within 125m and 500m of each site, respectively. We used GIS to explore a variety of scales for each index by drawing a buffer around each pot and calculating the milkweed/garden index for each buffer size. We varied the buffer size from 7–125m for milkweed and 36–500m for gardens, in increments of 1 m (with the lower bound on the buffer size constrained by having enough data to calculate a milkweed/garden index at that scale). In order to select the most appropriate scale for these resource indexes (i.e. to avoid making an arbitrary choice about at what scale resource context effects act), we used likelihood profiling. This involved constructing a GLM with fixed effects of the milkweed/garden index calculated for each scale (models further described below), then calculating the log likelihood of each model and selecting the scale that produces the maximum likelihood for our final model. We also used this approach to select a scale for aphid colony establishment time in response to milkweed index using a Weibull survival regression model (note that the aphid and monarch neighborhood scales were selected independently of each other). When assessing statistical significance of each predictor using likelihood ratio tests on these models, we included one additional degree of freedom in all tests because of the scale parameter implicitly estimated for each model via likelihood profiling.

Modeling approach

In order to test how neighborhood resource indexes related to per-pot monarch oviposition rates we constructed negative binomial GLMs (suitable for the overdispersed egg count data) predicting the total number of eggs each pot received over the whole season as a function of milkweed index × gardening index, where both predictors were centered and scaled at 0. Although we attempted to plant approximately equal numbers of milkweed stems in each pot, there was some variation in stem number across pots, so we included an offset in our models of the average number of stems of *A. incarnata* per pot across the season. This yields predictions for the negative binomial GLM that are on an eggs-per-stem basis.

Some pots also had more flowers or had actively blooming plants for longer than others, which could have caused variation in per-pot attractiveness to monarchs. To account for this, we tested whether the number of survey days that each pot had actively blooming stems of *A. incarnata* had an effect on the number of eggs laid, and found that there was no significant effect (slope = 0.004, $\chi^2 = 0.004$, df = 1, p = 0.9), and that estimates of the other effects were not substantially affected; as a result, we did not include any effect of flower blooms in subsequent models. We assessed significance of the milkweed index and garden index predictors and their interaction using likelihood ratio tests.

For quantifying speed of aphid colony establishment, we used a Weibull-distributed survival regression with a single predictor, neighborhood milkweed index, to model the response of days until colony establishment. The milkweed plants were sprayed with permethrin pesticide while grown in greenhouses by the suppliers, so on the day of planting there were no *A. nerii* present on any of the milkweed plants. Our survey period was 62 days, and in that time, 9 of the 20 sites never achieved ≥50 individuals, so colony establishment was recorded as never occurring and these sites were right-censored. We assessed significance of the neighborhood milkweed index predictor using a likelihood ratio test.

Statistical analysis and software

All statistical analyses were performed in R (v4.3.1)(R Core Team 2021). For data handling we used the tidyverse package (v2.0.0)(Wickham et al. 2019) with the included ggplot package (v3.4.1) as well as the patchwork package (v1.1.1)(Pedersen 2022) for graphing and plot layouts. We made maps with QGIS (v.3.22.14)(QGIS Association, 2022), with data sourced from MassGIS (Bureau of Geographic Information [MassGIS], Commonwealth of Massachusetts, Executive Office of Technology and Security Services). Milkweed counts were geocoded using the Google Geocoding API and we used the public Google Street View API to obtain garden locations. We used the MASS package (v7.3.60)(Venables and Ripley 2002) to fit negative binomial GLMs and the car package (v3.1.2)(Fox and Weisberg 2019) to test for statistical significance of each predictor using likelihood ratio testes. For neighborhood scale selection via likelihood profiling we used the bbmle package (v1.0.25)(Bolker 2022) to calculate maximum likelihoods and for spatial data processing used the sf package (v1.0.14)(Pebesma and Bivand 2023). We analyzed rate of aphid colony establishment using a Weibull-distributed survival regression with the survival package (v3.5.5) because some of our data were right-censored, and assessed significance of the milkweed predictor using a likelihood ratio test.

Results

Monarchs oviposited at all 20 pots in the study. We recorded 858 total eggs over the course of the season (range = 8–147 eggs/pot, mean = 42.9 eggs/pot) as well as 98 observations of larvae across all instars and 2 pupae (Table S1). Egg laying rates increased over the course of the season from June to August (Fig. S2). On a per survey basis, we recorded 0.30 eggs/stem (95% CI = 0.23–0.39). This was comparable to rates of oviposition in previously published reports from natural areas and gardens (Appendix B).

Our 20 study sites ranged in neighborhood milkweed index from 0.5–40.8 stems/acre for the 125m radius survey area around each pot (Fig. 2). For aphids, the maximum likelihood milkweed neighborhood size was 48m. For monarchs, the maximum likelihood neighborhood milkweed scale was 107m and the milkweed index at this scale had a range of 0.5–38.2 stems/acre. For monarchs, the maximum likelihood neighborhood garden scale was 207m, and flower garden index at this scale varied from 0% to 8.7% of front yards. Neighborhood milkweed index and gardening index at these scales were not significantly correlated (Fig. S1, Pearson's r = 0.21, df = 18, p = 0.4).

Monarch egg densities per plant were somewhat lower in neighborhoods with higher milkweed indexes (slope = -0.15 $\chi^2 = 5.06$, df = 2, p = 0.08; Table 1) and did not depend on gardening index, although the sign of the nonsignificant slope was positive (slope = 0.02, $\chi^2 = 1.56$, df = 2, p = 0.45; Table 1). These nonsignificant main effects reflect a significant interaction between neighborhood milkweed index and garden index (slope = -0.40, $\chi^2 = 8.59$, df = 2, p = 0.01)(Table 1, Fig. 3). The negative interaction indicated that at low milkweed indexes, gardening index was positively related to monarch oviposition, but at medium to high milkweed indexes, gardening index was either unrelated or negatively related to oviposition (Fig. 3).

Table 1: Summary of results of a negative binomial GLM predicting total monarch eggs laid as a function of neighborhood milkweed index × gardening index (both predictors scaled and centered at 0), with an offset of mean number of milkweed stems surveyed in the pot. We report likelihood ratio tests assessing statistical significance of each of the coefficients, with df adjusted to 2 because we also selected neighborhood size with likelihood profiling.

Coefficient	**Slope**	**χ^2**	**df**	**p**
Milkweed index	-0.15	5.06	2	0.08
Gardening index	0.02	1.56	2	0.45
Milkweed:gardening	-0.40	8.59	2	**0.01**

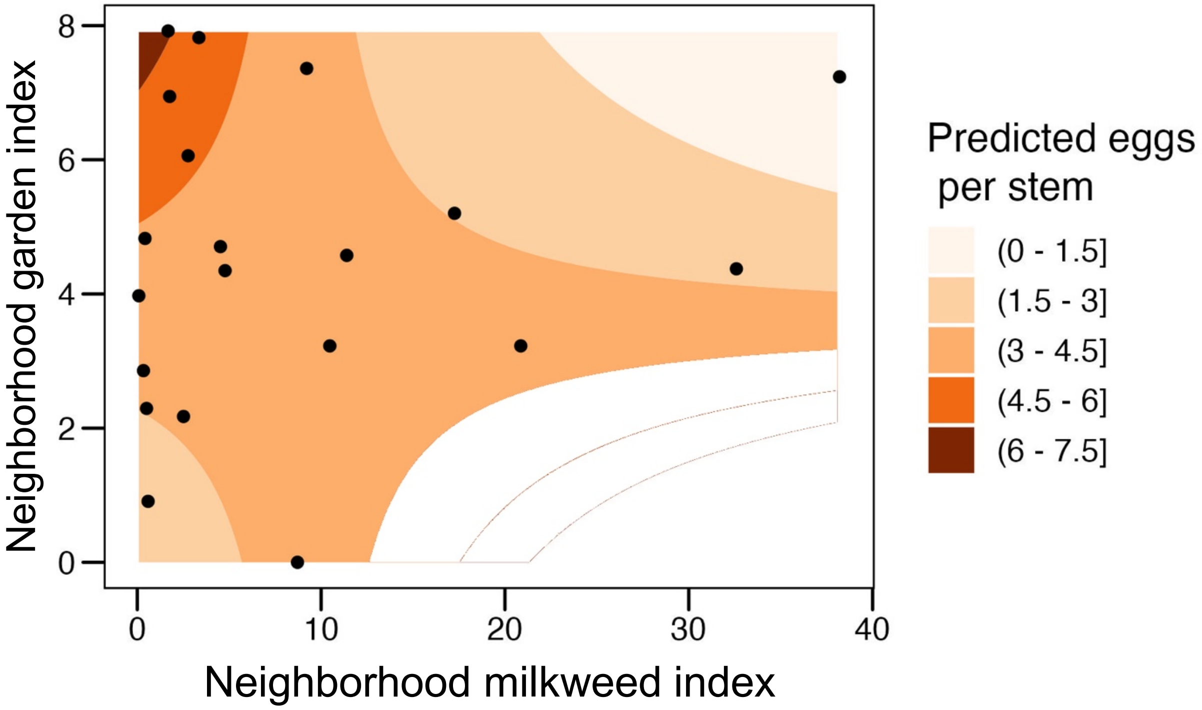


Fig. 3: Predicted monarch eggs per stem in response to neighborhood garden index (% of front yards with flower gardens, within 207m) and neighborhood milkweed index (front yard stems per acre, within 107m). Predictions are from a negative binomial GLM predicting whole season egg counts with an offset of avg. N stems. Darker orange indicates more eggs. Points show observations (N = 20 sites). We do not show all contours because of a lack of observations in some regions. Color breaks were chosen manually. There is a statistically significant negative gardening × milkweed interaction (Table 1).

Individual aphids (*A. nerii*) were observed at all sites, but colony establishment, which we defined as ≥50 individuals present, occurred at only 11 of 20 sites (55%). The neighborhood size selected by likelihood profiling for predicting the rate of aphid colony establishment as a function of milkweed index was 48m. The speed of aphid colony establishment was faster with increasing neighborhood milkweed index (Fig. 4, slope = -0.06, $\chi^2 = 6.41$, df = 2, p = 0.04).

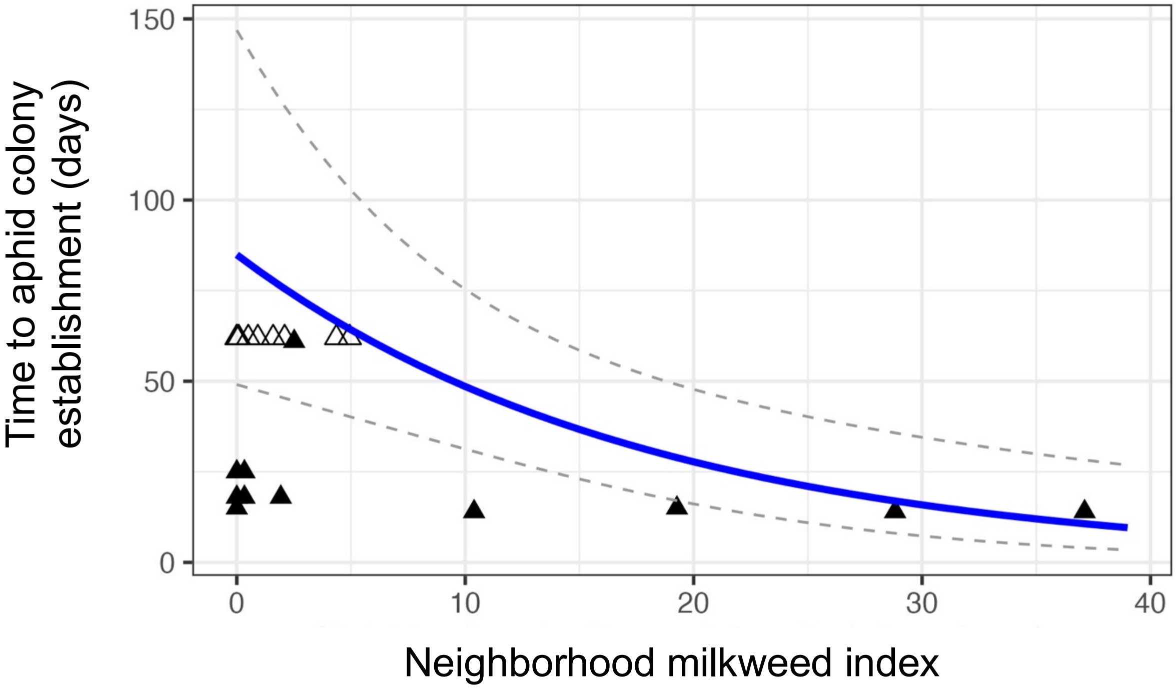


Fig. 4: Time to aphid colony establishment of each site as a function of neighborhood milkweed index, at the maximum likelihood neighborhood size of 48m. Colony establishment was defined as the date on which ≥50 aphids (*A. nerii*) were observed across all milkweed stems in a pot. The lines are the prediction of a Weibull-distributed survival regression with 95% confidence intervals. Filled triangles indicate days to colony establishment for each site, while empty triangles indicate sites where no colony establishment was observed over the 62-day period of the study (i.e. right-censoring occurred). The negative relationship is statistically significant (likelihood-ratio test, $\chi^2 = 6.41$, df = 2, p = 0.04).

Discussion

Our results provide evidence that neighborhood resource availability can alter host use in two common urban garden residents, monarch butterflies and milkweed aphids. We found responses to both local flower garden index (for monarchs) and milkweed index (for monarchs and aphids). We also observed widespread use of our study's small 0.6m wide containers; throughout the 20 sites, every milkweed pot received monarch eggs and had some amount of milkweed aphid activity recorded. Overall, we found that even small patches of urban habitat can experience consistent use from insects, but that the rate of use depends on neighborhood resource contexts.

For monarchs, neighborhood flower garden index was linked to higher rates of oviposition, but only in neighborhoods with low milkweed index. This complex pattern could be the result of a dilution effect for host density ultimately outweighing the attraction effect of gardens in neighborhoods with both high host and high garden availability. Past work has repeatedly found that butterfly eggs/larvae exhibit dilution at high host densities (e.g. Root and Kareiva 1984, Yamamura 1999), including for monarchs in natural and agricultural areas (Zalucki and Suzuki 1987, Pitman et al. 2018), and our results indicate a similar pattern for monarchs in cities. Previous studies have also found evidence of adult butterflies balancing their own needs with those of their offspring: females must seek nectar to maximize survival and fecundity, while offspring benefit from being laid on the highest quality host plants, which need not be co-located with the nectar (Janz 2005). In our study, such a phenomenon could help explain the peak oviposition rates occurring in high garden/low host neighborhoods, though it does not explain the null or even negative relationship between oviposition and gardens that we observed at high milkweed indexes.

The finding that patterns of pollinator habitat use can vary with context, i.e. some stems are used more than others, has implications for conservation in cities. Previous work in monarchs has reported variation in host use in response to *within* garden factors: spacing milkweeds in gardens further apart from other plants increases per-stem oviposition (Baker and Potter 2019) and adult monarch abundance is higher in gardens that have more flowers (Majewska et al. 2018). Our results echo these patterns, but at the larger scale of the neighborhood; for conservationists, we would predict that the maximum eggs per stem is yielded by adding milkweed to currently low milkweed/high garden density neighborhoods. However, this conclusion should be taken in the context that all of the 20 sites in our highly urbanized study area hosted at least some monarch eggs. Our pots were each just 0.6m across, yet this 5.6 m^2 of total habitat area supported over 800 eggs during a single breeding season, at egg densities comparable to or higher than natural settings (Appendix B). This is encouraging from a conservation perspective because it implies that host plant added anywhere in our study area had high potential to be used by monarchs, in spite of the fact that stems in some areas were used more than others. This provides additional ecological support for campaigns aiming to add habitat for monarchs and other insects in cities (Thogmartin et al. 2017, Derby Lewis et al. 2019).

For monarchs, our results also point to future directions for research. First, flower gardens are not the only source of nectar for monarchs, even in cities, as monarchs also readily visit an array of urban weeds for nectar. This makes our flower garden index a necessarily imperfect proxy for true nectar availability in a neighborhood. Perhaps it is only at the highest flower garden indexes we observed (>8% frequency) that gardens currently play a substantial role in the nectar landscape for urban monarchs. Another worthwhile future direction would be to understand the demographic and behavioral mechanisms that produce the patterns in monarch host use that we observed; for instance, testing whether there are more females present in neighborhoods with more eggs laid in them, or if each female in these neighborhoods tends to lay more eggs per host encounter, etc. Previous work has also found sex-specific effects of resource context on butterfly behavior which are not testable using only egg distributions; for instance, in the meadow brown butterfly, males engaged in distinctive mate-finding flight behavior specifically in patches with high nectar availability (Evans et al. 2020).

We observed a contrasting effect of neighborhood milkweed index for milkweed aphids, which supports one of the predictions of insect-plant density theories. Milkweed aphid colony establishment occurred faster in neighborhoods with higher milkweed indexes, with these high milkweed neighborhoods exhibiting colony establishment speeds more than double those of low milkweed neighborhoods. These aphids are a pest species whose traits align well with predictions for passive-dispersing contact searchers, which must by chance land on host; predictions from simulations and results from field data both suggest that aphid immigration rates are strongly dependent on patch area, specifically in comparison with butterflies, who have a more active visual/olfactory search modality (Andersson et al. 2013). In our data, the neighborhood scale selected by likelihood profiling for aphids was also less than half the size of that for monarchs (~50m vs. >100m), also consistent with shorter range, passive dispersal. These contrasting effects of resource contexts between butterflies and aphids are not unusual: previous work has suggested that there may be no universal host area/density responses in insects, and substantial variation across taxa is to be expected, probably linked to these kinds of life history and dispersal traits (Andersson et al. 2013, Hambäck et al. 2014). Our study suggests that these taxon-specific effects also hold for this pair of urban garden residents, in ways that partly support theoretical predictions.

Conclusions

In conclusion, our results support some predictions of basic ecological theories about insect foraging in relation to resource context. This connection is important because these theories were largely developed in natural and agricultural landscapes, not urban ecosystems. In spite of the fact that urban systems are under strong human influence, theories of these kinds can provide useful and testable predictions about urban animal populations and may be applicable more often than is typically thought; we can only know how applicable they are with further tests. Urban habitats also provide unique opportunities for ecologists, in that they exhibit particularly fine-grained variation or habitat patchiness, creating steep gradients in habitat availability over small areas. We hope that this study will inspire others to test whether theories from population and community ecology help us predict how some insect populations are able to persist and thrive in cities, and to assess which habitats are most important for that persistence.

Chapter 5 - Pollinator Gardens: Landscaping for Biodiversity in the 21st Century

Abstract

As global change threatens pollinator populations, conservationists have turned to cities as a new locale for habitat creation, with pollinator gardening showing particular promise. We integrate ecological data with research on landscaping preferences to show that while pollinator gardens have clear, substantial benefits for biodiversity over traditional landscaping, homeowners have been reluctant to widely adopt them owing to social controls on acceptable yard aesthetics and a general lack of knowledge. However, yard management is also socially contagious, meaning new preferences have the potential to spread through communities. With the goal of shifting norms and spreading ideas, we provide recommendations for gardeners and advocates that combine ecological value with benefits for homeowners, as well as a set of research questions whose answers would help us understand how gardens function as habitats. Pollinator gardening has unique potential to be a popular and cost-effective habitat creation tool, boosting biological resilience to global change and helping to unlock the untapped conservation potential of our cities.

Problem statement

Habitat loss is a leading threat to the maintenance of biodiversity. In addition to the direct effects of habitat loss *per se*, habitat loss indirectly limits resilience to other stressors, such as changing climate. In the 20th century, the conservation movement focused on protecting habitat in the remaining wilderness areas (Sarkar 1999). These efforts — though admirable and necessary — have not been sufficient to halt declines across widespread taxa like birds (Pimm et al. 2006) and insects (Wagner 2020). Among these declines, loss of pollinator populations is particularly conspicuous, because of the role pollinators play in maintaining food security.

Approximately 70% of crop species at least partially depend on animal pollination (Klein et al. 2007), often by wild pollinators that require natural habitat to persist.

In recent decades, the urban environment has emerged as a new frontier for habitat creation, especially in the form of pollinator gardening (Hall and Martins 2020). At first glance, urban lands might seem like unlikely targets for pollinator conservation because they look much less similar to wilderness than the rural, semi-natural landscapes used for agriculture, forestry, and grazing. However, they are important for at least two reasons. First, cities and suburbs are widespread and growing. Urban land cover is projected to grow by over 1 million km^2 from 2000 to 2030, meaning that by that date, a substantial majority of all urban lands on earth will have been created during the 21st century (Seto et al. 2012). In North America, these urban residential lands are currently dominated by nonnative turf grasses, which constitute the largest irrigated crop in the U.S. and cover an estimated 163,800 km^2 (Milesi et al. 2005), an area larger than the state of Georgia. The land management decisions that are made about these enormous areas will be of real conservation consequence for the tens of thousands of animal species that live in them. If just a modest fraction of urban green space were converted to pollinator gardens, cities may be able to support many pollinator species.

Second, conservation may be more economically compatible with urban than with semi-natural lands. In semi-natural landscapes, efforts to maximize profit often conflict with conserving pollinator habitat, so pollinator habitat creation and restoration come at an economic cost to farmers, ranchers and other rural landowners (Buckley and Crone 2008). In urban and suburban landscapes, lawns are maintained at considerable cost and effort by individual small landowners (Blaine et al. 2012, Harris et al. 2013). Changing management practices of these landowners could create habitat at a huge scale but with little additional economic cost.

Pollinator gardening also creates potentially desirable, well-liked landscapes, with minimal change to the usefulness of land. This is a recipe for a “win-win” situation in which pollinator habitat can be created with little top-down control or additional cost and largely through the voluntary spending of private, individual landholders.

State of the Art

Given this potential win-win situation, what can we do to make it happen? While much remains unknown about pollinator ecology and optimal garden design, incomplete ecological knowledge is not the main factor limiting adoption of pollinator gardens. We know that urban areas can harbor surprising pollinator diversity (e.g., on the order of a third or more of a region’s bee diversity, Ahrné et al. 2009, Fortel et al. 2014), similar species richness as nearby rural areas for some taxa (Baldock et al. 2015). As adults, many insect pollinators are generalists, and the factor most consistently linked to high pollinator diversity in cities is high flower cover and diversity around the sampling site (Ahrné et al. 2009, Bates et al. 2011, Quistberg et al. 2016, Majewska and Altizer 2020). Adult pollinators are mobile and appear to locate flowers even when they are planted in highly urbanized, otherwise unfavorable areas (Wenzel et al. 2020). We know less about how to make gardens that sustain pollinators throughout their life cycles, but the first steps are incorporating a diversity of types of nectar- and pollen-producing vegetation (Majewska and Altizer 2020), planting host plants for butterflies (Baker and Potter 2018), and providing nesting sites for bees (Fortel et al. 2016). Even without extensive ecological tuning, a moderately diverse pollinator garden provides far more conservation value than a yard composed only of turf grass or impervious surfaces (Wenzel et al. 2020).

Rather than ecological knowledge, the primary limit to the spread of pollinator gardens is the willingness of homeowners to adopt them. In North America, failure to conform to norms of "neatness" associated with turf grass is often perceived as a moral failing indicative of a lack of care for neighbors or community (Feagan and Ripmeester 1999, 2001, Robbins 2007, Harris et al. 2013). Even when landholders are discontented with conventional lawn care, they are reluctant to fall into nonconformity and/or feel they lack necessary knowledge (Larsen and Harlan 2006, Blaine et al. 2012, Harris et al. 2013). At the same time, the social nature of yard maintenance means that that pollinator gardening may be socially contagious. Neighbors overall tend to mimic the most popular landscaping choices in an area (Nassauer et al. 2009) and alternative yard care information can spread through conversation (Martini et al. 2014). These factors can lead to clusters of gardens forming (Hunter and Brown 2012). If we could understand how to initiate social contagion of pollinator gardening, the same social phenomena that maintain lawns as the dominant cover type today could one day cause pollinator gardening to emerge as a self-spreading idea.

Moving Forward

Given the state of the art, the best way to encourage pollinator gardening is to motivate social change. In other words, we need to make pollinator gardens easy and convenient for novice gardeners in order to build their social acceptability and popularity. With these principles in mind, we summarize recommendations that aim to: (I) distill the most important design elements for an effective pollinator garden into their easiest-to-adopt form (*Recommendations for gardeners*) and (II) summarize ways to motivate others to adopt pollinator gardening (*Recommendations for advocates*). For academics (and other researchers) who want to contribute to our ability to conserve biodiversity through pollinator gardening, we also (III) summarize ecological and biological research directions that best support the utility of pollinator gardens, given their social context *(Recommendations for researchers*).

Fig. 1: Examples of florally and structurally diverse pollinator gardens in Somerville and Cambridge, MA. Images from Google Street View 2018-20. Note the wide variation in management and design choices, all within the scope of the recommendations we provide.

I. Recommendations for gardeners

These recommendations are a starting set of easy-to-follow guidelines that could help novice gardeners plant pollinator gardens (examples in *Fig. 1*). Our aim is to complement existing guidelines targeted at experienced gardeners (see, e.g., Mader et al. 2011).

1. *Plant a diverse set of flowering plants*: Garden habitats with more plant species support greater pollinator diversity (Majewska and Altizer 2020) because each pollinator species visits a subset of flower species and attractiveness varies widely across plant taxa (Garbuzov and Ratnieks 2015). Gardens with higher floral diversity are also generally preferred by the public, thanks to their variation in flower color, size, and shape (Lindemann-Matthies and Bose 2007).
2. *Add vegetation structure to the yard:* Incorporating structural (physical) diversity, including bare soil and woody

plants, provides nesting habitat and food resources for many pollinator species (MacIvor et al. 2014, Fortel et al. 2016). This feature of pollinator gardens is also in line with public preferences, as survey participants' imagined ideal landscapes include substantial structural diversity (Lindemann-Matthies and Bose 2007).

3. *When possible, use native plant species and avoid problem plants:* Though non-native plants can support many native pollinators (Shapiro 2002), some specialist pollinators rely exclusively on native plants (Burghardt et al. 2009), which are also less likely to act invasively, offer inaccessible rewards (Corbet et al. 2001), or act as evolutionary traps whereby native pollinators are attracted to the plant but perform poorly on it (Nakajima et al. 2013). For landholders, native plants may also come with no increase to costs, as suggested by the finding that in cities, household income predicts exotic species diversity significantly better than native species diversity (Chamberlain et al. 2020).
4. *Minimize herbicide and pesticide use:* Pesticides can impair the health of garden-visiting pollinators (Larson et al. 2013) and herbicides reduce floral cover and diversity by removing weeds, which constitute important diet components for some urban pollinators (MacIvor et al. 2014, Larson et al. 2014). Reducing these chemical inputs would also lower costs and maintenance effort, two of the management factors homeowners report they are most concerned about (Blaine et al. 2012).
5. *Lawns can remain, but should be mowed infrequently:* Effective pollinator gardening does not require wholesale conversion of all outdoor space to flowers. Grass lawns, which are widely valued as safe spaces for leisure and play (Larson et al. 2009), can be mowed less frequently to minimize disturbance and allow weeds to bloom, which attracts more insects (Lerman et al. 2018). Maintaining taller, seminatural meadow areas

alongside conventional low-cut lawns can also be appealing to the public (Fischer et al. 2020) and can substantially reduce maintenance costs (Watson et al. 2020).

II. Recommendations for advocates

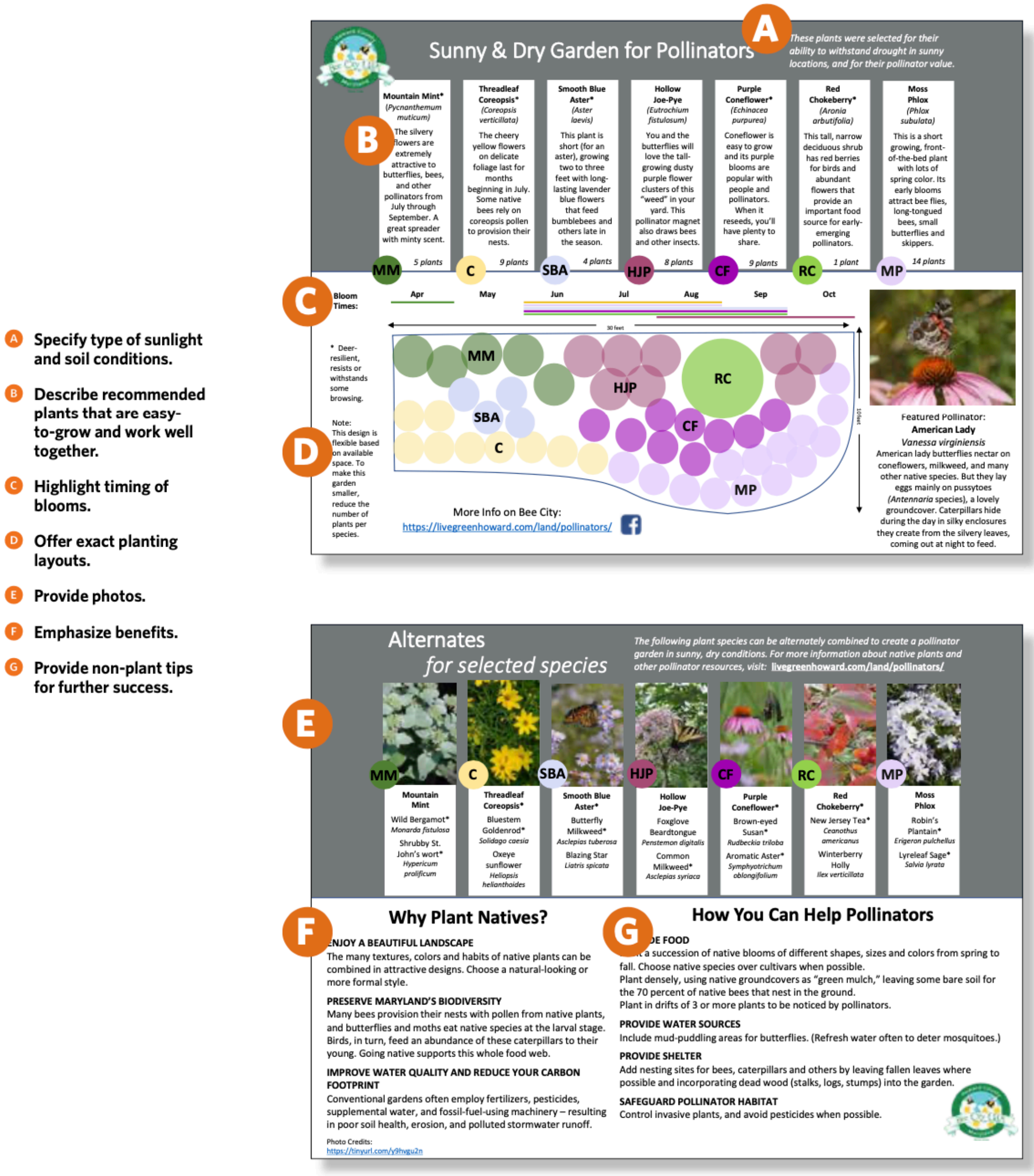
These recommendations are for individuals or organizations who want to promote pollinator gardening. At the present time, such groups often focus on educating master gardeners and other experienced individuals who self-select and actively seek out this information. Our recommendations are for organizations who particularly want to expand their reach to the general public as part of efforts to change wider social norms.

1. *Distribute easy-to-follow, scalable guidance on growing pollinator gardens:* Unlike other environmentally-conscious behaviors (e.g., recycling, Schultz 2002), a lack of knowledge is often a barrier to changing yard management practices (Harris et al. 2013, van Heezik et al. 2020). Given the potential tradeoff between complexity and likelihood of adoption of pollinator conservation guidance (Knapp et al. 2020), beginners should be taught simple and general principles (see *Fig. 2* for a dissection of an exemplary document). These might include an emphasis on easy-to-propagate species or may initially focus on harm reduction through reduced mowing or pesticide use.
2. *Aim for knowledge diffusion and social contagion:* Conventional, lawn-covered yard landscapes are a strong social norm (Feagan and Ripmeester 1999, Harris et al. 2013), and thus early-adopters of pollinator gardening take on some risk. However, these dynamics also lead to mimicry and thus social contagion: pollinator gardens become preferred in homeowner surveys once hypothetical neighbors have them too (Nassauer et

al. 2009). Advocates should recognize that the subsequent social pressure exerted by converting gardeners may be equally important as the initial gardens for long-term habitat creation.

3. *Emphasize beauty and ease of maintenance of native pollinator gardens:* Lawn owners generally prioritize achieving conventional aesthetics while minimizing costs in time or effort (Larson et al. 2009, Harris et al. 2013). Advocates should emphasize that pollinator-friendly planting can be cost-effective (Williams and Lonsdorf 2018) and beautiful, and they should combat any pre-existing beliefs that neighbors might dislike pollinator garden aesthetics (Peterson et al. 2012) and fears about potentially higher costs of unfamiliar practices (Harris et al. 2013).
4. *Combat policies that prevent pollinator-friendly practices from being adopted:* Pollinator gardening can be constrained by top-down forces such as municipal laws (e.g., lawn height limits, Sandberg and Foster 2005) and homeowners association rules, which convert social pressures into explicit contractual obligations about aesthetics (Turner and Stiller 2020). Advocates need to understand the motivation behind regulations – Are they due to safety issues such as visibility along crowded urban streets, or do they reflect popular but changeable beliefs about aesthetics and home values? – and then work to change rules where appropriate.
5. *Lead by example: the more gardens there are, the faster adoption occurs:* Directly creating gardens is a valuable tool for shifting norms and educating the public about the aesthetics of pollinator gardening, as well as its ecological benefits. In-person encounters with pollinator habitat create a social climate that is more accepting of and more interested in pollinator gardening (Hall and Martins 2020), and these improvements to

social climate might have redoubling effects down the road, thanks to the social contagion effect.



- **A** **Specify type of sunlight and soil conditions.**
- **B** **Describe recommended plants that are easy-to-grow and work well together.**
- **C** **Highlight timing of blooms.**
- **D** **Offer exact planting layouts.**
- **E** **Provide photos.**
- **F** **Emphasize benefits.**
- **G** **Provide non-plant tips for further success.**

Sunny & Dry Garden for Pollinators

These plants were selected for their ability to withstand drought in sunny locations, and for their pollinator value.

Mountain Mint* *(Pycnanthemum muticum)* The silvery flowers are extremely attractive to butterflies, bees, and other pollinators from July through September. A great spreader with minty scent. MM *5 plants*

Threadleaf Coreopsis* *(Coreopsis verticillata)* The cheery yellow flowers on delicate foliage last for months beginning in July. Some native bees rely on coreopsis pollen to provision their nests. C *9 plants*

Smooth Blue Aster* *(Aster laevis)* This plant is short (for an aster), growing two to three feet with long-lasting lavender blue flowers that feed bumblebees and others late in the season. SBA *4 plants*

Hollow Joe-Pye *(Eutrochium fistulosum)* You and the butterflies will love the tall-growing dusty purple flower clusters of this “weed” in your yard. This pollinator magnet also draws bees and other insects. HJP *8 plants*

Purple Coneflower* *(Echinacea purpurea)* Coneflower is easy to grow and its purple blooms are popular with people and pollinators. When it reseeds, you’ll have plenty to share. CF *9 plants*

Red Chokeberry* *(Aronia arbutifolia)* This tall, narrow deciduous shrub has red berries for birds and abundant flowers that provide an important food source for early-emerging pollinators. RC *1 plant*

Moss Phlox *(Phlox subulata)* This is a short growing, front-of-the-bed plant with lots of spring color. Its early blooms attract bee flies, long-tongued bees, small butterflies and skippers. MP *14 plants*

Bloom Times:

* Deer-resilient, resists or withstands some browsing.

Note: This design is flexible based on available space. To make this garden smaller, reduce the number of plants per species.

More Info on Bee City:
https://livegreenhoward.com/land/pollinators/

Featured Pollinator:
American Lady
Vanessa virginiensis
American lady butterflies nectar on coneflowers, milkweed, and many other native species. But they lay eggs mainly on pussytoes *(Antennaria* species), a lovely groundcover. Caterpillars hide during the day in silky enclosures they create from the silvery leaves, coming out at night to feed.

Alternates
for selected species

The following plant species can be alternately combined to create a pollinator garden in sunny, dry conditions. For more information about native plants and other pollinator resources, visit: **livegreenhoward.com/land/pollinators/**

MM	C	SBA	HJP	CF	RC	MP
Mountain Mint	**Threadleaf Coreopsis***	**Smooth Blue Aster***	**Hollow Joe-Pye**	**Purple Coneflower***	**Red Chokeberry***	**Moss Phlox**
Wild Bergamot* *Monarda fistulosa*	Bluestem Goldenrod* *Solidago caesia*	Butterfly Milkweed* *Asclepias tuberosa*	Foxglove Beardtongue *Penstemon digitalis*	Brown-eyed Susan* *Rudbeckia triloba*	New Jersey Tea* *Ceanothus americanus*	Robin’s Plantain* *Erigeron pulchellus*
Shrubby St. John’s wort* *Hypericum prolificum*	Oxeye sunflower *Heliopsis helianthoides*	Blazing Star *Liatris spicata*	Common Milkweed* *Asclepias syriaca*	Aromatic Aster* *Symphyotrichum oblongifolium*	Winterberry Holly *Ilex verticillata*	Lyreleaf Sage* *Salvia lyrata*

Why Plant Natives?

ENJOY A BEAUTIFUL LANDSCAPE
The many textures, colors and habits of native plants can be combined in attractive designs. Choose a natural-looking or more formal style.

PRESERVE MARYLAND’S BIODIVERSITY
Many bees provision their nests with pollen from native plants, and butterflies and moths eat native species at the larval stage. Birds, in turn, feed an abundance of these caterpillars to their young. Going native supports this whole food web.

IMPROVE WATER QUALITY AND REDUCE YOUR CARBON FOOTPRINT
Conventional gardens often employ fertilizers, pesticides, supplemental water, and fossil-fuel-using machinery – resulting in poor soil health, erosion, and polluted stormwater runoff.

Photo Credits:
https://tinyurl.com/y9hvgu2n

How You Can Help Pollinators

DE FOOD
a succession of native blooms of different shapes, sizes and colors from spring to fall. Choose native species over cultivars when possible.
Plant densely, using native groundcovers as “green mulch,” leaving some bare soil for the 70 percent of native bees that nest in the ground.
Plant in drifts of 3 or more plants to be noticed by pollinators.

PROVIDE WATER SOURCES
Include mud-puddling areas for butterflies. (Refresh water often to deter mosquitoes.)

PROVIDE SHELTER
Add nesting sites for bees, caterpillars and others by leaving fallen leaves where possible and incorporating dead wood (stalks, logs, stumps) into the garden.

SAFEGUARD POLLINATOR HABITAT
Control invasive plants, and avoid pesticides when possible.

Fig. 2: Anatomy of an effective guide to pollinator gardening targeted at beginners. This image was taken from guidelines developed by Howard County, MD for distribution to a broad audience, including novice gardeners. Note the clear plant guidance with pictures of flowers and the spatially precise planting layout. These features help beginners feel comfortable with starting a pollinator garden. Image adapted with permission from Howard County, MD Bee City USA.

III. Recommendations for researchers

We know that diverse native gardens are better than typical landscaping choices for most pollinator species. However, urban landscapes are also a novel ecosystem constructed by humans, whose form will thus never replicate natural landscapes. These research topics are recommended directions if we want to know whether pollinator gardens can substitute for — as opposed to supplementing — conservation in natural areas.

1. *Mechanisms that drive urban pollinator habitat quality:* Most data on urban pollinator ecology is correlative, describing patterns of diversity (see review by Majewska and Altizer 2020). For nearly all taxa, factors determining habitat quality are unknown, including garden-relevant factors like what resources are limiting across life stages (e.g., pollen vs. nest sites) and how far species disperse in cities. Understanding these mechanisms is central to understanding whether urban gardens can provide stand-alone "source" habitat for pollinators, as opposed to simply serving as habitat for populations that spill over from natural areas.
2. *Evolutionary and behavioral changes in cities:* Recent work has demonstrated genetic (Johnson and Munshi-South 2017) and behavioral (Sol et al. 2013) differences in animal populations from urban environments compared to rural ones, but the adaptive significance of most differences remains unclear and little is known about differences in pollinator populations. Identifying such differences could help characterize which elements of urban habitats are most important for a given species and help explain some of the substantial variation in urbanization tolerance across pollinator taxa.

3. *Optimal reserve design in social contexts and with many managers:* Optimal reserve design, the question of where and how to spend limited conservation resources, is an old problem, but studying its urban analogue requires acknowledging the distinct, irrational, and decentralized land management context of cities and drawing on the considerable social science literature on social contagion and emotions in yard care (Feagan and Ripmeester 1999, Robbins 2007, Harris et al. 2013). Leveraging this research could directly aid conservationists, e.g., by identifying nascent clusters of gardeners and prioritizing these areas for investment, using materials that emphasize pollinator gardening's benefits within homeowners' pre-existing priorities.
4. *What pitfalls should be avoided when creating urban pollinator habitats?:* We advocate simple, proscription-light messaging in part because most pitfalls in pollinator gardening are not well characterized: outside of an obvious few (e.g., excluding locally invasive species), most problems are more complex (e.g., evergreen tropical milkweed is a popular garden plant with clearly disruptive effects on monarch butterfly migration [Majewska and Altizer 2019], but as it is a suitable host plant, its presence may or may not make garden habitats a net negative for monarch populations). Biologists should investigate such potentially harmful practices, but pollinator gardening advocates should be careful not to overstate the evidence or overcomplicate messaging, because ease of adoption is key to large scale habitat creation.
5. *What are achievable conservation targets for urban pollinators?:* Although replacing a lawn with a diverse flower garden almost invariably leads to greater pollinator diversity in that yard, it is unknown whether city- or region-wide pollinator diversity increases given an increase in the number of gardens. Aside from these largely untested — yet

> much-heralded — ambitions for boosting urban biodiversity at larger scales, pollinator gardens provide other potential conservation benefits worthy of research, such as a capacity for buffering pollinators from global change impacts by increasing population sizes, as well as favorably altering public perceptions of insect conservation (Hall and Martins 2020).

Climate Solutions

Global change and the associated modern extinction crisis are very serious yet very complex problems. This complexity can be overwhelming, and the problems' scales can make an average person feel powerless. However, the impacts of climate change do not occur in isolation. Habitat creation increases (and, conversely, habitat loss decreases) species' resilience to climate change. If species do not have sufficient habitat, they may experience overcrowding or search time limitation, both of which decrease population growth. Larger populations are able to withstand greater shocks, and also are more likely to have the capacity to evolve to new environments through genetic change. The availability of suitable habitat also constrains the ability of species to shift their ranges in response to shifting windows of suitable climate conditions.

Pollinator gardens are a direct and immediate solution to one dimension of climate change. They have the direct effect of making pollinator populations less habitat limited, and therefore more resilient to climate change. They also help connect people to biodiversity in a real and immediate way. We do not yet know whether pollinator gardens can be a substitute for natural habitats, i.e. for how many taxa they can support self-sustaining urban populations;

ecological research in this area is a high priority. However, we do know that urban and suburban lands are a large and growing segment of the landscape and that pollinator gardens, even if imperfect, are far superior to traditional landscaping choices, such as turf lawns. Making pollinator gardens accessible to the general public has the added benefit of possibly leading to social contagion. Rather than competing with other economic interests, they could become a landscaping option that spreads simply because it is beautiful and popular. Even if the ultimate goal is a landscape of sophisticated and fine-tuned gardens, pollinator gardens that are "good enough" are a first step towards shifting the social norms away from monoculture lawns and towards heterogeneous and diverse urban landscapes.

Pollinator gardening serves as a powerful potential habitat creation solution for a group of animals threatened by global climate change and habitat loss. As a conservation measure, it is especially well-suited to the urban context: it engages with private landowners about activities they already spend substantial amounts of time and money on and encourages them to create landscapes that typically do not conflict with other desired uses, which are also widely seen as beautiful. Because these ecologically beneficial practices are also likely to be socially contagious, every dollar spent on creating more pollinator gardeners has the potential to redouble in its conservation benefits, through the passive, natural spread of information and aesthetic preferences. By taking into account the practicalities that make urban conservation a very different enterprise than traditional wilderness conservation, as we have done here, ecologists and conservationists can more easily identify and overcome the barriers to large-scale changes in urban land management and can leverage patterns of human behavior to their advantage, and to the advantage of biological resilience in an era of global change.

Chapter 6 - Conclusion

For some of the same reasons that pollinator gardening is a promising conservation practice, it presents unique challenges and questions for ecologists and other researchers. Its conceptual flexibility makes it more broadly appealing to participants, yet difficult to study or guide (Chapter 1); it is increasing in popularity but still rare (Chapter 2); its high visibility can make it socially contagious (Chapter 3) yet can also constrain its spread (Chapter 5); its ecological impacts are promising yet poorly characterized and complex (Chapter 4).

In my dissertation, I attempted to use multiple perspectives to begin understanding pollinator gardens holistically, as ecological and human spaces. I aimed to connect processes across spatial scales, from within yards (patterns of floral diversity within gardens, Chapter 2), to along streets (contagion of gardening between neighbors, Chapter 3), to across neighborhoods (garden densities between neighborhoods, Chapters 2 and 4). I also attempted to assess how the clustered patterns I observed in flower gardens (Chapters 2 and 3) might be ecologically relevant for insects (Chapter 4). In addition, I used findings from the social sciences to contextualize gardens as deeply personal, emotional spaces, in order to help make the case that effective conservation efforts involving pollinator gardens should remain conceptually flexible (Chapter 1) and focused not only on ecological perspectives of optimizing habitat quality but also on the qualities that make gardens appealing to the humans that voluntarily create them (Chapter 5).

A key contribution of my work is to provide evidence that pollinator gardening may be socially contagious among nearby neighbors (Chapter 3). Pollinator gardening fits into a broader trend of urban conservation on residential parcels, and it presents issues exemplary of that field. For several years, a leading concern among ecologists studying residential lands has been that creating habitat using this patchwork of independent small landholders will create disconnected and small patches, each of which are not likely to support self-sustaining animal populations on their own. This leads to questions about how to 'scale up' from single yards to many nearby yards (e.g. Goddard et al. 2010). While contagion has previously been discussed as a possible factor, its importance has been understated (particularly for small organisms who usually move shorter distances, like pollinators), and explicit evidence for contagion in yard landscaping has only rarely been reported. If pollinator gardening is socially contagious, this means that there is a self-organizing process that is 'scaling up' gardens already, without the intervention of ecologists or conservationists.

My dissertation also links human behavior with ecological outcomes in cities, which is a second major challenge for urban ecology. Urban ecology is a relatively new field, expanding most rapidly within the past two or three decades. Given that urban systems are produced by the interaction between already-complex natural ecological processes with similarly difficult-to-predict human behavior, it is perhaps unsurprising that grand unifying theories have thus far been elusive for urban ecologists. My approach to coping with this problem was to study how theories of human behavior *interact* with theories of basic ecological processes. In some cases, we found that standard ecological theories did not hold in interesting ways, e.g. that floral species richness in yards was unrelated to the size of each lot (Chapter 2), suggesting that human management may be the more dominant driver of per-yard diversity than patch area. In other cases, predictions from basic ecology were upheld, e.g. aphid colony establishment rate was positively related to host density and monarch butterfly oviposition rates were negatively related to host density (Chapter 4). In a third set of cases, ecological theories provided compelling future directions based on my results, e.g. habitat connectivity and other landscape ecology concepts as ways to study the impact of social contagion on pollinator gardening habitat structure (Chapter 3).

In my view, pollinator gardening really is an idea whose time has come, with its ability to make a meaningful difference for both pollinators and people in an era of mounting threats to biodiversity and widespread alienation from nature. Yet there is so much left to find out about how these complex and dynamic spaces work. The tools of basic ecology have much to offer these efforts, by providing theories to stimulate new testable hypotheses and allowing quantitative explorations of how these gardens are created and how they function.

APPENDIX 1A: Supplemental Material for Chapter 2

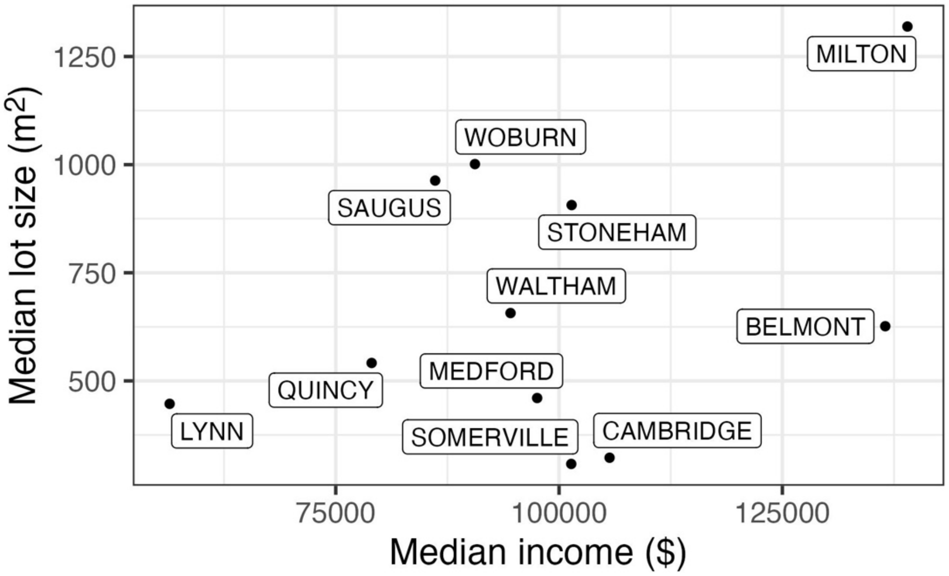


Fig. A1: The relationship between average per-tract median lot size (sq. m) and average per-tract median household income for the 11 study cities. Income is infl. adjusted 2019 dollars, from American Community Survey for time period 2015-2019 and lot sizes are from MassGIS tax assessment records. The linear relationship is not statistically significant (Pearson's r = 0.37, df = 9, p = 0.27).

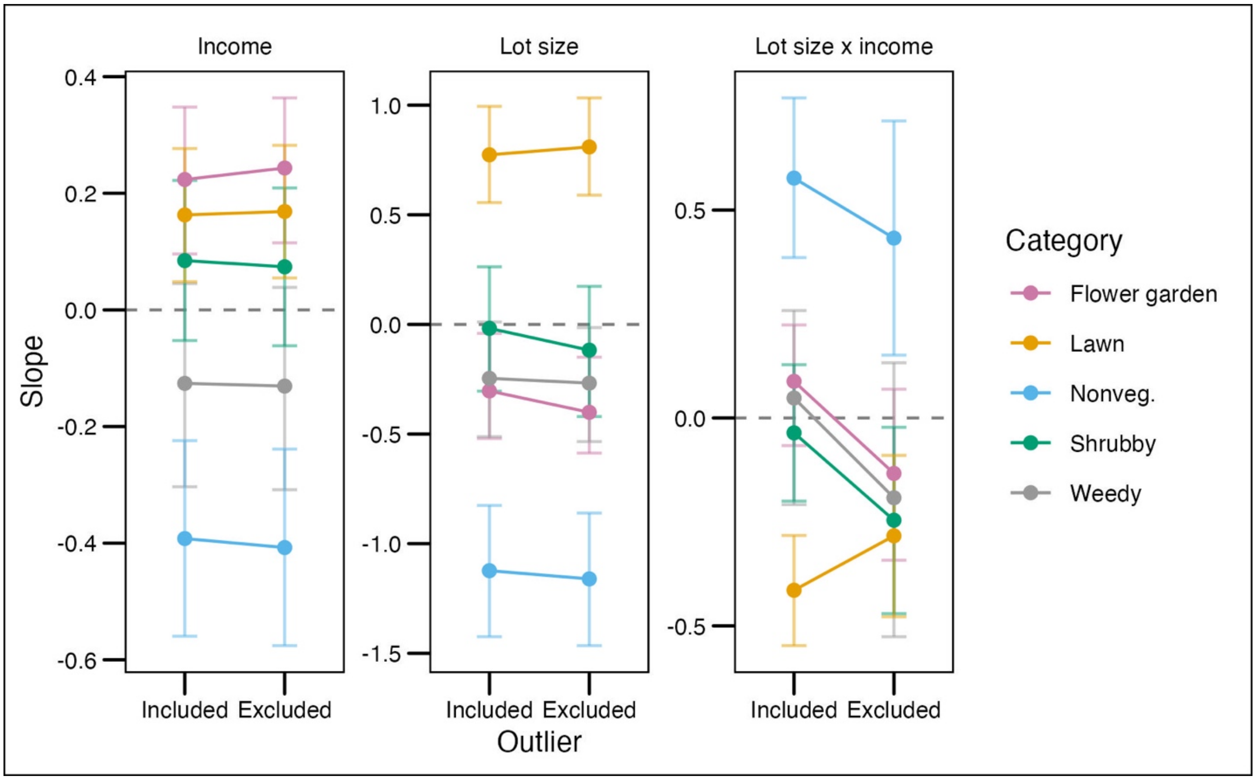


Fig. A2: A comparison of model slope estimates with 95% confidence intervals, including or excluding a single outlier census tract with very high median lot size (+8 SD above mean). In all analyses in the main manuscript, the outlier is excluded. Note that the scale of the y-axis has been allowed to vary across panels to facilitate comparison of the effect of excluding the outlier.

Table A1: Top 30 most common flowering morphospecies, sorted in descending order by percentage of yards present. Includes both spontaneous and cultivated species.

Species	N Yards	% Yards
Oxalis stricta	360	69.4
Trifolium repens	247	47.6
Mollugo verticillata	203	39.1
Hosta spp.	197	38
Erigeron canadensis	183	35.3
Spergularia rubra	164	31.6
Rosa spp.	156	30.1
Lepidium spp.	148	28.5
Hydrangea macrophylla	122	23.5
Petunia spp.	116	22.4
Hemerocallis fulva	105	20.2
Hieracium spp.	104	20
Taraxacum spp.	101	19.5
Cynanchum louiseae	98	18.9
Hemerocallis lilioasphodelus	84	16.2
Plantago lanceolata	82	15.8
Solanum nigrum spp.	79	15.2
Pelargonium x hortorum	77	14.8
Commelina communis	74	14.3
Rhododendron spp.	74	14.3
Impatiens spp.	72	13.9
Salvia spp.	68	13.1
Campanula rapunculoides	66	12.7
Erigeron annuus	66	12.7
Rudbeckia spp.	64	12.3
Tagetes patula	63	12.1
Capsella bursa-pastoris	62	11.9
Leucanthemum spp.	61	11.8
Hibiscus syriacus	60	11.6

Table A2: Summary statistics of the study cities. All metrics are summarized as the mean of all studied tracts in each city. Income is therefore the mean of per-tract median household income, lot size is the mean of median lot size, etc. N lots refers to the number of lots in our study tracts.

City	Income ($)	Lot size (m^2)	Area (km^2)	N Lots	Lot dens. (lots/km^2)	% Renting	% White	% Bach Dgr
Lynn	56409	447	29.91	16624	556	53.8	47.3	17.6
Quincy	79020	541	44.84	18112	404	45.9	62.7	45
Saugus	86134	963	29.37	7890	269	17	90.3	28.1
Woburn	90585	1001	33.52	9378	280	36.8	80.7	44.6
Waltham	94567	657	35.64	10907	306	45.7	70.7	52.9
Medford	97549	460	21.88	12440	569	44	73.3	54
Somerville	101367	308	10.7	9900	925	65.9	77	65.8
Stoneham	101410	907	17.21	5645	328	27.8	89.6	46.7
Cambridge	105658	322	18.4	8018	436	62.5	67.9	78
Milton	136460	718	34.46	7863	228	10.4	73.5	61.9
Belmont	136520	626	12.22	6343	519	32.7	77.1	75.9

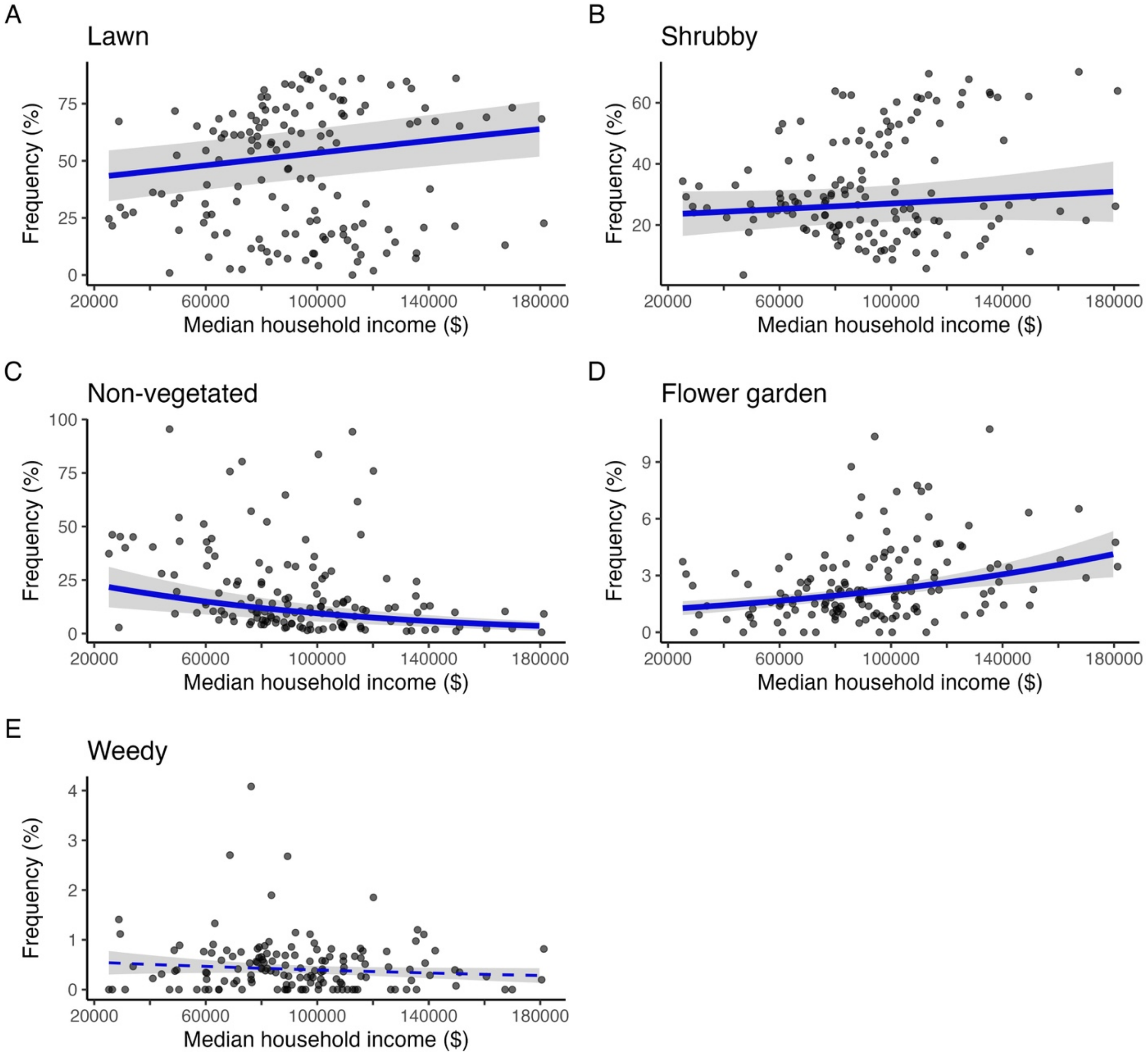


Fig. A3: The relationship between frequency of each lot type and income across each of the five yard type categories: (a) lawn, (b) shrubby, (c) non-vegetated, (d) flower garden, and (e) weedy lots. The blue line is the prediction of a binomial GLMM with fixed effects of income × lot size and random effects of city and census tract, with lot size fixed at the mean. Error bars show 95% confidence intervals. Thick lines show a significant relationship and thin dashed lines show non-significant relationships at the 95% level, based on likelihood ratio tests. The prediction lines do not always pass directly through the raw data because of the presence of multiple fixed effects, as well as random effects, in the model (i.e. the lines are not fit only to the raw points as shown).

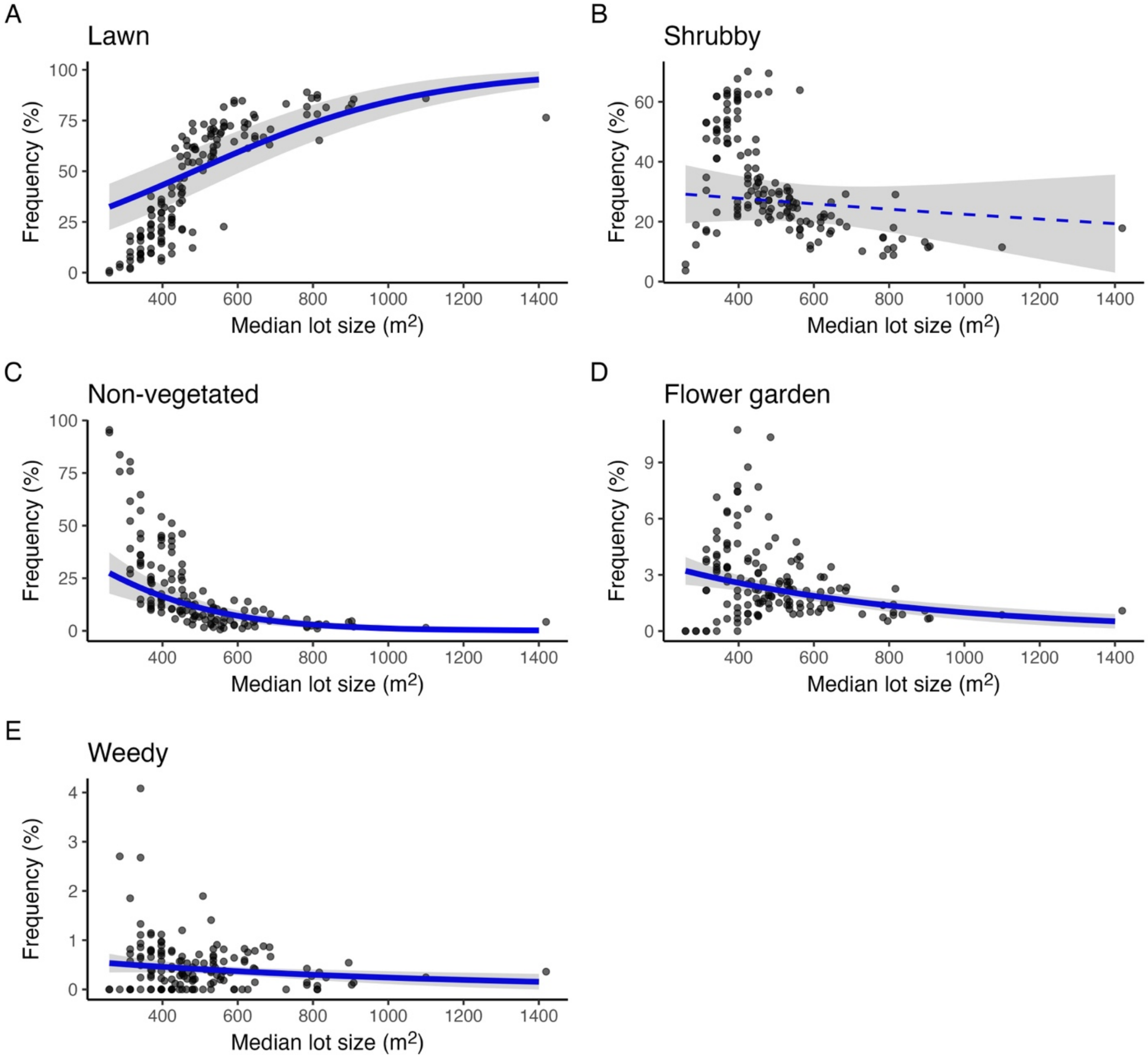


Fig. A4: The relationship between frequency of each lot type and lot size across each of the five yard categories: (a) lawn, (b) shrubby, (c) non-vegetated, (d) flower garden, and (e) weedy lots. The blue line is the prediction of a binomial GLMM with fixed effects of income × lot size and random effects of city and census tract, with income fixed at the mean. Lot size is the median per-tract. Error bars show 95% confidence intervals. Thick lines show a significant relationship and thin dashed lines show non-significant relationships at the 95% level, based on likelihood ratio tests. The prediction lines do not always pass directly through the raw data because of the presence of multiple fixed effects, as well as random effects, in the model (i.e. the lines are not fit only to the raw points as shown).

Table A3: Summary of model results for supplemental demographic predictors. For these models, we used a binomial GLMM with random effects of city and census tract and fixed effects of all the predictors (additive only). All predictors were medians collected at the census tract level and then centered and scaled. χ^2 statistics are for likelihood ratio tests.

Yard Type	Variable	Slope	χ^2	Df	P
Lawn	Income	-0.03	0.107	1	0.74
Lawn	**Lot size**	**0.62**	**42.875**	**1**	**<0.0001**
Lawn	**Renter %**	**-0.28**	**14.498**	**1**	**<0.0001**
Lawn	White %	0.11	2.365	1	0.12
Lawn	Bachelor's %	0	0	1	0.99
Shrubby	Income	-0.01	0.004	1	0.95
Shrubby	Lot size	-0.2	3.148	1	0.08
Shrubby	Renter %	0.01	0.01	1	0.92
Shrubby	White %	-0.1	1.545	1	0.21
Shrubby	**Bachelor's %**	**0.46**	**12.178**	**1**	**<0.001**
Non-vegetated	Income	0.03	0.062	1	0.8
Non-vegetated	**Lot size**	**-0.91**	**46.491**	**1**	**<0.0001**
Non-vegetated	**Renter %**	**0.5**	**21.225**	**1**	**<0.0001**
Non-vegetated	White %	0.08	0.64	1	0.42
Non-vegetated	**Bachelor's %**	**-0.66**	**17.434**	**1**	**<0.0001**
Garden	Income	0.07	0.659	1	0.41
Garden	**Lot size**	**-0.39**	**24.87**	**1**	**<0.0001**
Garden	Renter %	0.04	0.263	1	0.61
Garden	White %	0.05	0.662	1	0.42
Garden	**Bachelor's %**	**0.27**	**8.978**	**1**	**<0.01**
Weedy	Income	0.1	0.396	1	0.53
Weedy	**Lot size**	**-0.29**	**4.629**	**1**	**<0.05**
Weedy	Renter %	0.26	3.934	1	0.05
Weedy	White %	0.11	0.908	1	0.34
Weedy	Bachelor's %	-0.25	1.947	1	0.16

Table A4: Model summary for negative binomial GLMs/GLMMs predicting species richness in individual yards. Lot size and income were each centered and scaled. Lot size is on a per-lot basis. Income is assigned to tract-level median household income. The final model for cultivated species richness had the structure lot type + income x lot size. The final model for spontaneous species richness had the structure lot type + income + lot size, with a random effect of census tract. χ^2 statistics are for likelihood ratio tests.

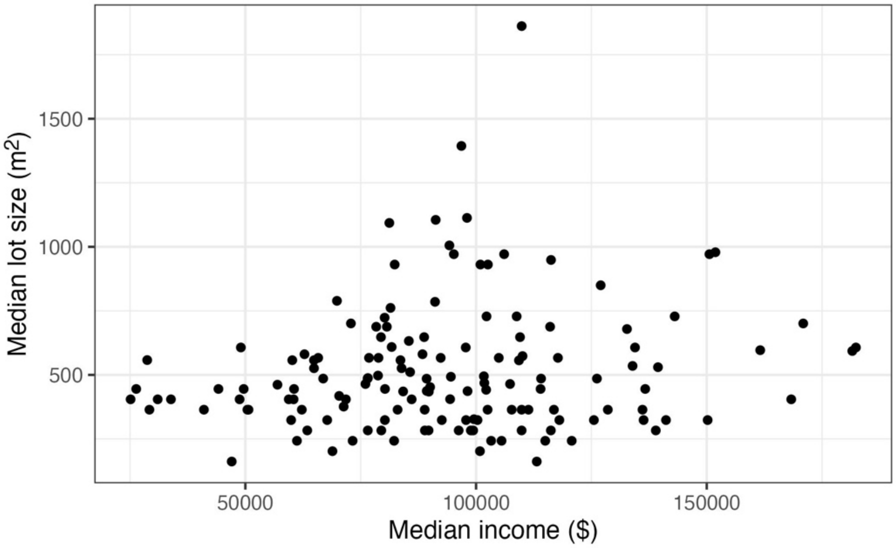
Plant Community	**Variable**	**Slope**	**χ^2**	**Df**	**P**
Cultivated	**Lot type**	**NA**	**208.59**	**4**	**<0.0001**
Cultivated	**Income**	**0.12**	**9.03**	**1**	**<0.01**
Cultivated	Lot size	0.01	1.31	1	0.25
Cultivated	**Income:Lot size**	**0.09**	**4.5**	**1**	**<0.05**
Cultivated	*Lot type:Lot size*[1]	*NA*	*2.23*	*4*	*0.69*
Cultivated	*Lot type:Income*[1]	*NA*	*8.46*	*4*	*0.08*
Cultivated	*Lot type:Income:Lot size*[1]	*NA*	*8.69*	*4*	*0.07*
Spontaneous	**Lot type**	**NA**	**42.03**	**4**	**<0.0001**
Spontaneous	**Income**	**-0.07**	**3.99**	**1**	**<0.05**
Spontaneous	Lot size	0	0	1	0.96
Spontaneous	*Income:Lot size*[1]	-0.05	*0.61*	*1*	*0.43*
Spontaneous	*Lot type:Lot size*[1]	NA	*7.93*	*4*	*0.09*
Spontaneous	*Lot type:Income*[1]	*NA*	*4.02*	*4*	*0.40*
Spontaneous	*Lot type:Income:Lot size*[1]	*NA*	*1.13*	*4*	*0.89*

[1] *Non-significant interaction removed from the final model used for inference. Test statistics for these terms are from the full model. Test statistics for other terms are from the final, reduced model*

APPENDIX 1B: Assessing collinearity of predictors (Chapter 2)

When selecting the cities used in this study, we attempted to decouple two factors that are generally positively correlated in our region — lot size and income — in order to estimate their independent effects on yard management. At the city level, lot size and income were not significantly correlated, as intended by our site selection (see Fig. A1). However, a non-significant positive correlation remained at the smaller, census tract level (Fig. B1; Pearson's r = 0.15, t = 1.86, df = 142, p = 0.06).

Fig. B1: Relationship between lot size and income for the 144 census tracts in the study, with per tract median lot size (m^2) and household median income (infl. adjusted 2019 dollars, from American Community Survey for time period 2015-2019).



In order to test whether collinearity was a problem for interpreting estimates from models including both of these predictors, we used two methods. First, we calculated VIF, the variance inflation factor, to estimate how much inflation to slope standard error had occurred as a result of collinearity. Second, we compared the slopes for interaction models with both covariates to models with only one covariate included, to test if the slopes were substantially altered (e.g. flipping signs) by including both covariates in the same model, which would indicate that slopes for the interaction model might be unreliable for interpretation.

We calculated VIF values using the vif function from the car package (v3.1.2) in R (v4.1.2) with the omnibus multinomial model of yard type frequencies, which included fixed effects of income and lot size (here with no interaction because interactions alter interpretation of VIF). Using this model, lot size VIF = 6.4 and income VIF = 2.2. These values are below the commonly-used cutoff of 10, but for the lot size value may be high enough to cause concern.

We therefore followed up with comparisons of univariate and interaction models to understand how estimates of each coefficient affected each other (Fig. B2). Note that for weedy yards, there were convergence warnings and confidence intervals could not be estimated, so for the purposes of this figure the weedy yard models have only a random effect of census tract; the other models have random effects of both city and census tract, as in the main text.

In this comparison, none of the effects flipped sign when included in the same model, none of the effects changed from significant to non-significant, and effect sizes were similar.

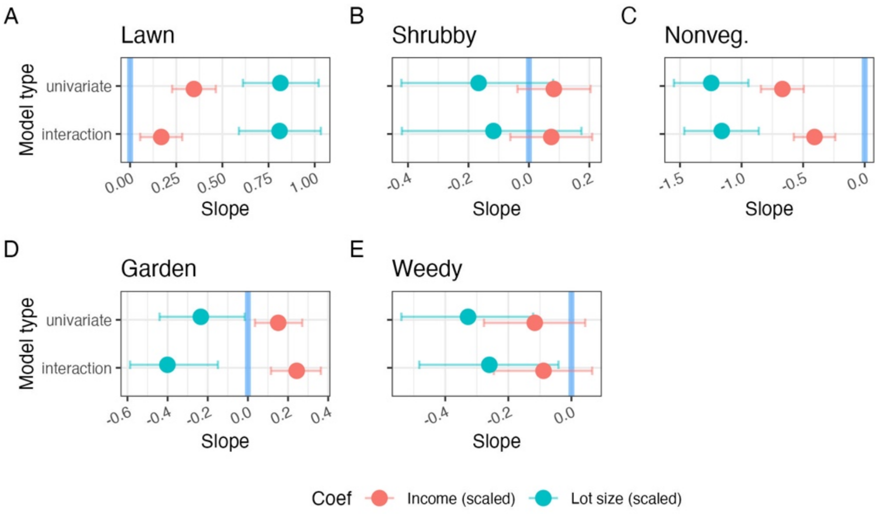


Fig. B2: The effect sizes (slopes) for models with income and lot size included in the same model (with an interaction) or with only one of the two in a model (both cases with city and census tract as random effects). Error bars show 95% confidence intervals.

Taking these two diagnostics into account, the significant effects we observed are not being driven by collinearity, so we proceeded with including both lot size and income in models.

APPENDIX 1C: Consistency and accuracy of Google Street View Scoring (Chapter 2)

The utility of Google Street View scores as a representation of floral richness in yards depends in part on scorer consistency and on the accuracy of how well scored images correspond with conditions on the ground. Here, we report details of how image scorers varied in their assessments of yards and also how accurately Street View scores represented on-the-ground yard assessments using the subset of yards we visited in person to perform floral surveys.

Two scorers gathered all the Street View data, here denoted as scorer A and scorer B. Each image was scored once (other than the quality control checks on all gardens and weedy yards by A.M.). Scorer A assessed 26,800 images (27%) and Scorer B assessed 73,247 images (73%)(note that this total is greater than the ~86,000 addresses analyzed in the manuscript because it includes images that were assessed but categorized as unscoreable).

To assess repeatability, or how often scorers agreed when assessing the same image, we gave each scorer the same set of 999 random images and asked them to assess them in the same way as the rest of the data. Overall, the absolute agreement between scorers was 75% (752 out of 999 images received the same score from both scorers).

In order to test whether variation between scorers would affect the outcome of our analysis, we performed the same analysis from the main manuscript separately using the data gathered by each scorer. In general, using data from only Scorer A or Scorer B does not substantially affect our inferences (Fig. C1). The direction of the slope of each of the main effects of income and lot size remains the same in the subsets of Scorer A or B data and in the full data set. Statistical significance does change in some cases, but this is unsurprising given the substantial reduction in sample sizes when excluding one scorer's data — from a statistical power perspective, recall that although there are tens of thousands of total addresses in each scorer's data set, there are only dozens to hundreds of scored lots *per tract*, which is part of why such large sample sizes are required for this analysis. The interaction term appears somewhat more sensitive to scorer identity; this interaction is not a key part of our inference (see main text of this paper), particularly for the categories that were most sensitive to scorer identity (non-vegetated and shrubby yards).

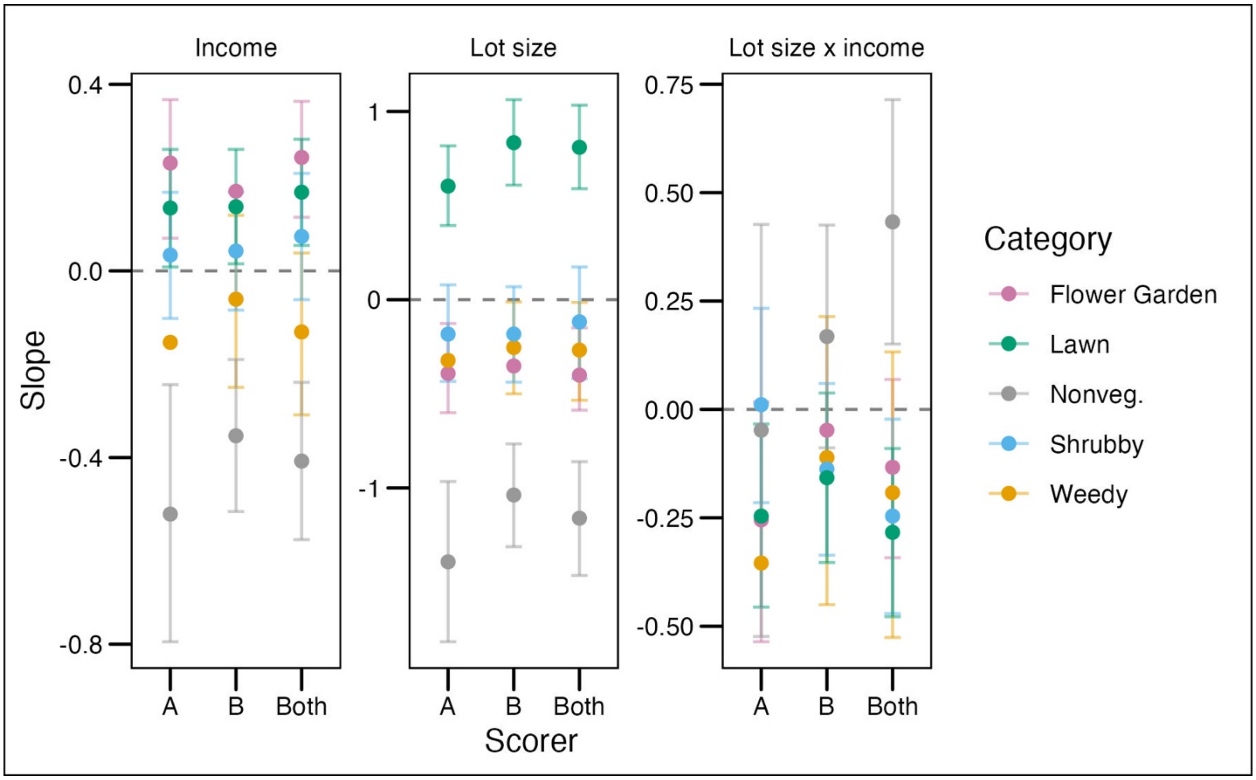


Fig. C1: Model slope estimates with 95% confidence intervals estimated using data from only Scorer A, only Scorer B, or both scorers combined (both combined is the data used in the main manuscript). Models are of the same structure as the main analysis, a binomial GLMM predicting frequency of each category at the census tract level using fixed effects of income, lot size, and their interaction, with random effects of city and census tract. Two confidence intervals could not be estimated by the model (for data subsetted by scorer). Predictors are centered at 0 and scaled. Note that the scale of the y-axis has been allowed to vary across panels to facilitate comparison between the scorers.

We also can compare the match between Google Street View scores and on the ground assessments. To make this assessment, we qualitatively categorized each yard we visited in person, based on field notes describing the yard and the species lists. Note that we did not quantitatively assess % cover of turfgrass, shrubs, or impervious surface, which would be interesting to assess if similar studies are done in the future. For flower gardens, the category that was our primary focus, performance was good: 86.8% of addresses scored as flower gardens on Google Street View had flower gardens when visited in person. For the addresses that were inaccurately scored on Google Street View, the imagery was predominantly relatively old (i.e. >10 years old, pers. obs.), suggesting that if Google's public API supported constrained time ranges, this method could have improved performance. Street View scores also performed well for lawns, the most abundant yard type, with 90.6% of addresses scored as lawns on Google Street View being lawns when visited in person. For the other categories, performance was somewhat lower: 67.3% for shrubby, 62.1% for non-vegetated, and 55.7% for weedy.

APPENDIX 2: Supplemental Material for Chapter 3

Supplemental analysis:

Our analysis is based on the assumption that demographic factors do not substantially vary at the small scale of our within-census-block analysis. Instead, these demographic factors tend to vary at larger grains, like the census block group or tract levels (hence our inclusion of random effects of city, tract, and block group in our models). To explore this assumption, we quantified similarity in tax-assessed home valuations across the range of the 1st to 30th neighbors away in our data set. We found only weak declines in correlations of total tax assessed value between neighbors 1–30 (Fig. S1). In addition, correlations in tax-assessed home value did not significantly decline from the 1st to 15th nearest neighbors. Tax assessed values are not equivalent to income, and we do not have per-household demographic information to test whether those factors would follow the same trends, but we expect similar patterns to hold across most demographic factors, wherein neighbors tend to be relatively demographically similar to each other at the scale of 1 to 15 neighbors. Because in our data the strongest garden clustering occurs at the 1 to 15 neighbor scale, especially in the 1–5 neighbor scale, this suggests we are measuring the results of contagion, not merely demographic similarity between neighbors.

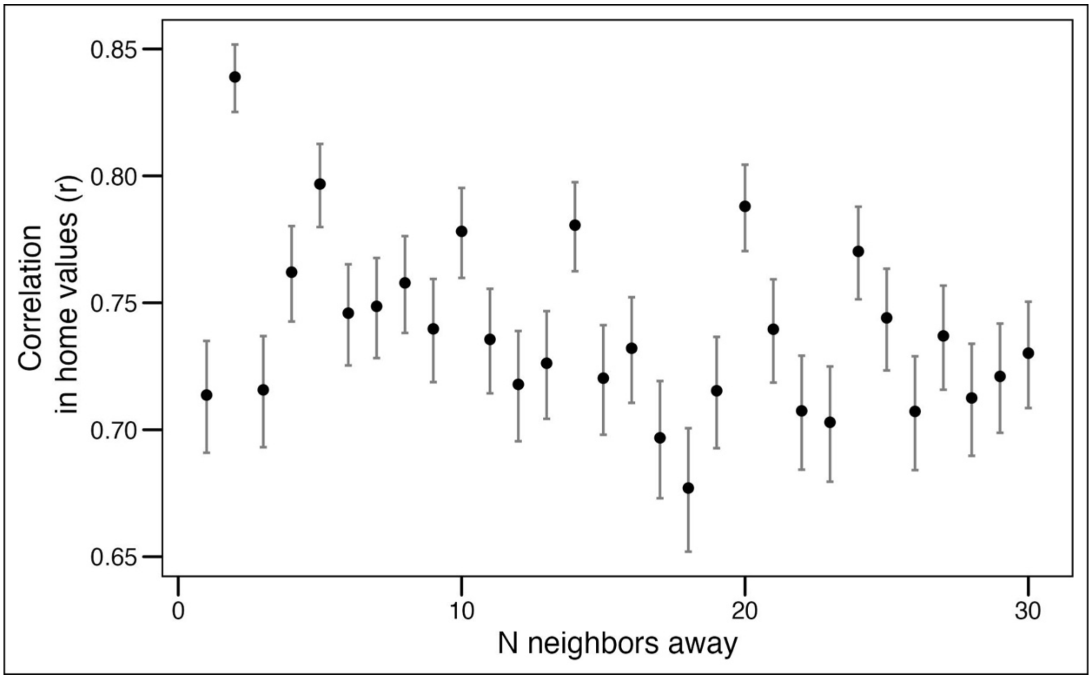


Fig. S1: The Pearson's correlation coefficients between the total tax assessed value of a focal address (building plus land valuations) and its 30 nearest neighbors. The error bars show 95% confidence intervals around each point estimate of r. The correlation coefficient declines significantly but weakly over the 1st to 30th neighbor range (linear regression, slope = -0.0015, $F_{1,28} = 4.7$, $p = 0.04$). Over the range of 1st to 15th neighbors, there is no significant decline in correlation for home values (linear regression, slope = -0.002, $F_{1,13} = 0.9$, $p = 0.4$).

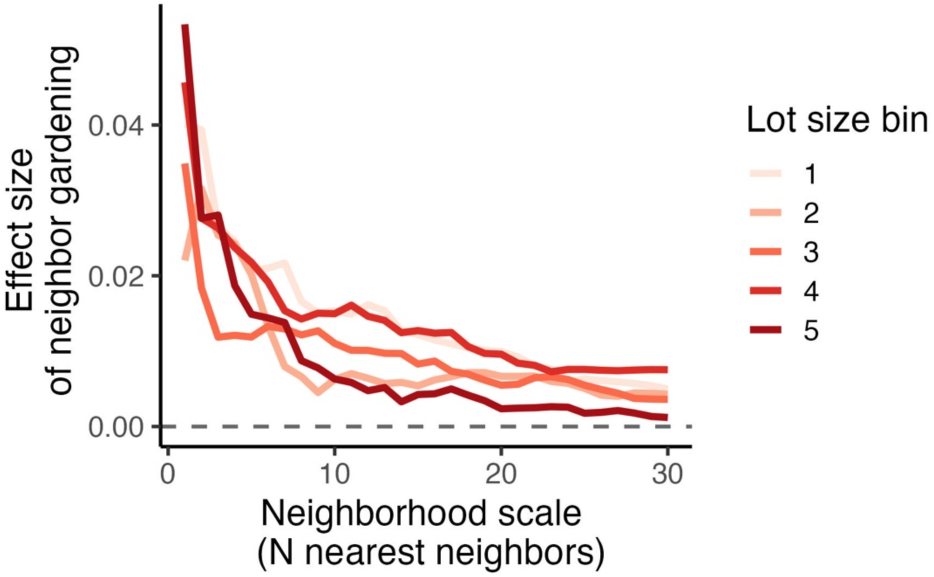


Fig. S2: Across lot size bins, the effect of a neighbor gardening on the prevalence of flower gardening as a function of how far away the neighbor is. Using the same approach for each bin as Fig. 2, effect size is calculated using a binomial GLMM estimating the probability of being a flower garden with a fixed effect of the neighbor being either a garden or a random non-garden, and random effects of city, census tract, and census block group. Positive values for effect size indicate elevated prevalence of gardens within the set of N neighbors away from a flower garden. Confidence intervals are not shown, for visual simplicity. Lot size bins are ordered from smallest to largest, so bin 1 = small lots and bin 5 = large lots.

APPENDIX 3A: Supplemental Material for Chapter 4

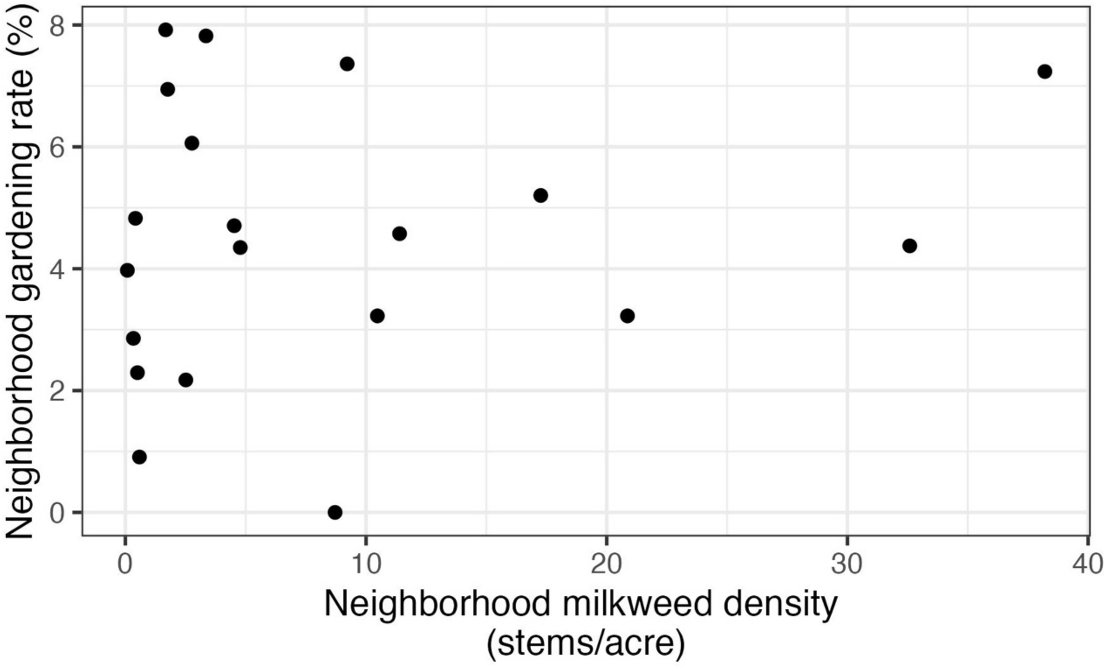


Fig. S1: Gardening rate (% of front yards with flower gardens) vs. milkweed density (N total stems per acre within the survey area), with neighborhood sizes of 207m for gardening and 107m for milkweed density, selected via likelihood profiling. The linear relationship is not statistically significant (Pearson's r = 0.16, t = 0.70, df = 18, p =0.49).

Table S1: Total number of observations of monarchs of each life stage in the pots, summed across all parks and all surveys. 'L1' = first larval instar, etc. Individuals were not uniquely marked and we cannot attempt to account for repeated sightings of the same individuals, except for the largest instars (L4, L5) and pupae.

Life stage	N observations
Eggs	858
L1	64
L2	28
L3	2
L4	1
L5	1
Pupae	2

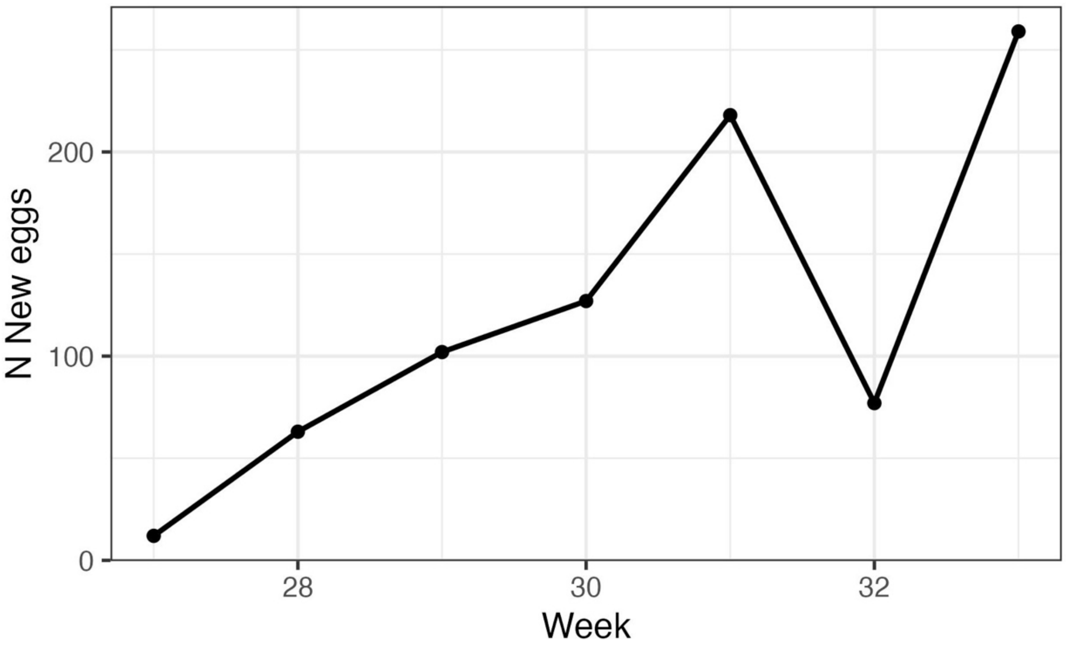


Fig. S2: Total new monarch eggs laid each week, summed across all sites. The x-axis is given in week of the year and covers the dates July 4 through August 19.

APPENDIX 3B: Comparison to past studies (Chapter 4)

We compared our observed monarch eggs densities per stem to three past studies, in order to assess whether our pots supported comparable levels of oviposition to previous reports. These past estimates were obtained using the following sources:

- Cutting & Tallamy (2015): reported mean and SE for 'eggs per plant per visit' in their Table 1; reported for natural sites and gardens separately, and for each of two study years separately
- MLMP [Monarch Larva Monitoring Project](Stenoien et al. 2015; data downloaded from Table S3 in Marini and Zalucki 2017): mean 'maximum eggs per stem per site', reported annually by region; for our purposes we averaged across the period 1998–2014 for the northeast region in Jul.–Aug.; includes both natural sites and gardens
- Geest et al. (2019): pers. comm. from the author, mean eggs per stem per survey; includes both natural sites and gardens.

The inclusion of both natural sites and gardens does not have substantial impacts for comparing these estimates of oviposition rates because rates are broadly similar in both habitat types.

We observed comparable oviposition rates to past reports (Fig. B1).

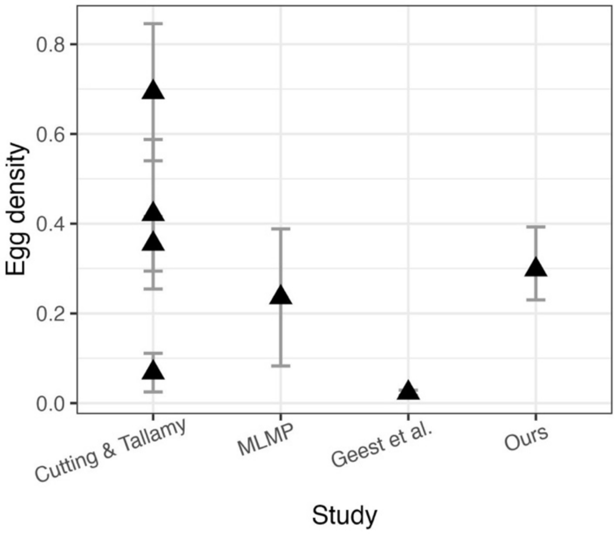


Fig. B1: Comparison of our study's overall mean observed monarch oviposition rate to past estimates. Egg density is calculated as the average eggs per survey per stem. Triangles show mean values and error bars show 95% confidence intervals calculated using reported SE for the past studies. Our estimate and confidence intervals were calculated using a negative binomial GLM with an offset of log(stems).

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