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LETTER

Multiple ecosystem service synergies and landscape mediation of biodiversity within urban agroecosystems

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Abstract

Ecosystem services (ESs) are essential for human well-being, especially in urban areas where 60% of the global population will live by 2030. While urban habitats have the potential to support biodiversity and ES, few studies have quantified the impact of local and landscape management across a diverse suite of services. We leverage 5 years of data (>5000 observations) across a network of urban community gardens to determine the drivers of biodiversity and ES trade-offs and synergies. We found multiple synergies and few trade-offs, contrasting previous assumptions that food production is at odds with biodiversity. Furthermore, we show that natural landscape cover interacts with local management to mediate services provided by mobile animals, specifically pest control and pollination. By quantifying the factors that support a diverse suite of ES, we highlight the critical role of garden management and urban planning for optimizing biodiversity and human benefit.

KEYWORDS
ecosystem function, food system, pest control, pollination, trade-offs

INTRODUCTION

Biodiversity-mediated ecosystem services (ESs) are ecosystem processes that contribute to human well-being (Daily, 1997; MEA, 2005), including pollination, carbon sequestration and food production, among many others, and are currently valued at >$33 trillion annually worldwide (IPBES, 2016). While humans benefit from a wide array of ESs, they also differentially impact the quality and quantity of services provided through their habitat management activities (Dade et al., 2019; Dainese et al., 2019; Goldstein et al., 2012). This is particularly true in agroecosystems where crop biomass often negatively correlates with biodiversity, highlighting potential conflicts in optimizing multiple ESs (Landis et al., 2018). Given predictions of increasing trade-offs between crop production and biodiversity (Lawler et al., 2014), it is essential to characterize how multiple categories of ES shift across landscapes (Felipe-Lucia et al., 2014; Gomes et al., 2020; Li et al., 2017; Raudsepp-Hearne et al., 2010). While recent work reveals that ES categories can exhibit synergies and trade-offs (positive/negative correlations) (Smith et al., 2013), little is known about relationships between biodiversity and ES within urban landscapes (Howe et al., 2014) and the role of local habitat management and landscape composition as underlying mechanisms regulating trade-offs and synergies (Boerema et al., 2017; Dade et al., 2019; Hatt et al., 2018).

Furthermore, some metrics of biodiversity and ESs may be contingent on the interaction between local

habitat complexity and landscape composition (Hatt et al., 2018; Martin et al., 2019; Seibold et al., 2019; Tscharntke et al., 2005, 2012). The intermediate landscape-complexity hypothesis posits that loss of landscape-level complexity (e.g. natural landscape cover) negatively impacts animal biodiversity and ESs in simple local habitats (e.g. habitats with low-vegetation diversity) due to losses in colonization from the surrounding natural landscape, but may have little impact within complex local habitats where biodiversity and ESs are locally supported (sensu Tscharntke et al., 2005, 2012). In other words, local habitat complexity can have stronger effects on biodiversity and ESs in intermediate landscapes compared to very simple or very complex landscapes. In this way, local habitat complexity, often measured as local herbaceous plant richness (Diehl et al., 2013; Stein et al., 2014), may critically impact ecosystem function within human-dominated landscapes. Specifically, while local habitat and landscape composition may interact to impact biodiversity and ESs, a range of landscape-moderated resource concentration and dilution effects have been observed (reviewed in Tscharntke et al., 2012), particularly in the case of mobile ES providers, such as pollinators and natural enemies (Lichtenberg et al., 2017; Tscharntke et al., 2016). For example, if few animal foragers are present in simple landscapes, resource 'dilution' may occur, where foragers spread out when local resources increase at a site, resulting in a reduction in per-resource visitation (Doublet et al., 2019; Otway et al., 2005; Root & Kareiva, 1984; Yamamura, 1999) and lower ES provisioning. If many foragers are present in simple landscapes, resource 'concentration' may occur, where more foragers visit when local resources increase at a site, resulting in an increase in per-resource visitation (Sih & Baltus, 1987; Totland & Matthews, 1998; Wenninger et al., 2016) and higher ES provisioning. Both 'dilution' and 'concentration' effects may also be strengthened, weakened or unaffected by increasing landscape complexity (Figure 1). Even though intermediate landscape-complexity theory has been critical at predicting animal biodiversity and ESs, it has rarely been evaluated in urban areas, despite evidence for its existence in the ecologically and economically important urban agroecosystem (Ballare et al., 2019).

Urban agroecosystems, which include community gardens, private gardens and urban farms and orchards, are relevant to both biodiversity and food production goals of cities (Lin et al., 2015) and are expanding globally (Siegner et al., 2018), contributing an estimated 15–20% of the world food supply (Hodgson et al., 2011). They are also ideal systems for exploring the mechanisms underlying trade-offs and synergies across biodiversity and ESs, given high local habitat heterogeneity (Lin et al., 2015) and direct connection to local food security (Alig et al., 2004; Lovell, 2010). Urban agriculture is a critical asset to food security where spatial inequities have created limited access to fresh produce

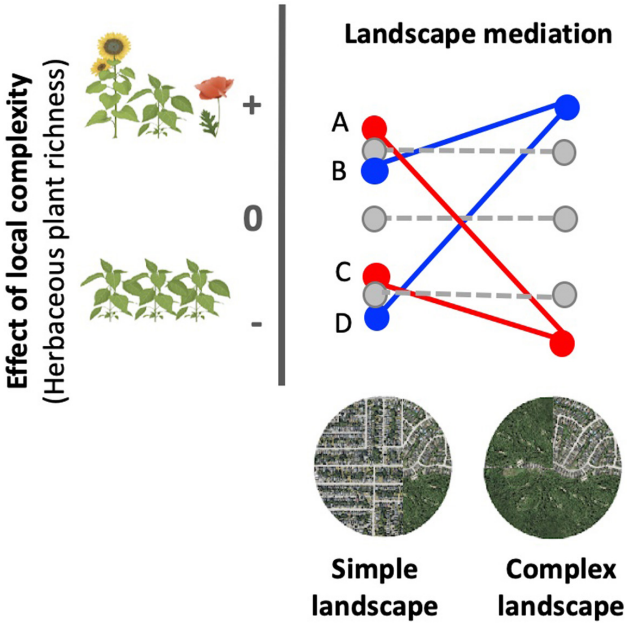

FIGURE 1 Conceptual framework visualizing landscape-specific management synergies and trade-offs, which describe the positive and negative impacts of local complexity (herbaceous plant richness) on animal biodiversity and ecosystem services, that are mediated by landscape complexity (natural habitat cover). Four hypothesized responses are visualized: (A) local complexity has a weakened concentration effect (starts positive, becomes more negative) with increasing landscape complexity, (B) local complexity has a stronger concentration effect with increasing landscape complexity (starts positive, becomes more positive), (C) local complexity has a stronger dilution effect with increasing landscape complexity (starts negative, becomes more negative) and (D) local complexity has a weaker dilution effect (starts negative, becomes more positive) with increasing landscape complexity (blue = more positive effect of local complexity, red = more negative effect of local complexity and grey = no change in effect of local complexity with increasing landscape complexity).

by reduced proximity to markets, financial limitations and inadequate transportation (Thomas, 2010; Ver Ploeg et al., 2009; De Master & Daniels, 2019). While studies from rural agroecosystems have characterized food production as at odds with biodiversity (Foley et al., 2005; Glamann et al., 2015; Tilman et al., 2011; but see Hanspach et al., 2017), this relationship has never been rigorously explored in urban agroecosystems, despite the role of gardeners as both local habitat managers and direct beneficiaries of ESs (Lin et al., 2015). Previous work in urban agroecosystems has explored variation in single services or service providers (Bennett & Lovell, 2019; Rocha & Fellowes, 2018), with few studies investigating multiple services (Clarke & Jenerette, 2015; Dennis & James, 2016; but see Cabral et al., 2017). Furthermore, a tendency to use narrow service- or provider-specific sampling and modelling approaches for each metric has limited the opportunity to evaluate relationships across biodiversity and ES metrics (Boyd & Banzhaf, 2007; Seppelt et al., 2011). This gap in the biodiversity-ES literature, coupled with the increasing relevance of urban

agriculture for global food security, highlights an urgent need to understand potential trade-offs and synergies across multiple metrics of biodiversity, food-security and well-being.

We used 15 data sets collected over 5 years from a network of urban agroecosystems to investigate synergies and trade-offs across seven categories (22 metrics) of ESs and two categories (18 metrics) of mobile animal ecosystem service providers (ESPs) (sensu Kremen, 2005; Kremen et al., 2007). We ask two main questions (I) *Are there synergies and trade-offs across biodiversity and ESs, and do local and landscape management factors drive these relationships?* and (II) *Are the impacts of local complexity on biodiversity and ESs mediated by landscape complexity?* We investigate multiple ESs (pest control, pollination, climate regulation, carbon storage, water conservation, food production and gardener well-being), as well as two ESPs (natural enemies and pollinators), to test the following hypotheses: (H1): Direct trade-offs are more frequent than synergies among and between ESs and ESPs in urban agroecosystems, (H2): Local and landscape management serve as critical mechanisms underlying synergies and trade-offs among ESs and ESPs and (H3): Landscape complexity mediates the effect of local agroecosystem management on ESs and ESPs, especially ESs provided by mobile animals.

MATERIALS AND METHODS

Study system

Between 2013 and 2017, we collected data three to five times from May to September within 28 urban community gardens in the central coast of California, USA (see Egerer, Arel, et al., 2017; Philpott & Bichier, 2017) (Figure S1). During each garden visit, we counted the number and species of trees and shrubs within a 20 × 20 m plot and measured herbaceous plant species richness, flower abundance and ground cover composition (percent bare soil, rocks, grass, mulch) within four (2013–2015) or eight (2016–2017) randomly placed 1 × 1 m quadrats in the plot (see Philpott & Bichier, 2017).

Landscape composition

We quantified landscape composition within 2 km of each garden using data from the 2011 National Land Cover Database (NLCD, 30 m resolution) (Homer et al., 2015). The 2 km buffer size is inclusive of typical foraging distances for our focal animal taxa (arthropods and birds) and the time period is closest to the average sampling year (as in Cohen et al., 2021; Philpott & Bichier, 2017). We calculated the percent of natural landscape cover (comprised of deciduous forest, evergreen forest, mixed forest, shrub/scrub and grassland/herbaceous), which ranged between 0 and 61.2%, with spatial statistics tools (ArcGIS v. 10.1) (ESRI).

Ecosystem services

In the same gardens, we measured seven ESs: pest control, pollination, climate regulation, carbon sequestration, water storage, food production and human well-being (Table S1). We evaluated four pest control metrics (ES-Pest-control)—three measuring prey removal (see Philpott & Bichier, 2017) and one measuring parasitism (see Egerer, Liere, et al., 2018). We evaluated six pollination metrics (ES-Pollination)—two measuring open pollination success (see Cohen et al., 2021), three measuring fruit set (the proportion of flowers developing into fruits) and one measuring conspecific pollen deposition. We evaluated one climate mitigation metric (ES-Climate)—variation in daytime garden temperatures (see Lin et al., 2018), one carbon sequestration metric (ES-Carbon)—soil organic matter (see Egerer, Ossola, et al., 2018) and one water conservation metric (ES-Water) – soil water holding capacity (see Egerer, Ossola, et al., 2018). We included five food production metrics (ES-Food)—four measuring weight or volume of focal crops (see Cohen et al., 2021) and one assessing gardener-reported food production. We evaluated four human well-being metrics (ES-Well-being) that describe gardener perceptions of well-being derived from gardener survey data (see Egerer, Philpott, et al., 2018) (see Supporting Information and Table S1 for details).

Mobile ecosystem service providers

We evaluated biodiversity levels for putative ESPs, specifically mobile animals that (a) consume or have non-consumptive negative effects on herbivores (ESP-Natural-enemy) or (b) visit flowers to collect pollen and nectar (ESP-Pollinator). We evaluated 14 metrics for natural enemies sampled with a variety of traps (pitfalls, sticky traps), visual surveys and point counts (Table S1). We quantified abundance and species richness for ants (Hymenoptera: Formicidae), carabids (Coleoptera: Carabidae), spiders (Arachnida: Araneae) (see Egerer, Arel, et al., 2017; Otoshi et al., 2015; Philpott et al., 2019), ladybeetles (Coleoptera: Coccinellidae) (see Egerer, Bichier, et al., 2017) and insectivore birds (Animalia: Aves) (see Mayorga et al., 2020). We quantified abundance and family richness for parasitoids (Hymenoptera: Parasitica) (see Burks & Philpott, 2017) and all arthropods (see Philpott et al., 2020). We evaluated four metrics for pollinators sampled with netting, pan-trapping and non-lethal observation (Table S1). We quantified abundance and richness of bees (Hymenoptera: Apidae) (see Plascencia & Philpott, 2017; Quistberg et al., 2016) and pollinators (Hymenoptera, Diptera, Coleoptera and Lepidoptera) (see Cohen et al., 2021). For all 18 metrics, we

extrapolated richness using the Chao1 index (Chao, 1987), which accounts for uneven sampling and undersampling, using the vegan package in R (Oksanen, 2013).

Statistical analyses

We define *direct synergies and trade-offs* as significant positive and negative correlations between any two biodiversity and ES metrics, *management synergies and trade-offs* as significant positive and negative relationships between biodiversity and ESs driven by a change in a single local or landscape management factor (as in Bennett et al., 2009; Tomscha & Gergel, 2016), and *landscape-specific management synergies and trade-offs* as significant positive or negative relationships between biodiversity and ESs driven by the interaction between local vegetation complexity, characterized by herbaceous plant richness, and landscape complexity, characterized by natural landscape cover (Figure 1). We selected herbaceous plant richness because it includes the focal vegetation of urban gardens (weeds, crops and ornamentals), is correlated with local vegetation cover and complexity and is commonly used to capture local vegetation complexity (Diehl et al., 2013; Stein et al., 2014). We selected natural landscape cover as it is correlated with landscape-level heterogeneity and richness, often used to capture landscape complexity (Tscharntke et al., 2005, 2012), and interacts with local habitat management to impact mobile ESPs within urban areas (Ballare et al., 2019). Unlike a metanalysis, which compares patterns across independent studies (Glass, 1976; Harrison, 2011), we leverage 5 years of data in the same study system, where we can investigate the impacts and interactions between a standardized set of environmental variables (as seen in rural agricultural systems, e.g. Werling et al., 2014, Robertson et al., 2012) but for the first time in urban agricultural systems.

Direct synergies and trade-offs between ecosystem services and ecosystem service providers

To quantify *direct synergies and trade-offs*, we conducted three sets of correlation analyses (Washbourne et al., 2020) between each of the 22 ES and 18 ESP metrics, and across all ES and ESP metrics (Figure 2, Figures S2, S3). We averaged each metric across years to obtain a single value per site and then conducted Pearson correlations using the R package corrplot (Wei, 2021). To reduce potential type I errors associated with multiple testing within the three sets of correlation analyses (231, 153 and 780 comparisons) while also minimizing type II errors, we controlled for false discovery rates using the Benjamini–Hochberg procedure (Benjamini & Hochberg, 1995) with a conservative threshold of 0.05 (Verhoeven et al., 2005).

Management synergies and trade-offs and landscape-specific management synergies and trade-offs across ecosystem services and ecosystem service providers

To quantify *management synergies and trade-offs*, as well as *landscape-specific management synergies and trade-offs* across the 22 ES and 18 ESP response metrics, we used generalized linear mixed effects models with the glmer function in R. Because many local and landscape predictor variables were correlated, we prioritized variables previously found to be ecologically meaningful in describing biodiversity and ESs in our study system, specifically those related to garden size, ground cover, tree and shrub abundance, floral abundance and herbaceous plant richness (Egerer, Arel, et al., 2017; Egerer, Liere, et al., 2018; Otoshi et al., 2015; Philpott & Bichier, 2017; Quistberg et al., 2016) and included an interaction between local-level herbaceous plant richness and natural landscape cover (as in Ballare et al., 2019). We then calculated a variance inflation factor (VIF) for each model set using the car package in R (Fox & Weisberg, 2018) and ensured all VIF scores were below 4. Using this process, all models contained five unique fixed local and landscape predictor variables: garden size (ha), mulch ground cover (per m^2), number of trees and shrubs (per 400 m^2), number of flowers (per m^2), herbaceous plant richness (per m^2, estimated using Chao index for repeated samples), natural landscape cover (percent in 2 km radius) and the interaction between these latter two terms, with year and garden as random effects for datasets with multiple years. For ES and ESP response metrics for which previous studies documented impacts of animal biodiversity, focal crop abundance, agricultural landscape cover, plot structure or housing opportunity, we added these predictor variables, but only if their inclusion did not lead to VIF scores above 4 (see Supporting Information for additional details).

For the response ES and ESP metrics, we used a Poisson error distribution for count data and a Gaussian error distribution for all non-integer metrics. For a subset of non-integer metrics, we used a log10 transformation to better fit assumptions of normality. For response variables that were proportions or success/failure ratios, we used a Binomial error distribution (Table S1). For most models, we used predictor variable values measured in the same month as ES and ESP response data; however, for seven response variables measured weekly, we used raw herbaceous plant richness data specific to each survey week and included week as an additional random effect (Table S1). For all models, we standardized continuous predictor variables using the scale function in R such that a value of zero represents the mean value for that variable, and a positive or negative represents a higher or lower value relative to the mean. For all models, we ran model selection using the MuMIn package (Barton, 2012) and selected the top model for each of the response variables based on the AICc values. For models where the AICc

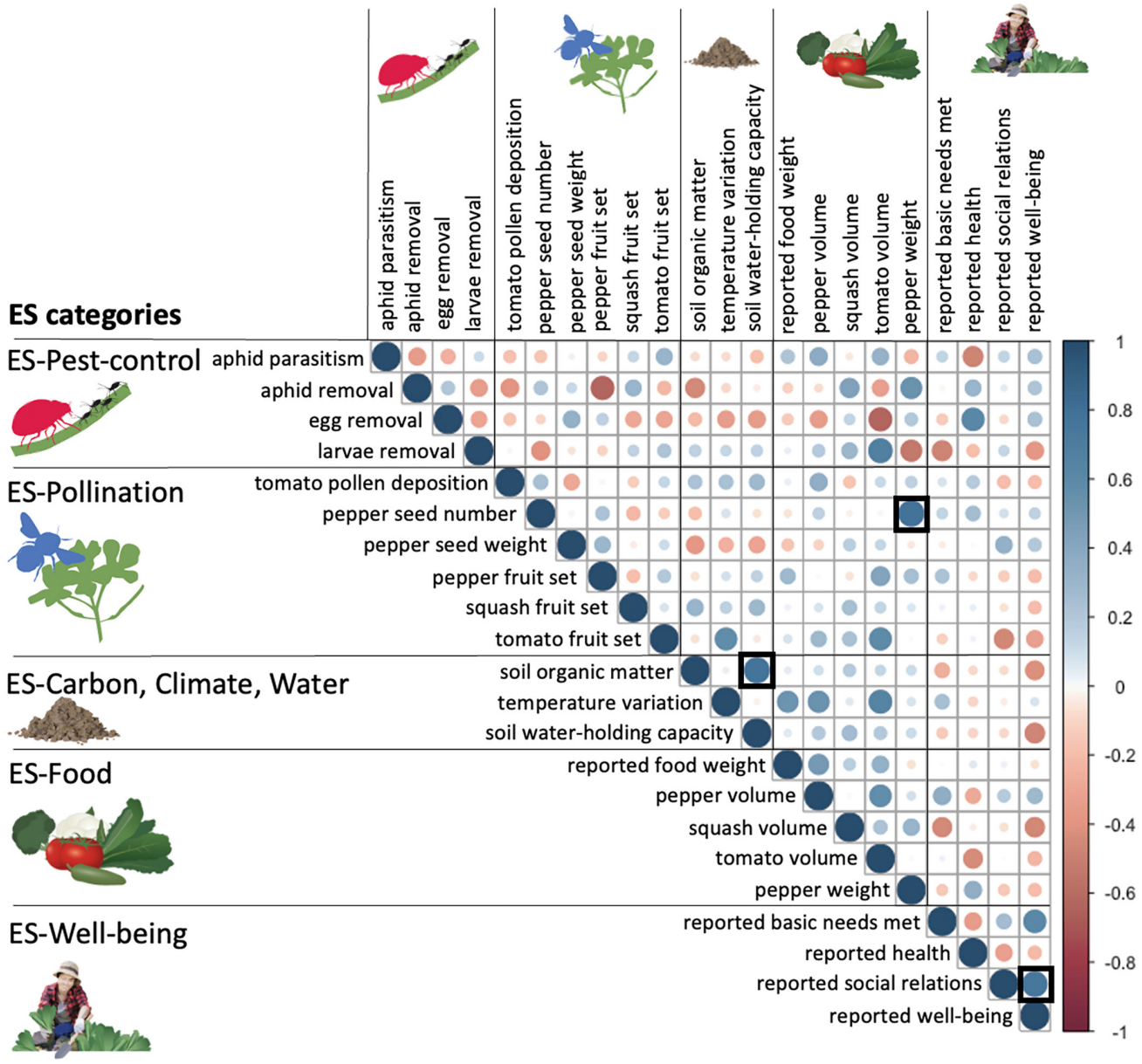

FIGURE 2 Direct ecosystem service (ES) synergies and trade-offs shown as correlations between ES categories (separated by black lines) and metrics within. Only Benjamini–Hochberg adjusted significant *p*-values are boxed in black, and the size of the circle indicates the absolute value of the corresponding correlation coefficient (red = negative, blue = positive).

for the top model was within two points of the next best model, we calculated conditional model averages (as in Coux et al., 2016; Philpott & Bichier, 2017). We chose the conditional model average given the standardized large set of predictor variables (Table S6), and our interest in detecting all local habitat and landscape composition factors that may have even weak significant effects (sensu Grueber et al., 2011) on the response ES or ESPs. To reduce potential type I errors associated with multiple testing (209 comparisons in ES models, 132 comparisons in ESP models), we implemented the Benjamini–Hochberg procedure with a conservative threshold of 0.05.

To visualize *management trade-offs and synergies*, we displayed the direction and portion of models with significant local and landscape predictors for each ES or ESP category. Specifically, we defined *management trade-offs and synergies* as differential response to changes in local or landscape variables (negative = management-trade-offs, positive = management-synergies) and divided the number of models for which we found significant predictors (positive or negative) by the total number of models evaluated for each ES or ESP category (Figure 3). This allowed us to visualize and compare *management trade-offs and synergies* for each ES and ES category.

To visualize *landscape-specific management synergies and trade-offs* across the 22 ES and 18 ESP response metrics, we first referred to the literature and noted past definitions of 'simple' landscapes as those with 1–20%

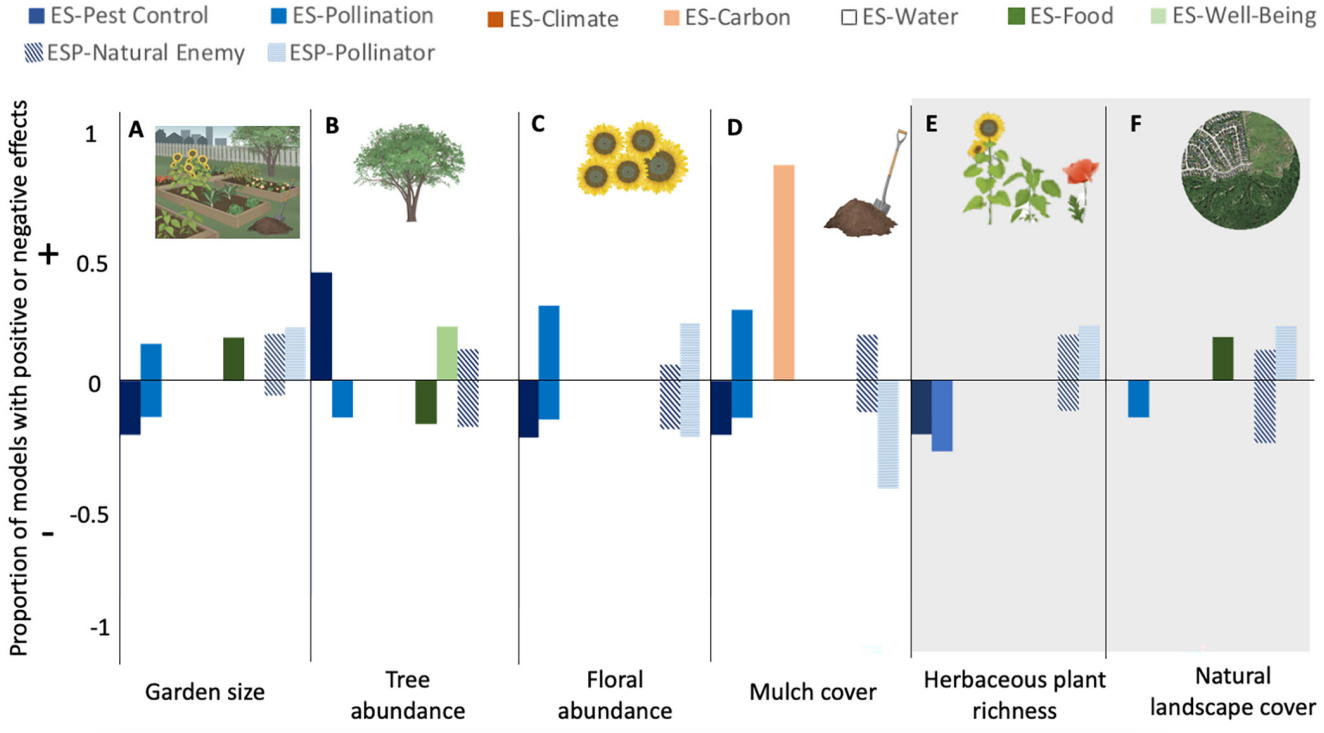

FIGURE 3 Response to local and landscape management characteristics (in separate panels, listed on the bottom) and resulting trade-offs between ecosystem services (ES) and mobile ecosystem service providers (ESPs). Proportion of models with significant positive or negative effects of the management characteristics are depicted, where local management characteristics include (A) garden size, (B) tree abundance, (C) floral abundance, (D) mulch cover and (E) herbaceous plant richness (when natural landscape cover is held at the mean), and where landscape management includes (F) natural landscape cover (when herbaceous plant richness is held at the mean). The two interacting management characteristics are shaded in grey (Tables S2 & S6).

non-crop cover and complex landscapes as those with >20% non-crop cover (reviewed in Tscharntke et al., 2005). We then visualized model coefficients for herbaceous plant richness in both 'simple' landscapes, defined here as when natural landscape cover in the landscape is held at the mean value (~16% across years in our datasets) and increasingly 'complex' landscapes (> ~16% natural landscape cover), where the coefficient for the interaction captures the effect of this increase. We visualized all models for which herbaceous plant richness was included as a predictor in the best model and plotted significant changes in the effect of herbaceous plant richness on the ES and ESP response variables, given increases in natural landscape cover (Figure 4).

RESULTS

Direct synergies and trade-offs between ecosystem services

We documented three significant synergies and no significant trade-offs between the 22 ES metrics. Across the ES comparisons, 55.4% of all correlations were positive while 44.6% were negative. ES-Food had largely positive correlations with ES-Carbon, ES-Climate, ES-Water and ES-Pollination, but had mixed correlations with ES-Pest-control and ES-Well-being (Figure 2). We documented three significant synergies and no trade-offs between the 18 ESP metrics, where 59.5% of all correlations were positive and 40.5% were negative (Figure S2). Across all ES and ESP comparisons, we documented six significant synergies and no trade-offs, where 54.5% of all correlations were positive and 46.5% were negative. We found no significant trade-offs or synergies between ES-Food and any of the ESPs (Figure S3).

Management synergies and trade-offs across ecosystem services and ecosystem service providers

We documented significant *management synergies and trade-offs* across the seven categories of ESs (Figure 3, Tables S2–S6). Garden size had predominantly positive effects on ES-Food, ESP-Natural-enemy and ESP-Pollinator, mixed (positive and negative) effects on ES-Pollination and negative effects on ES-Pest-control (Figure 3A). Tree and shrub abundance had positive effects on ES-Pest-control and ES-Well-being, mixed effects on ESP-Natural Enemy and negative effects on ES-Pollination and ES-Food (Figure 3B). Floral

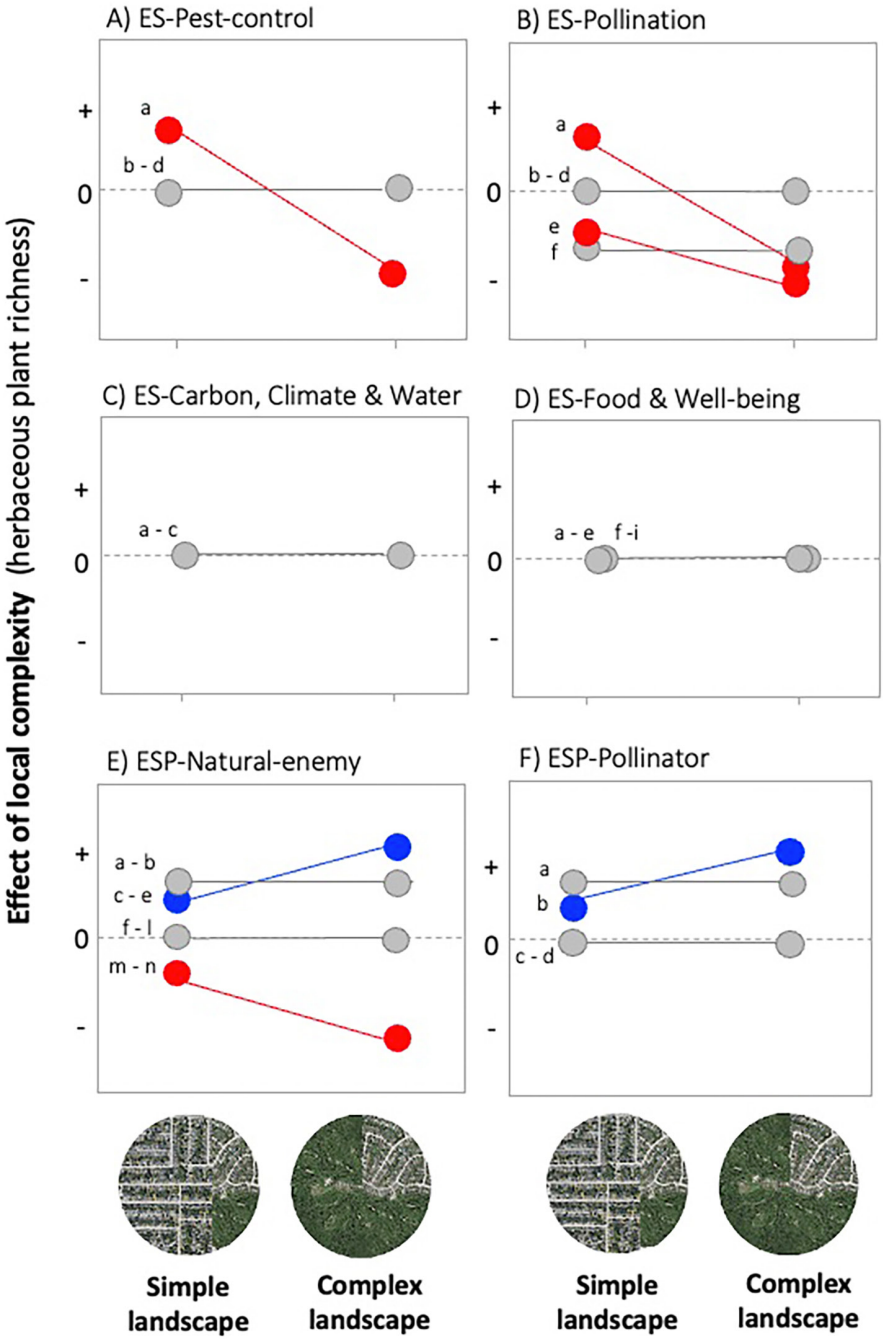

FIGURE 4 Impacts of local herbaceous plant species richness on ecosystem services (A–D) and mobile ecosystem service providers (E–F) in two landscape contexts, where simple landscapes represent those surrounded by mean natural landscape cover and complex landscapes represent those with greater than mean natural landscape cover. Red lines indicate a significant negative effect of herbaceous plant richness, blue lines indicate a significant positive effect of herbaceous plant richness and grey lines indicate no significant change in effect of herbaceous plant richness, with increasing natural landscape cover. ES-Pest-control services (A) are aphid parasitism (a), aphid removal, egg removal and larvae removal (b–d). ES-Pollination services (B) are tomato pollen deposition (a), squash fruit set, tomato fruit set and pepper seed weight (b-d), jalapeño seed number (e), and pepper fruit set (f). ES-Carbon, Climate and Water services (C) are coefficient of variation of °C temperature, soil carbon composition and soil water holding capacity (a-c). ES-Food and Well-being services (D) are volume of tomatoes, squash and pepper, weight of peppers and reported food production (a-e) and reported basic needs met, reported health, reported social relations and reported well-being (f–i). ESP-Natural enemies (E) are number of natural enemy families and abundance of ladybeetles (a-b), abundance of spiders, abundance of natural enemies, abundance of carabids (c-e), species richness of ants, species richness of carabids, species richness of spiders, species richness of ladybeetles, abundance of parasitoids, family richness of parasitoids, species richness of insectivorous birds (f–l), the abundance of ants and abundance of insectivore birds (m-n). ESP-Pollinators (F) are abundance of pollinators (a), abundance of bees (b), pollinator species richness and bee species richness (c-d).

abundance had mixed effects on ESP-Pollinator and ES-Pollination and predominantly negative effects on ES-Pest-control and ESP-Natural-enemy (Figure 3C). Mulch cover had positive effects on ES-Carbon, mixed effects on ES-Pollination and ESP-Natural-enemy and negative effects on ES-Pest-control and ESP-Pollinator (Figure 3D). Herbaceous plant species richness (when natural landscape cover is held at the mean) had predominantly positive effects on ESP-Pollinator, mixed effects on ESP-Natural Enemy and negative effects on ES-Pollination and ES-Pest Control (Figure 3E). Natural landscape cover (when herbaceous plant richness is held at the mean) had positive effects on ES-Food and ESP-Pollinator, mixed effects on ESP-Natural-enemy and negative effects on ES-Pollination (Figure 3F).

Landscape-specific management synergies and trade-offs for ecosystem services

We documented significant interactions between herbaceous plant richness and landscape complexity for nine metrics; three that showed negative impacts and six that showed positive impacts of local herbaceous plant richness in simple landscapes (where natural landscape cover is held at the mean) (Figure 4). With increasing landscape complexity, the positive impact of herbaceous plant richness becomes more negative (weakened concentration effect) for one ES-Pest-control and one ES-Pollination metric, and the negative impact becomes more negative (stronger dilution effect) for another ES-Pollination metric (Figure 4A,B). None of the ES-Climate, ES-Carbon, ES-Water, ES-Food or ES-Well-being metrics were significantly predicted by herbaceous plant richness and its interaction with landscape complexity (Figure 4C,D). For ESPs, with increasing landscape complexity, the positive impact of herbaceous plant richness became more positive (stronger concentration effect) for three ESP-Natural-enemy metrics, the negative impact became more negative (stronger dilution effect) for two other ESP-Natural-enemy metrics (Figure 4E), and the positive impact became more positive (stronger concentration effect) for one ESP-Pollinator metric (Figure 4F).

Landscape context also shifted synergies and trade-offs among ESs and ESPs. In simple landscapes (where natural landscape cover is held at the mean), two ES and four ESP metrics were positively impacted by herbaceous plant richness (concentration effect) while one ES and two ESP metrics were negatively affected by herbaceous plant richness (dilution effect); however, in increasingly complex landscapes, three ES metrics were more negatively impacted by herbaceous plant richness (weakened concentration and stronger dilution effect), while six ESP metrics became stronger in their respective concentration and dilution effects.

DISCUSSION

In this study, we synthesize multiple years of data across a suite of 40 biodiversity and ES metrics to reveal multiple synergies across urban landscapes. Specifically, we show that synergies dominate direct correlations between ES and biodiversity metrics, with no significant trade-offs related to food production. Furthermore, we demonstrate that surrounding landscape context mediates the response of many animal biodiversity and ES metrics to local complexity, creating new landscape-specific management synergies and trade-offs.

Direct synergies dominate for both ecosystem services and mobile ecosystem service providers

Across the ES and ESP metrics, we found that all significant direct correlations were positive; in particular, the ESs related to food production were positively correlated with services related to pollination, carbon, water and climate. While recent reviews have described an abundance of both ES synergies (Dade et al., 2019) and ES trade-offs, they have also expressed concern over reporting biases that may influence interpretations of such trade-offs (Howe et al., 2014). In our synthesis, we not only evaluated all possible trade-offs and synergies but also controlled for study region, spatial scale, time period and model composition. Interestingly, we did not document any synergies or trade-offs between food-related ESs and animal biodiversity metrics. Thus, optimizing food production is not inherently at odds with biodiversity conservation within urban agroecosystems. We emphasize that our results focus on urban agroecosystems, where gardens represent high-diversity habitat patches relative to the urban landscape; specifically, our study system is located in a region experiencing one of the fastest rates of population growth in the state of California (Lin & Egerer, 2020). Given this urban context, our results contrast much of the ES and development literature, which has traditionally focused on rural intensive agricultural systems and has often emphasized trade-offs between biodiversity and food production (e.g. Foley et al., 2005). Our comprehensive and standardized synthesis adds support to evidence of positive food and biodiversity relationships (Hanspach et al., 2017) and argues that urban agroecosystems serve as critical habitats where biodiversity and ES synergies dominate.

Local habitat management factors significantly drive ecosystem services, resulting in multiple synergies and trade-offs

Our work reveals a number of classic and unexpected management synergies and trade-offs, mediated by local

habitat factors and landscape composition. First, tree abundance within gardens produced ES synergies and trade-offs, displaying positive effects on pest control and gardener well-being but negative effects on pollination and food production. Urban trees provide habitat for natural enemies (Barth et al., 2015; Threlfall et al., 2016; Wood & Esaian, 2020), aesthetic benefits (Egerer et al., 2019; Nowak & Dwyer, 2007; Ordóñez Barona et al., 2016), recreation benefits (Bjerke et al., 2006) and cultural or historical value for residents (Dwyer et al., 1991). Unsurprisingly, the management trade-off we documented with crop production has also been noted outside of urban systems (reviewed in Luedeling et al., 2016), where local tree cover can reduce pollination success (Lindgren et al., 2018) and compete for water and soil nutrients (Bayala et al., 2015), limiting photosynthetically active radiation (Kessler, 1992). Because temporal overlap with crop growth, and thus competition for resources, is often the underlying factor mediating negative interactions (reviewed in Luedeling et al., 2016), we posit that staggering trees and crops spatially or temporally could reduce these ES trade-offs.

Second, we found evidence that mulch is a key predictor of ES management synergies and trade-offs as it positively correlates with soil carbon storage, but negatively correlates with pest control and pollinator abundance. In urban agriculture, mulching can enhance soil quality (Beniston & Lal, 2012) and increase carbon storage through soil structural enhancement (Gregory et al., 2016; Tresch et al., 2019). Many gardeners use mulch to suppress weeds and maintain 'tidy' spaces, which are a social norm in Western culture (Robbins, 2007) and reflect perceived usability of the ecosystem (Chollet et al., 2018; Unterweger et al., 2017). In both rural and urban settings, mulch management trade-offs have been frequently documented, where mulch additions alter natural arthropod predator biodiversity levels (Arnold et al., 2019; Dudás et al., 2016) and bird community composition (Munyenyembe et al., 1989), reduce habitat availability for ground nesting bees (McFrederick & LeBuhn, 2006; Threlfall et al., 2015) and may also reduce weedy species, upon which native pollinators forage (O'Connell et al., 2021).

Other notable ES management trade-offs in our system were driven by vegetation management, where floral abundance had negative impacts on natural enemies and pest-control but mixed effects on pollinators and pollination services. While rare, past work suggests that some natural enemy groups may indeed be negatively impacted by floral cover (Wyckhuys & O'Neil, 2007). On the other hand, floral abundance can variably affect urban pollinators (Buchholz & Egerer, 2020; Hung et al., 2019; Lowenstein et al., 2019) depending on pollinator functional group; specifically, in rural agroecosystems, some pollinators exhibit dilution effects (lower visitation when resources are higher), while others exhibit concentration effects (greater visitation when resources are higher) in response to floral resources, even in the same landscapes (Jha & Vandermeer, 2009; Veddeler et al., 2006). Thus, the mixed effects in pollination services evident in our synthesis are likely to occur in systems where pollination is mediated by functionally distinct taxonomic groups.

Both natural enemies and pollinators (ESPs) experienced predominantly positive effects from increased garden size, while pollinators exhibited additional positive responses to herbaceous plant richness and natural landscape cover. In terms of synergies, past urban research indicates that garden size positively impacts bee abundance and richness (Matteson & Langellotto, 2010; Pardee & Philpott, 2014) and that patch size correlates with natural enemy communities and predation (Fenoglio et al., 2013). Likewise, urban floral richness (correlated with herbaceous plant richness in our study) is highly predictive of pollinator diversity and abundance (Ballare et al., 2019), and vegetation complexity correlates with abundance and richness of natural enemies (Langellotto & Denno, 2004) especially in highly urbanized landscapes (Bennett & Gratton, 2012). Natural landscape cover or proximity has been shown to mediate both increases and decreases in pollination success (Gaines-Day & Gratton, 2016; Ricketts et al., 2008), and similar mixed effects on pest control (Bennett & Gratton, 2012; Burkman & Gardiner, 2014), with negative effects potentially driven by support of pest populations, lowered habitat suitability for natural enemies (reviewed in Tscharntke et al., 2016) and existence of alternative floral resources for pollinators (Gaines-Day & Gratton, 2016).

Landscape-specific management synergies and trade-offs exist only for mobile ecosystem service providers and their associated ecosystem services

We documented clear landscape-specific management synergies and trade-offs for mobile ESPs (ESP-Natural-enemy and ESP-Pollinator) and their ESs (ES-Pest-control and ES-Pollination), and no landscape-specific management synergies or trade-offs for the remaining services (ES-Climate, ES-Carbon, ES-Water, ES-Food or ES-Well-being). Often, the response of ESPs and associated ESs followed the predictions of the intermediate landscape-complexity hypothesis (Tscharntke et al., 2005, 2012), where the positive effects of local complexity (herbaceous plant richness) were diminished with increasing landscape complexity, seen in weakened concentration effects or stronger dilution effects with increasing natural landscape cover in the landscape. However, in contrast to predictions, we found that for many natural enemy and pollinator metrics, the effects of local complexity were more positive with increasing landscape complexity. This pattern can occur when more complex urban landscapes support a species pool of animal foragers that can more actively respond to local garden-level complexity (as in Ballare et al., 2019).

In rural agricultural landscapes, landscape context mediates the impacts of local management for arthropod richness (reviewed in Batary et al., 2011; Lichtenberg et al., 2017), pollinator abundance and richness (Kennedy et al., 2013), predation (Birkhofer et al., 2016), parasitism (Jonsson et al., 2015) and pollination (Nicholson et al., 2017). Though few urban parasitism studies have tested for an interaction between local and landscape variables or have failed to detect landscape effects (Bennett & Gratton, 2012; Lowenstein et al., 2017), research on urban birds and arthropods has indeed documented local-landscape interactions, where impacts of local vegetation depended on landscape complexity levels and were distinct for each functional group (Frey et al., 2018). Ballare et al. (2019) also found that locally simplified urban agroecosystems exhibited greater bee abundance and diversity in response to landscape-level natural cover compared with locally complex urban grasslands; to our knowledge, no other previous work has documented landscape-dependent impacts of local management on urban pest control and pollination services.

While categories of ESs may spatially cluster or covary (Raudsepp-Hearne et al., 2010) or demonstrate trade-offs and synergies depending on landscape type (Felipe-Lucia et al., 2014), we provide the first study to evaluate and document landscape-specific management synergies or trade-offs, where landscape context *mediates* the negative (trade-off) or positive (synergy) response of ES categories to local complexity. Most prior work focuses on larger-scale land use and services (Dobbs et al., 2014; Goldstein et al., 2012; Grafius et al., 2016) over time (Gomes et al., 2020), indicating that such changes can lead to new trade-offs and that synergies in ESs and may be spatially aggregated by landscape type (Li et al., 2017). While at least one study has examined the impact of fine-scale local habitat management on the delivery of multiple ESs (Tamburini et al., 2016), previous work has not evaluated habitat management as a key factor underlying ES synergies or trade-offs, despite the importance of habitat composition for mobile-agent based ESs (Kremen et al., 2007).

Interestingly, our analyses also reveal that animal-mediated ESs and their putative ESPs often respond to different local management and landscape factors, and thus biodiversity metrics do not always predict ES levels. For example, if trophic interactions are less top-down and more bottom-up regulated, where vegetation properties predict pest abundance via strong lower trophic-level processes (e.g. Denno et al., 2002), then pest-control ESs and ESPs may be decoupled. These results are also consistent with previous urban ecology studies, where fruit set is best predicted by local habitat management (Bennett & Lovell, 2019) or where pollinator diversity or abundance may not consistently predict fruit set because of differences in floral morphology and visitation rates across plant species (Lowenstein et al., 2015). This is likely because complementarity between mobile ESPs depends not only on the plant species they visit, but also the time and place of the visitation (Blüthgen & Klein, 2011; Hoehn et al., 2008). Additionally, if interspecific competition between ESPs results in niche shifts or increased specialization (sensu Inouye, 1978), then the impacts of pollinator diversity on plant reproduction may only be evident when surveying the entire plant community, not a subset of focal species. Furthermore, past work has documented that natural enemy impacts on herbivore suppression depend on the focal species examined (Letourneau et al., 2009) and that antagonistic interactions between natural enemy species can hinder overall pest control (Alyokhin & Sewell, 2004; Brown et al., 2011), altering the relationships between natural enemy biodiversity and pest control.

CONCLUSIONS

We show that urban agroecosystem management heavily impacts both animal biodiversity and ES metrics and that urban food production is not at odds with the conservation of biodiversity and ESs. Enhancing tree abundance outside of crop beds can avoid pollination and food production trade-offs, and mulching only within crop beds can reduce trade-offs with pest control and pollinators, while simultaneously boosting soil carbon services. Furthermore, our study is the first to demonstrate that landscape composition mediates the effect of local agroecosystem management on ESs provided by mobile animals, specifically pest control and pollination. Thus, while within-garden management critically impacts animal biodiversity and related ESs, the strength and the direction of this relationship often depends on natural cover in the landscape. As urbanization and food access concerns increase across the globe, our work highlights the positive role of urban agroecosystems in supporting a broad range of ESs while simultaneously benefitting local food production.

AUTHOR CONTRIBUTIONS

SP, ME and SJ conceived of the idea with support from PB, HC, HL, BL and AL. SP, ME and SJ gathered datasets and executed analyses. All the authors discussed the results and participated in writing the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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