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Context matters: contrasting ladybird beetle responses to urban environments across two US regions

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Abstract: Urban agroecosystems offer an opportunity to investigate the diversity and distribution of organisms that are conserved in city landscapes. This information is not only important for conservation efforts, but also has important implications for sustainable agricultural practices. Associated biodiversity can provide ecosystem services like pollination and pest control, but because organisms may respond differently to the unique environmental filters of specific urban landscapes, it is valuable to compare regions that have different abiotic conditions and urbanization histories. In this study, we compared the abundance and diversity of ladybird beetles within urban gardens in California and Michigan, USA. We asked what species are shared, and what species are unique between urban regions. Moreover, we asked how beetle diversity is influenced by the amount and rate of urbanization surrounding sampled urban gardens. We found that the abundance and diversity of beetles, particularly of unique species, respond in opposite directions to urbanization: ladybirds increased with urbanization in California, but decreased with urbanization in Michigan. We propose that in California water availability in gardens and the urbanization history of the landscape could explain the divergent pattern. Thus, urban context is likely a key contributor to biodiversity within habitats and an important consideration for sustainable agricultural practices in urban agroecosystems.

Keywords: urban gardens, biological control, impervious surface, urbanization rate, Michigan, California

Introduction

Urbanization is changing biodiversity patterns and population distributions in cities across the world [1,2]. Urban environments are characterized by changes in abiotic [3] as well as biotic conditions [4]. For example, greater amounts of impervious surface in cities causes urban heat island effects, which increases the temperatures of cities [5] and within urban green spaces [6]. Light pollution from buildings and car traffic extends the duration and intensity of light availability, affecting the circadian rhythms of biotic elements [7]. Irrigation of lawns, parks and gardens adds water resources and maintains the presence of vegetation for organisms to exploit [8,9]. Moreover, the abundance and distribution of species and resources (habitat/food/shelter) in urban areas are often supplemented or altered across time and space [1,10].

Changes in environmental conditions and resource availability have different effects on different taxa and species [1,11]. Some species are able to persist and thrive in altered urban environments, while environmental filters and competition can cause other species to decline [12]. The species that thrive, what some consider "urban exploiters", are often habitat generalists that are able to live, exploit resources and reproduce in diverse, resource poor environmental conditions [2]. On the other hand, specialist species with particular habitat (food, shelter) requirements may be more sensitive to -- and decline with -- increasing urbanization because cities do not have the vegetation or resources to support these species [13]. The negative effect(s) of urbanization on species life history and functional traits may lead to biotic homogenization and declines in species richness within urban habitats [14].

The rate at which urbanization occurs (i.e., the speed at which land is converted to impervious surface) could further affect the diversity and distribution of species abundance and richness within urban habitats, and their ability to adapt to certain urban conditions. The percent impervious surface is forecasted to increase by 1.5 million km^2 by 2030 [15,16]. Moreover, because cities have distinct development histories, socio-cultural and demographic trends [17], it is important to understand whether and how biodiversity will respond to increasing urbanization (and associated qualitative and quantitative aspects) across multiple urban environmental contexts [16,18]. Elucidating whether certain organisms respond differently or not between unique regions can inform conservation agendas and urban sustainability broadly for various cities across the world [1,19].

Urban agroecosystems such as community and home gardens are high quality habitats that conserve considerable amounts of biodiversity in cities [20]. These systems are heavily managed by people predominantly for the purpose of cultivating fresh vegetables, fruits, flowers and herbs for self consumption [21–23]. Because urban agroecosystems are usually vegetated and irrigated [24], they provide food and shelter for many arthropods. Certain arthropod groups, for example pollinators and natural enemies, are in turn important for providing ecosystem services like crop pollination and pest control. Previous studies have shown that these arthropod groups are less abundant in gardens where surrounding levels of urbanization are high [25,26]. However, groups respond differentially to urbanization and at different spatial scales [27,28]. Some arthropod groups and species in urban environments including urban agroecosystems may actually increase with urbanization [29,30]. For example, insect pollinator species diversity is greater in some urban regions compared to surrounding suburban and agricultural areas [30–32]. Currently, it is unclear whether these patterns are regional phenomenon or if these trends are generalizable to other urban regional contexts. We argue that this question warrants further investigation, requiring research that draws comparisons of arthropod biodiversity across spatially distinct regions. Yet studies in urban agroecosystems that compare and synthesize findings across regions with different environmental conditions are rare [33].

Here, we combine data on ladybird beetle abundance and species richness collected from comparable urban agroecosystems in two distinct geographical regions to test whether the response of ladybird beetles to urbanization differs by the environmental context and urbanization history. Ladybird beetles are charismatic arthropods in agroecosystems that provide key natural pest control services, particularly of herbivorous aphids, mites and scale insects [34–36]. Because urban agroecosystems are situated amongst dense human populations, they tend towards organic, environmentally-friendly, and human-health conscious forms of management [37]. Thus, natural pest control is particularly important for these agroecosystems. In this study, we asked: 1) Does the relationship between urbanization (percent impervious surface, rate of development) and predator (ladybird beetle) systems in urban agroecosystems change with environmental context (region)? 2) Which species are shared by, and which are unique to urban agroecosystems of different regions? 3) Do shared species respond differently to urbanization measures in the region than unique species?

Methods

Study Regions

We worked in two regions in the USA – California and Michigan – to collect ladybird beetle data in urban community gardens in these regions (Figure 1). In California, we collected ladybird beetle data from 18 urban gardens in the California central coast in Santa Clara, Santa Cruz, and Monterey counties, which have estimated population densities of 274, 232, and 50 people/sq. km, respectively (2010-2014 U.S. census period) [38]. In Michigan, we collected ladybird beetle data from 13 urban gardens in Washtenaw county, which have an estimated population density of 192 people/sq. km [38]. The gardens in both regions are surrounded by different amounts of impervious surface. Moreover, the gardens differ in vegetation and groundcover composition and structure, but because they are all community gardens, differences in composition and structure are assumed relatively similar between regions. The gardens range in size from 444 to 15,525 m^2 in California and from 54 to 8,778 m^2 in Michigan, and are separated by approximately >2 km in California and >0.5 km in Michigan. All of the gardens have been cultivated for 1 to 47 years and do not use chemical pesticides and insecticides.

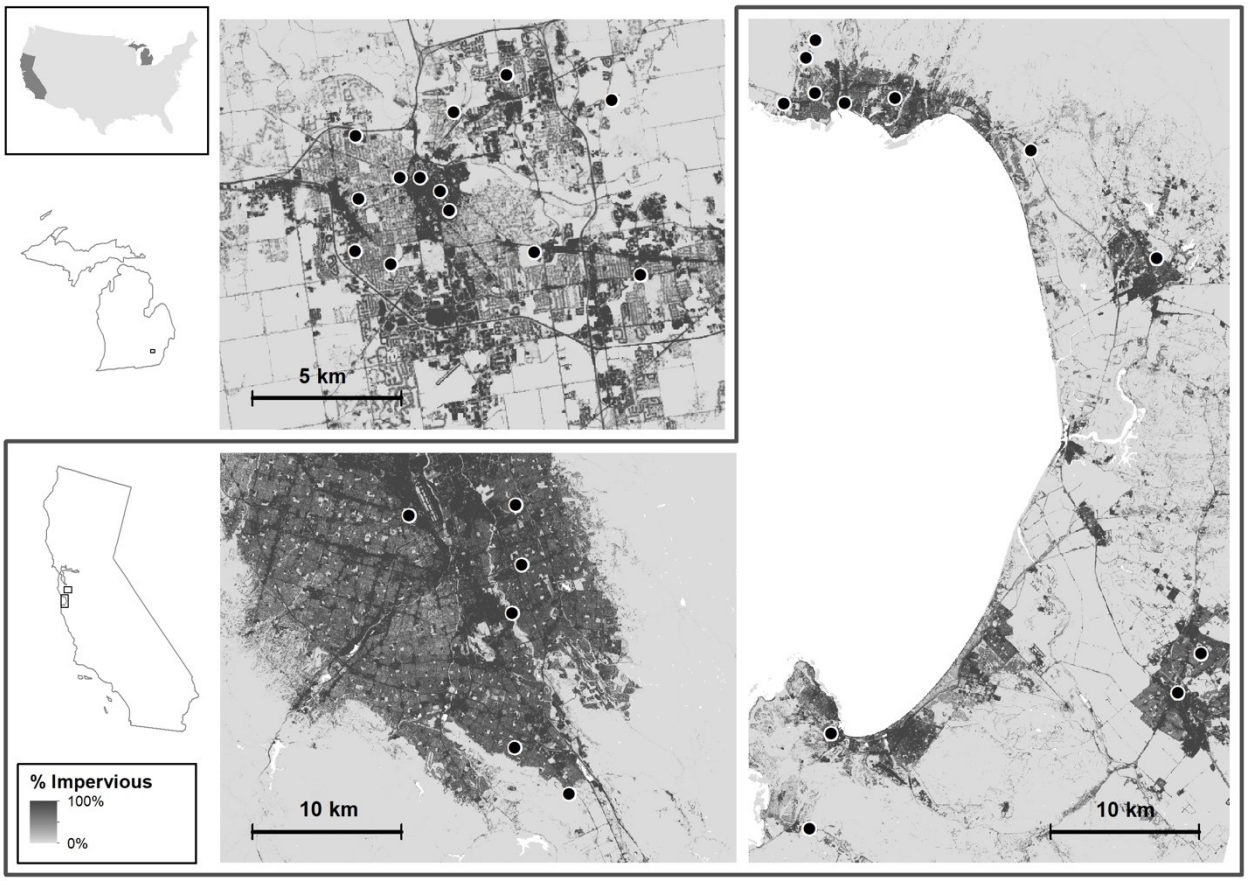

Figure 1. Study regions in Michigan (a) and in California (b) where community gardens (black circles) were sampled. Increasing percent impervious surface (NLCD 2011) shown with increasing shaded color.

Ladybird beetle sampling

To assess ladybird beetle communities in the gardens, we used visual and trapping methods in both regions. In California, we sampled for adult beetles with visual surveys and sticky traps within 20 m^2 plots at the center of each of the 18 gardens six times during summer 2014 (17–20 June, 7–10 July, 27–30 July, 19–21 August, 8–10 September, 29 September–1 October). Within the 20 m^2, we visually surveyed vegetation and ground cover for adult beetles in eight randomly placed 0.5 x 0.5 m sub-plots. We collected all individuals observed and stored them in vials with ethyl alcohol. At four random locations within the plots, we also placed a 3" x 5" yellow sticky trap card (BioQuip

Products Inc) on a galvanized wire stake for 24 h. In Michigan, we sampled for adult beetles by visually surveying five sentinel potted pea plants (*Pisum sativum* var. Dwarf grey) placed at each of the 13 gardens in Washtenaw County. Any ladybird beetle adults on plants were counted and identified to species. In addition, we swept surrounding vegetation in gardens for adult ladybird beetles using 10 full sweeps of a 0.2 m diameter net. All Michigan gardens were surveyed twice a week from May 14 to July 20, 2012. Sampling effort was consistent in all sites in each region throughout the sampling periods: in Michigan, the same two researchers conducted the sampling within the respective area for 30 min; in California, the same researcher conducted the sampling within the respective area for 60 min. The slight differences in sampling methods and years sampled between regions introduces some limitations discussed later in our conclusions.

We identified all ladybird beetles on traps and in vials to species using identification guides [39] and online resources [40,41]. Total abundance for each site for each species, total species richness, and total species diversity (Shannon's Diversity Index H) was tabulated across the months. Species diversity includes the relative distribution of species' abundances and was calculated using the vegan package in R [42]. For the analysis, we categorized species present in both California and Michigan as "shared species," and categorized species that were not both present in California and Michigan as "unique species."

Urban landscape analysis

To measure current levels of urbanization and to assess urbanization history, we summarized 1) the mean percent impervious surface surrounding gardens, and 2) the rate at which percent impervious surface has increased over time. For both regions (California, Michigan), we used the package "raster" in R (v 3.4.1) [43,44] to calculate the mean percent impervious surface within buffers of 10, 100, 500, 1000, 2000, 3000 m spatial scales surrounding each garden site based on land cover data from the US Geological Survey's National Land Cover Database (NLCD) 2011 Percent Developed Imperviousness dataset [45]. Here, a high total percent impervious surface indicates higher degrees of urbanization, and a low percent impervious surface indicates low degrees of urbanization. To calculate the rate of percent impervious surface change over time (henceforth "urbanization rate"), we collected this data at three time periods, as provided by the NLCD: 2001, 2006, 2011. Urbanization rate was calculated as the slope of the regression across these three time periods.

Statistical analysis

We ran species accumulation curves to test whether species richness had been sufficiently sampled in both California and Michigan. The expected number of species in each geographic region was calculated using a sample-based rarefaction method known as the Mao Tau estimator [46]. Both regions show evidence that richness was sufficiently sampled, exhibiting saturation in their species accumulation curves (Supplementary Figure 1).

We first modeled abundance and richness for each region at multiple spatial scales to determine the best scale at which ladybird beetles respond to urbanization. We built seven generalized linear models (GLM) at 0, 10, 100, 500, 1000, 2000, 3000 m spatial scales assuming Poisson error distributions for count data. The model with the lowest Akaike Information Criterion (AIC) was selected as the best spatial scale for each each region [47].

Urbanization rate was calculated by taking the slopes of linear regressions between time and impervious surface (NLCD: 2001, 2006, 2011) for each garden at a scale of 500 m. This was the buffer scale determined earlier to be significant for Michigan. California beetles best responded to impervious cover at 100 m, but at this scale urbanization rate did not vary by garden. Thus we only analyzed effects of urbanization rate on ladybird beetle abundance, species richness and species diversity at 500 m for both regions. We also ran Pearson's r tests between values of urbanization rate and impervious surface at both 100 and 500m to test for correlations between explanatory variables. Urbanization rate and impervious surface were not significantly correlated (Supplementary Table 2).

To determine whether ladybird beetles significantly responded to percent impervious surface or urbanization rates, we constructed GLMs at the spatial scale appropriate for the region and predictor variable as described above. Abundance and species richness GLMs assumed Poisson error distributions, and diversity GLMs assumed Gaussian. All GLMs were then fit by Laplace approximation and goodness of fit determined by Wald Z tests [47]. This is what we refer to in text as Poisson and linear regressions.

Results

We found 16 ladybird beetle species in California and eight species in Michigan over the sampling periods across the regions (Table 1). Species diversity index values were higher in California (ranging from 1.3 to 2.5 for all species) than in Michigan (ranging from 0 to 1.5). Only four species were shared by California and Michigan, including: *C. septempunctata, C. Sanguinea, H. axyridis* and *O. v-nigrum*. Thus, 12 species in California and four species in Michigan were unique to that region.

Table 1. Ladybird beetle species sampled in California and in Michigan. We present: the respective region the species was found in, their feeding habits, the ecological role that they play in agroecosystems, their nativity in their respective region [39,48,49], and their current geographic distribution in the USA [39–41]. (CA = California; MI = Michigan; NA = North America)

Species	Region observed	Feeds on	Ecological function in agroecosystems	Origin	Distribution in US
Adalia bipunctata	CA	aphids and mites	predator / pest control	native	West coast, Northeast, few Midwest records (historically most of US and Canada)
Coccinella californica	CA	mostly aphids	predator / pest control	native	West coast CA
Cycloneda polita	CA	mostly aphids	predator / pest control	native	West coast US and British Columbia
Hippodamia convergens	CA	mostly aphids	predator / pest control	native	Throughout US and western Canada
Hyperaspis quadrioculata	CA	aphids and scale insects	predator / pest control	native	Central to south CA
Nephus binaevatus	CA	aphids and scale insects	predator / pest control	non-native	Central to south CA
Psyllobora vigintimaculata	CA	fungus	fungus and mildew control	native	Throughout US and Canada
Scymnus cervicalis	CA	mites and scale insects	predator / pest and mite control	native	East US to south CA
Scymnus coniferarum	CA	mites and scale insects	predator / pest and mite control	native	CA and scattered west NA records
Scymnus marginicollis	CA	mites and scale insects	predator / pest and mite control	native	CA to British Columbia; scattered NA records

Scymnus nebulosus	CA	mites and scale insects	predator / pest and mite control	native	South CA to Canada
Stethorus punctum	CA	mites and scale insects	predator / pest and mite control	native	West coast US; Northeast, west to north Great Plains
Coleomegilla maculata	MI	mostly aphids	predator / pest control	native	East NA to southwest US
Cryptolaemus montrouzieri	MI	mites and scale insects	predator / pest and mite control	non-native	Throughout US
Hippodamia variegata	MI	mostly aphids	predator / pest control	native	Northeastern to middle US and Canada
Propylea quatuordecimpunctata	MI	mostly aphids	predator / pest control	non-native	Throughout NA (native to the Palaearctic)
Coccinella septempunctata	MI, CA	mostly aphids	predator / pest control	non-native	Throughout NA (native to the Old World)
Cycloneda sanguinea	MI, CA	mostly aphids	predator / pest control	native	West to south CA; NC and FL
Harmonia axyridis	MI, CA	mostly aphids	predator / pest control	non-native	Throughout US and southern Canada, except northern Rockies
Olla v-nigrum	MI, CA	mostly aphids	predator / pest control	native	Throughout US, except ME and Pacific Northwest

Total ladybird beetle species abundance, richness and diversity (shared and unique species) were best explained by percent impervious surface at a 100 m spatial scale in California, but was best explained at a 500 m spatial scale in Michigan (Supplementary Table 1). Total ladybird beetle species abundance and species diversity significantly increased with percent impervious surface in California, but significantly declined with percent impervious surface in Michigan (Table 2; Figure 2). Total species richness also generally increased in California and decreased in Michigan with percent impervious surface (Table 2). The divergent trend between regions was similar for shared species: shared species abundance, richness and diversity significantly increased in California with greater impervious surface, but was not significant in Michigan (Table 2). Unique species abundance also significantly increased with impervious cover in California, while unique species abundance significantly decreased in Michigan (Table 2; Figure 2). Of note, impervious surface cover gradients were comparable between California and Michigan.

In response to the rate of urbanization surrounding gardens, ladybird beetle abundance and species diversity increased with faster urbanization rates in California (Table 2; Figure 3). Whereas, in Michigan it was not significant for all response measures (Table 2; Figure 3). Species diversity of shared ladybird species significantly increased with faster urbanization rates for both regions (Table 2; Figure 3). The abundance of unique species significantly increased in California and decreased in Michigan with faster urbanization rates (Table 2; Figure 3).

Table 2. Results of regressions predicting ladybird beetle abundance (AB), richness (RI) and Shannon's Diversity Index (SH) as a function of percent impervious surface (IS) and urbanization rate (UR). Scale indicates the spatial scale in meters used to calculate predictor variables IS and UR. Coefficients and P values are derived from Wald Z tests, which assess

goodness of fit of generalized linear models to data assuming Poisson error distributions (AB, RI) or Gaussian error distribution (SH).

Dataset	Region	Scale	Predicted	Predictor	Coefficient	P value
All	MI	500	AB	IS	-0.015	**0.01**
All	CA	100	AB	IS	0.019	**<0.001**
All	MI	500	RI	IS	-0.018	0.08
All	CA	100	RI	IS	0.009	0.06
All	MI	500	SH	IS	-0.013	**0.02**
All	CA	100	SH	IS	0.006	**0.05**
Shared	MI	500	AB	IS	-0.001	0.92
Shared	CA	100	AB	IS	0.031	**<0.001**
Shared	MI	500	RI	IS	-0.016	0.29
Shared	CA	100	RI	IS	0.021	**0.05**
Shared	MI	500	SH	IS	-0.003	0.54
Shared	CA	100	SH	IS	0.007	**0.09**
Unique	MI	500	AB	IS	-0.023	**0.004**
Unique	CA	100	AB	IS	0.018	**<0.001**
Unique	MI	500	RI	IS	-0.020	0.16
Unique	CA	100	RI	IS	0.004	0.46
Unique	MI	500	SH	IS	-0.005	0.44
Unique	CA	100	SH	IS	0.003	0.76
All	MI	500	AB	UR	-3.524	0.15
All	CA	500	AB	UR	2.231	**<0.001**
All	MI	500	RI	UR	0.932	0.77
All	CA	500	RI	UR	2.292	0.11
All	MI	500	SH	UR	1.372	0.55
All	CA	500	SH	UR	2.331	**0.04**
Shared	MI	500	AB	UR	3.710	0.22
Shared	CA	500	AB	UR	1.925	0.29
Shared	MI	500	RI	UR	4.665	0.23
Shared	CA	500	RI	UR	2.024	0.50
Shared	MI	500	SH	UR	2.698	**0.09**
Shared	CA	500	SH	UR	3.110	**0.02**
Unique	MI	500	AB	UR	-10.88	**0.01**
Unique	CA	500	AB	UR	3.376	**<0.001**
Unique	MI	500	RI	UR	-4.020	0.47
Unique	CA	500	RI	UR	1.705	0.33

Unique	MI	500	SH	UR	-1.506	0.48
Unique	CA	500	SH	UR	1.473	0.24

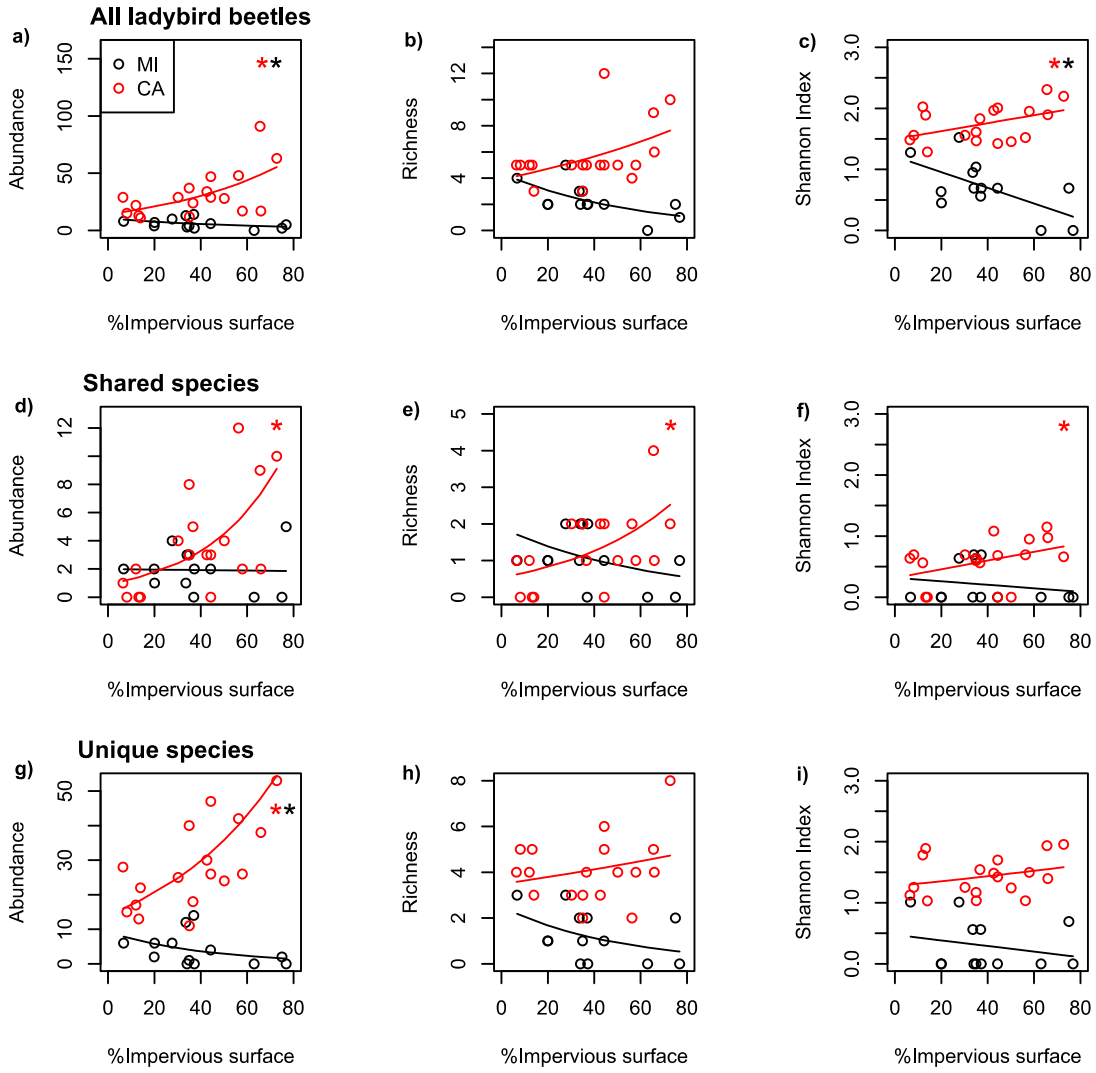

Figure 2. Effect of impervious surface on abundance, richness and diversity of ladybird beetles.

Regressions of abundance and richness of Michigan (black lines and points) and California ladybird beetles (red lines and points) as a function of % impervious surface at 500 m for MI and 100 m for CA. All species combined (a-c, top row), species that are shared by both CA and MI (d-f, middle row) and species unique to each region (g-i, bottom row). * indicate significant regressions ($P < 0.05$). In (b) Poisson regressions for MI and CA are partially significant ($P < 0.10$).

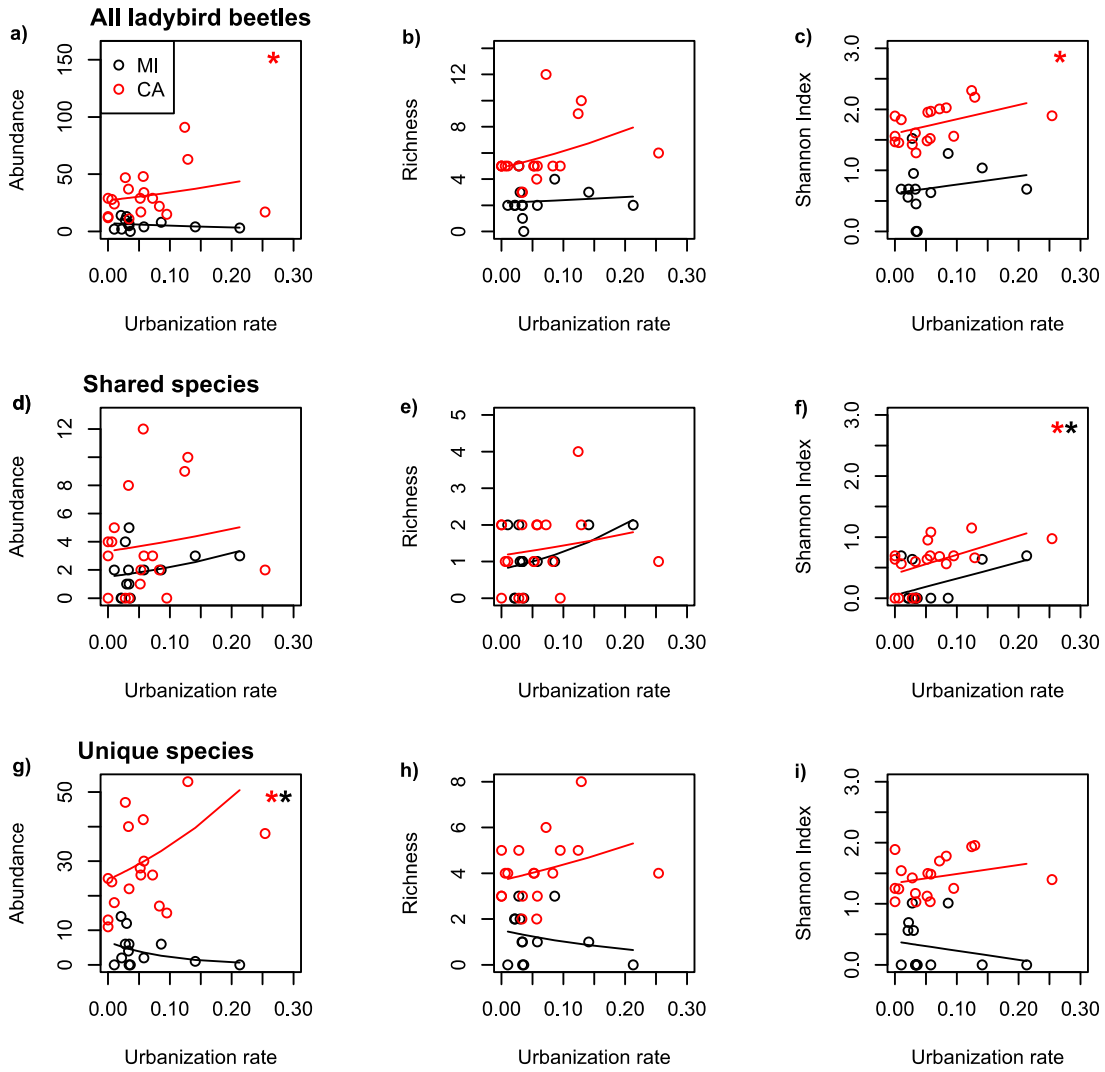

Figure 3. Effect of urbanization rate on abundance, richness and diversity of ladybird beetles. Regressions of abundance and richness of Michigan (black lines and points) and California ladybird beetles (red lines and points) as a function of urbanization rate at 500 m. All species combined (a-c, top row), species that are shared by both California and Michigan (d-f, middle row) and species unique to each region (g-i, bottom row). * indicate significant regressions ($P < 0.05$)

Discussion

The influence of urbanization on biodiversity can change with environmental (regional) context. This comparative study between two urban regions in the US – California and Michigan – shows that organisms respond differently to urbanization depending on region. Ladybird beetles have a contrasting response to the intensity of urbanization as well as the rate at which urbanization occurs in different regional contexts, and we found only a single unidirectional positive relationship between species diversity and urbanization rate between regions. Moreover, this trend is most evident for the abundance of all species and unique species. We hypothesize that the effect of urbanization on unique species is driving this divergent pattern.

Our first question was whether the relationship between urbanization and ladybird beetles in urban agroecosystems changes with environmental context. We found that urban gardens are supporting more abundant and diverse ladybird beetle populations in more urban areas in California, while in Michigan, ladybird beetles in urban gardens decline in abundance, species richness and diversity with increasing amounts of impervious cover and faster urbanization rates in some instances. Urbanization is clearly driving the abundance, species richness and behavior of

ladybird beetles in California, as we have found in previous studies [29,50]. However, we show that this is not the case in another environmental context (Michigan). Though not specifically sampled in urban gardens, a majority of taxa decline in abundance and species richness with urbanization [2]. This is particularly apparent for vertebrates [18], but is also often the case for invertebrates [51–53]. In contrast, plant species generally increase with urbanization presumably because non-native species introductions outweigh extinctions in this group and because plants have smaller geographical ranges than mobile organisms [54]. Organisms with larger ranges may be more sensitive to urbanization because urbanization can fragment migratory corridors [55,56]. Given that we observed divergent geographical responses to urbanization most strongly for unique ladybird species but one similar response to urbanization of shared species (in diversity), differences in dispersal ranges could possibly explain our results. If California-specific beetles have larger geographical ranges than Michigan beetles, our results would be consistent with the dispersal hypothesis. However, we did not find strong evidence for this hypothesis in our results, because the reported geographic distribution for these species – often related to species dispersal ability and range size [57] – is relatively narrow for California beetles versus Michigan beetles (Table 1).

It is important to note however, that though general trends in taxonomic responses to urbanization exist, all taxa that have been examined at multiple spatial scales or contexts exhibit some degree of divergence in responses to urbanization (6.9 to 33.3% of studies in a given taxon report different responses to urbanization depending on context) [2,28,30,58,59]. At larger spatial scales, urbanization is correlated with dense human populations that also coincide historically with nutrient-rich and biodiverse regions [60,61]. McKinney suggests that this can produce an apparent positive effect of urbanization on species abundance and richness [2]. Moreover, the longer periods of warm temperatures due to urbanization (i.e., urban heat island effects) may increase insect population abundance because of increased reproductive capacity [62], a common physiological response for arthropods [63]. At smaller spatial scales, local effects including management intensity and the destruction of habitat and pollution may impose negative effects of urbanization on species abundance and richness [64]. However, our results do not support this hypothesis given that ladybird beetles responded negatively to urbanization at larger spatial scales in Michigan, and positively at smaller spatial scales in California (Figure 2, Table 1).

The rate of urbanization, not only the amount of impervious surface, was important for explaining beetle abundance and diversity but exhibited different patterns depending on the group. Interestingly, while the abundance and diversity of unique species similarly diverged in regional responses to urbanization rate as to amount of impervious surface, shared species all showed positive unidirectional responses to urbanization rate. The predictor variables are not significantly correlated, and thus could theoretically have divergent effects (Supplementary Table 2). Urbanization rates were actually relatively similar in California and in Michigan (at 500 m), which could explain why shared species had similar responses in each region while unique species had opposite responses. The differences in ladybird biodiversity between regions is therefore likely best explained by a species-level response: specifically, the response of unique species to California versus Michigan. Indeed the strongest pattern from our study is the response of unique species to both the percent impervious surface and to the rate of urbanization, with abundance of unique beetles significantly increasing in California but decreasing in Michigan. This suggests that there are environmental filters at regional as well as local scales for species' traits that allow them to thrive in more urban areas and habitats [12,65] in California, and that in Michigan, those species are not present. Only species with traits that allow them to persist in urban environments should similarly increase with increasing rates of urbanization across regions. Indeed traits including habitat, diet breadth and foraging efficiency have explained the global expansion of the ladybird species *Harmonia axyridis* into urban areas [66,67]. The similar unidirectional response of shared species to urbanization rate in our study supports this hypothesis.

Thus, our results may be explained by the legacy of land use change in each region and species' life histories/traits. California gardens have more species and more unique species that are not found in Michigan. Michigan gardens have fewer species, and 50% of those species were also

297 found in California gardens. Most of the shared species across regions are aphidophagous (eat
298 aphids), while in California the unique species to the region largely eat mites, scales and fungus
299 (Table 1). For example, the fungus feeder *Psyllobora vigintimaculata* is very abundant in California
300 and has a different life history than other species (Supplementary Figure 2). The presence of species
301 with these feeding preferences could be because of the industrial agricultural crops grown within
302 and near our urban garden sites in California, historically and currently. Some of the region was
303 once an orchard landscape, known as the "Valley of Heart's Delight", that has historically grown
304 diverse fruit and nut trees [68]. Generally, fruit trees and landscaped shrubs are often prone to
305 scale, mite and mealybug pest damage along with crops like strawberries and tomatoes [69]. As
306 discussed earlier, human populations preferentially settle in biodiverse areas (or "biodiversity
307 hotspots") [61,70], and cities can coincide with threatened species distribution [71,72], possibly
308 explaining positive relationships between ladybirds and urbanity. The legacy of agriculture in turn
309 has permanent effects on ecosystems, and the influx of nutrients and irrigation can also create
310 biodiversity hotspots [60]. Natural enemies were historically introduced from e.g. New Zealand
311 and Australia for biological control of pests in the orchards. For example, the Dusky ladybird
312 beetle, *Nephus binaevatus*, was released into California from New Zealand in 1922 to help control
313 mealybugs in orchards [73]. This non-native species is observed only in the California garden sites,
314 particularly in very urban sites in Santa Clara county that were once orchards. Our sampled garden
315 sites in California contain diverse fruit trees such as citrus and stone fruit. Thus some of the unique
316 ladybird beetles like *N. binaevatus* and also *Coccinella septempuctata* are legacies of agricultural
317 industrialization and urbanization unique to California, and/or may be present in gardens due to
318 the availability of their prey/host.

319 The ladybird beetles in California -- particularly those that are unique -- may be more likely
320 able to withstand environmental disturbance because they have been historically used in human-
321 dominated systems for e.g. biological control. Non-native species to a region often have a greater
322 ability to survive in a variety of habitats -- including disturbed habitats -- than native species [74]. In
323 disturbed urban landscapes, more abundant species are habitat generalists and/or non-native to a
324 region [2,75]. These species have ecological traits that allow them to exploit resources and persist
325 [76], and environmental filters of urban habitats have been used to explain taxonomic differences
326 between urban habitats [12,77]. Most (though not all) of the ladybird species that we observed in
327 Michigan sites are native species from the greater Northeast and Midwest region (Table 1). This
328 could explain why abundance and richness of beetles declines with urbanization in Michigan: many
329 of the species are native and are less likely to survive and adapt to environmental disturbances like
330 urbanization as non-native and invasive species [78].

331 Abiotic factors associated with urbanization and different environmental contexts may better
332 explain the contrasts in ladybird diversity patterns in California and Michigan agroecosystems.
333 Ladybirds must avidly consume water (dew, rain) for their survival [79], and water availability
334 often drives their movement ecology and life cycle [80]. Thus climate patterns (temperature,
335 precipitation) can affect ladybird distribution [39,79], and significant climatic contrasts between
336 regions could explain divergent patterns in ladybird abundance and richness in gardens. In
337 comparison to Michigan, which has a temperate climate with four defined seasons, California has
338 on average warmer temperatures throughout the year and two seasons, one dry (summer; April to
339 September) and one wet (winter; October to March). In California, urban gardens in the summer
340 dry months (with <1 cm precipitation per month much in the form of fog) may provide an
341 important irrigated habitat in comparison to the surrounding urban matrix. Indeed supplemental
342 irrigation in cities maintains and supports biodiversity during drought events [9,81,82], as
343 California experienced during the time of this study. Michigan has an opposite precipitation pattern
344 with relatively wet summers, receiving on average 8 to 9 cm/month in the summer [83]. Thus,
345 limited water availability in the urban matrix may not affect arthropod distributions as strongly in
346 Michigan. On the other hand, urban gardens in California may act as critical sources of water, food,
347 and shelter and promote greater ladybird beetle foraging and fecundity rates [79], ultimately
348 increasing their populations. If this is the case, then urban gardens in California may function as

sources of populations rather than sinks, as has previously been suggested for biodiversity in urban habitats [1,25,84,85]. To test this hypothesis, we suggest examining habitats outside of gardens in these respective regions and their local conditions (in water availability, prey) to see whether ladybird abundance and diversity conservation is greater within gardens versus outside of gardens in natural habitats [86] and if it is explained by local conditions.

The slight differences in sampling methods and years sampled between regions are caveats in our study. Specific sampling methods as well as annual variation within regions may influence differences between regions. Moreover, although we only focused on landscape factors to understand the ecology of urban agroecosystems across regions, local garden attributes including vegetation characteristics could also be important for species distribution [87,88]. Indeed, these caveats are generally the cruces of comparative studies and synthesis research. Although such studies are critical, comparing biodiversity assessments from multiple regions and research groups are inherently challenging to conduct and to analyze due to inconsistencies among methodological approaches in ecology, and research funding and timing. Given these limitations, this work shows strong relationships between landscape factors and local biodiversity with available comparable data across two regions. This is a first step towards a greater understanding of regional effects on urban biodiversity.

Conclusion

Ladybird beetles provide important pest control services and understanding their responses to urbanization can inform sustainable agricultural management in urban gardens. In this comparative study using urban agroecosystems as a field system, we show that organisms like ladybirds exhibit opposite responses to urbanization in different regional environmental contexts. Thus we cannot expect universal responses of organism groups to urbanization. Based on previous research, region-specific responses to urbanization appear ubiquitous. Spatial scale is currently presumed to have a positive correlation with species abundance and diversity in increasingly urban environments. Here, we show that at least for ladybird beetles that is not the case. We suggest that region-specific responses are more likely due to the environmental factors (abiotic, biotic), urbanization history of the region, and the natural histories of species specific to each region. The natural history of species that are unique to urban agroecosystems could impart insight into how urban areas may be designed to conserve species that are more sensitive to urban environments. Future urban ecology research should seek to draw more comparisons across distinct regions rather than generalizing responses of biodiversity to urbanization.

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