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Local and landscape correlates of coccinellid species richness, abundance, and assemblage change along a rural–urban gradient in Quintana Roo, Mexico

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Abstract

Coccinellids are important predators and provide important ecosystem services. The coccinellid fauna, drivers of assemblage composition, and species richness in the tropics are poorly known. We studied changes in species composition of coccinellids in domestic gardens along a rural-urban gradient in southeastern Mexico and identified the local and landscape variables that determine abundance and species richness. We surveyed coccinellids through monthly visual surveys, yellow sticky and pan traps in nine domestic gardens, and measured local variables (flower and prey abundance, plant diversity, garden size, temperature, and relative humidity), and gathered information on landscape heterogeneity in buffers around gardens (0.05 km, 1 km, and 3 km radius). We collected 40 coccinellid morphospecies, including two exotic species: *Chilocorus nigrita* and *Delphastus catalinae*. Coccinellid species composition differed along the gradient. Assemblages did not exhibit a nested pattern; species turnover was the main contributor of observed beta diversity. Overall coccinellid abundance was highest in the suburban zone, while overall species richness was highest in the rural zone. Mean abundance and mean species richness did not vary significantly along the gradient. The gradient negatively affected coccinellid diversity; diversity was highest in the rural zone which harbored several exclusive species. At the local scale, coccinellid abundance and species richness correlated positively with prey abundance and temperature, and negatively with plant diversity. Urbanization filtered more than half the species in the community, yet urban gardens in southeastern Quintana Roo, especially those providing abundant prey, might assist coccinellid conservation.

Abstract in Spanish is available with online material

KEYWORDS

biodiversity conservation, domestic gardens, exotic coccinellids, ladybeetles, tropics, urban entomology, urban green spaces, Yucatan Peninsula

1 | INTRODUCTION

Ladybeetles (Coleoptera: Coccinellidae) are an important and speciose insect group that occur in an array of ecosystems, but disturbance and presence of exotic species may affect their diversity. There are approximately 6000 known species of coccinellids (Seago et al., 2011; Ślipiński et al., 2011), most of which are considered beneficial due to their predatory nature, and their ability to reduce pest insect populations (Hagen, 1962; Hodek et al., 2012; Ipert, 1999).

Diversity and abundance of coccinellids may be influenced by several local and landscape variables. At the local scale, prey availability (Rocha et al., 2018) and presence of alternative adult and larval food sources (nectar, honeydew, pollen, fungi; Lundgren, 2009) are influential. Moreover, landscape structure and composition may determine their abundance, richness (Egerer et al., 2017; Rocha et al., 2018; Woltz & Landis, 2014) and assemblage composition (Gardiner et al., 2009; Grez et al., 2019; Liere et al., 2019). Species-specific biological traits can also explain spatial distribution patterns (Comont et al., 2012). In addition, coccinellid assemblages experience compositional changes due to the presence of exotic species (e.g., Alyokhin & Sewell, 2004; Masetti et al., 2018). How these variables affect coccinellids has been documented mainly in temperate countries, where drivers include agriculture intensification, climate change, invasions of non-native species, and habitat degradation and loss through urbanization (Comont et al., 2014; Honek et al., 2017).

Conservation of coccinellids and the ecosystem services they provide is crucial, but knowledge concerning factors influencing their richness and abundance within different ecosystems is lacking in the tropics. Despite recent advances in knowledge of tropical coccinellids (e.g., González & Větrovec, 2021; Nestor-Arriola & Toledo-Hernández, 2019; Rodríguez-Vélez, 2018), diversity in the tropics is still largely unexplored. Tropical species have distinct life histories and physiologies; furthermore, ecological communities are assembled differently across latitude (Sheldon, 2019) and different community responses to disturbance may be expected compared with those in temperate regions.

Deforestation followed by urbanization creates a gradient of natural habitat loss toward the urban core of cities (McKinney, 2002), and the physical changes and the resultant biotic environment along the different zones (rural, sub-urban, and urban areas) of this gradient may affect coccinellids. Recent studies from temperate and subtropical regions describe coccinellid communities along a rural to urban gradient, or in urban ecosystems, such as gardens (e.g., Egerer, Arel, et al., 2017; Egerer, Bichier, et al., 2017; Grez et al., 2019; Liere et al., 2019; Rocha et al., 2018), but studies from tropical urban areas are lacking. In temperate zones, species composition of other arthropods changes along rural to urban gradients (Ishitani et al., 2003; Niemelä & Kotze, 2009); with several invertebrate studies showing increasing species richness with urbanization (McKinney, 2008). Increases in species richness in moderately urbanized areas could follow predictions from the intermediate disturbance hypothesis (Connell, 1978; Wootton, 1998), suggesting that local species diversity should be maximal at moderate levels of disturbance. However, even within a taxonomic group, different species respond differently

to urbanization (Magura & Lövei, 2021). In general, urbanization negatively affects arthropods (Faeth et al., 2011; McKinney, 2008), but no global pattern emerged in recent meta-analyses, and effects of urbanization on abundance, diversity, and richness of arthropods remains controversial (Fenoglio et al., 2020; Magura & Lövei, 2021).

Urban green spaces harbor numerous species of coccinellids (Egerer, Bichier, et al., 2017; Gardiner et al., 2014; Grez et al., 2019; Liere et al., 2019; Rocha et al., 2018), but assemblages depend on local and landscape factors (Egerer, Bichier, et al., 2017). The degree to which green spaces conserve biodiversity also depends on urbanization (Grez et al., 2019). Local factors identified as important correlates of coccinellid species richness and/or abundance in urban settings in temperate or subtropical regions include vegetation complexity, size of green spaces, type and abundance of ground cover, number of flowers (Egerer, Bichier, et al., 2017), plant diversity, and prey abundance (Rocha et al., 2018). At the landscape level, proportions of impervious surface (Rocha et al., 2018), agricultural land cover (Grez et al., 2019), and natural areas surrounding green spaces (Egerer, Bichier, et al., 2017), at certain spatial scales, are influential.

We aim to fill knowledge gaps on coccinellids in the tropics, specifically in domestic gardens (e.g., households) along an urbanization gradient in the southeastern portion of the Yucatan Peninsula, Mexico. We address four research questions: (1) Does coccinellid species composition change along a rural to urban gradient? (2) Are species poor assemblages a subset of species rich assemblages? (3) Does coccinellid abundance, species richness, and diversity differ along the rural to urban gradient? (4) Which local and landscape factors are correlated with coccinellid abundance and species richness in domestic gardens in southern Quintana Roo? We hypothesize that species assemblages will vary significantly between zones of the rural to urban gradient and that assemblages will present a nested pattern. We expect that the urban zone will have lower species richness and will be a nested subset of rural and suburban assemblages. We hypothesize that richness and abundance of coccinellids will differ along the gradient. According to the intermediate disturbance hypothesis, we hypothesize that suburban gardens will harbor more species and higher abundance.

2 | METHODS

2.1 | Sampling sites

We worked in the state of Quintana Roo in the southeastern part of the Yucatan Peninsula, Mexico; the study site included the coastal city of Chetumal (Figure 1). The vegetation consists mainly of tropical forest (Islebe et al., 2015), arboreal secondary vegetation (Cortina Villar et al., 1999), and coastal mangroves. The region has a warm sub-humid climate with rainfall during the summer and the driest season during March and April, according to the classification of Köppen modified by García (1973). We selected nine domestic ornamental gardens along the gradient, three in the rural zone (R1-3) about 8–14 km away from the city, three in the edge of the city (suburban zone, SU1-3) and three in the urban core (urban zone, U1-3) (Figure 1; see Text S1 and Table S1 for garden details).

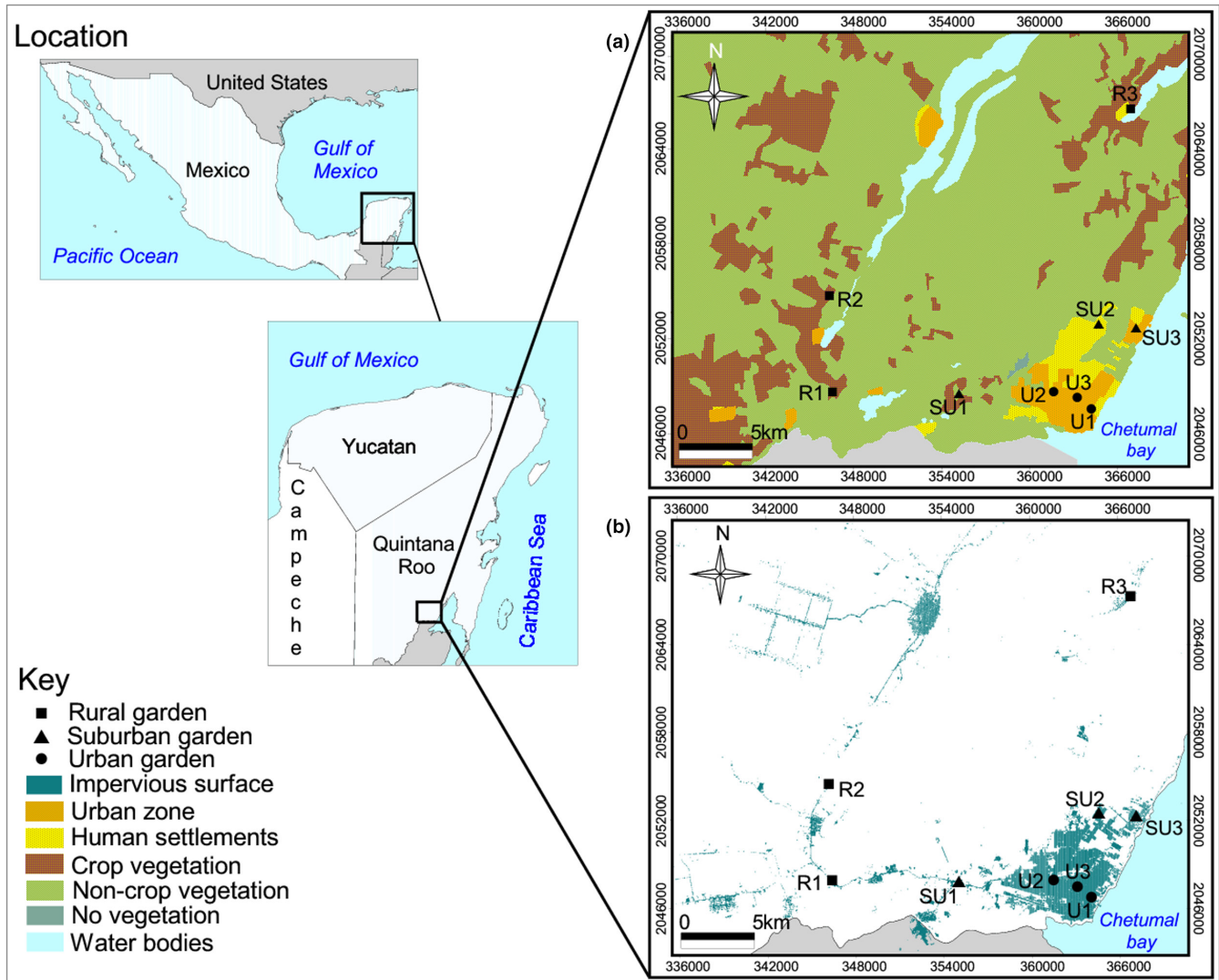


FIGURE 1 Area of study and location of domestic gardens sampled along a rural to urban gradient. Land cover types in 2015 (top right), and impervious surface coverage in early 2018 (bottom right). Circles: urban gardens; triangles: suburban gardens; squares: rural gardens

2.2 | Coccinellid sampling and identification

We sampled coccinellids monthly, from January 2018 to February 2019 with 3 methods: visual surveys during 1.5–2 h/site, yellow sticky traps (11.5 × 24.5 cm, Feromnis Group, Mexico) and yellow pan traps (20 cm diam.). During visual surveys, we examined all plants and collected all coccinellids present (eggs, larvae, pupae, and adults). We placed coccinellids in plastic jars covered with a fine mesh for further observations. We placed larvae in separate containers to prevent cannibalism. We randomly distributed four sticky traps and four pan traps containing 300 ml of water and a few drops of detergent (Egerer, Arel, et al., 2017) in each garden and collected them after 24 hrs. We placed traps 1–1.5 m above the ground; sticky traps were suspended on tree or shrub branches, while the pan traps were placed on any surfaces above ground. We distributed traps further apart in larger gardens in order to cover most of the area, and closer in small gardens due to the limited dimensions of the plots.

We sorted coccinellids into morphospecies using online identification keys (Gordon, 1985). For specimens that could not be

identified using keys, DNA from representative specimens was extracted and barcoded, and CO1 sequences were used to delineate molecular operational taxonomic units as part of an independent study (see Catzim et al., 2022; dataset DS-QROOCOCC, doi:dx.doi.org/10.5883/DS-QROOCOCC in boldsystems.org). Field sampling comply with the current laws of Mexico and was carried out under permit number FAUT-0277 issued by the Secretaría de Medio Ambiente y Recursos Naturales, Mexico.

2.3 | Local factors

We recorded flower abundance, plant diversity, prey abundance, temperature, and relative humidity at each sampling, and noted garden area. To quantify flower abundance, we counted all flowers in the garden using a hand tally counter. We counted large solitary flowers individually and large racemose inflorescences as one flower. To determine plant species diversity, we listed all plant morphospecies (except grasses) and recorded their estimated frequencies. We

assessed abundance of potential prey items (e.g., coccids, aphids, psyllids, whiteflies, citrus blackflies, and mites (Nedvěd & Honěk, 2012)) on sticky traps and pan traps and also on ten 10-cm long plant shoots in each garden. We measured temperature and relative humidity in situ with a digital hygro-thermometer. We measured garden area with high resolution satellite images in the program Google Earth Pro.

2.4 | Landscape characterization

We included percent cover of several land cover types, and land cover diversity within three buffers (0.5 km, 1 km, and 3 km radius) surrounding each garden calculated using Geographic Information Systems (GIS) version 3.3. We selected 3 km as the largest buffer zone since it represents the dispersal range reported for some coccinellids in North America (Gordon, 1985) and because characteristics at this scale correlate with coccinellid richness and abundance (Egerer, Bichier, et al., 2017).

To calculate the percent cover of each land cover type, we analyzed the most recent land cover data available (2015) from the Mexican National Institute of Statistics and Geography (INEGI) with ArcView GIS 3.2. To reduce the number of land cover types, we grouped vegetation types in two categories: (1) Crop vegetation and (2) Non-crop vegetation (see detailed information of land type grouping in Table S2). To calculate percent of impervious surface (buildings, asphalt, pavement), we used ENVI 5.3 for a supervised classification of a Landsat 8 satellite image from January 2018 (USCG, 2018) (Figure 1). Some vegetation was replaced by impervious surface between 2015 and 2018; so, we used combined data of both maps; hence, percent impervious surface coverages used for analyses were an updated version of the 2015 land cover data.

2.5 | Other factors

In the study area, there is a dry season (March–May), a rainy season (June–October), and a “cold-dry” season known as “*nortes*” (November–February; SEDATU, 2018). Assemblage composition of coccinellids shifts seasonally (Honek et al., 2015). Thus, we included seasonality and precipitation as possible correlates of coccinellid richness and abundance because of their direct influence in resource availability fluctuation. We obtained average monthly precipitation data from the nearest meteorological stations of the National Commission of Water (CONAGUA).

2.6 | Data analyses

We performed all analyses with statistical software R version 3.6.1 in R Studio version 1.2.5042 (RStudio Team, 2020). To estimate total coccinellid abundance and species richness, we used pooled data

from all capturing methods. However, to avoid accumulating biases related to the effectiveness of different sampling methods, we only used visual survey data for comparison of coccinellid abundance, species richness, diversity, and species composition along the gradient; this method captured most species compared with the others (Table S3).

2.6.1 | Species composition along the rural to urban gradient

We visualized garden groupings along the gradient with a non-metric multi-dimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity of coccinellid assemblages using the “metaMDS” function. To test for significant differences in species composition along the gradient, we performed a permutational multivariate analysis of variance (PERMANOVA) using the “adonis” function. We used the function “betadisper” to check for homogeneity of multivariate dispersion. All functions are found in the “Vegan” package (Oksanen et al., 2019).

2.6.2 | Are urban coccinellid assemblages a subset of rural assemblages?

To determine if gardens with lower species richness were a subset of gardens with higher species richness, we used Nested metric based on Overlap and Decreasing Fill (NODF; Almeida-Neto et al., 2008). This metric yields values between 0 (no nestedness) and 100 (perfect nestedness) based on the presence-absence data. To estimate the significance of overall nestedness, we compared the observed nestedness score with that obtained from simulations (999) of a null model performed using the “oecosimu” function in the “Vegan” package. We followed the same procedure to determine if zones with lower species richness were a subset of zones with larger species richness. Species richness per zone was obtained by pooling species data from gardens within each zone. We also evaluated beta diversity among gardens and among zones; we used functions in the “betapart” package (Baselga et al., 2021) to separate the nestedness component (species loss) from the spatial turnover component (species replacement) to evaluate their contribution to the variation of the species composition of the assemblages as proposed by Baselga (2010).

2.6.3 | Coccinellid abundance, species richness, and diversity along the rural to urban gradient

Total abundance per zone was calculated by the sum of all abundances from gardens embedded within zones. To analyze differences in coccinellid mean abundance along the gradient and to account for repeated sampling of gardens over time, we fitted a Linear Mixed-Effect model (LMM) with the function “lmer” in the LME4 package

(Bates et al., 2015). First, we evaluated clustering in abundance data due to our nested design (gardens within zones of the gradient) and date of sampling (month) through Interclass Correlation Coefficients (ICC) with a null model that included coccinellid abundance as our response variable and “month” and “gardens within zones” as random effects. The variable “month” had no clustering effect and was removed from the final model. Abundance data were transformed ($\log + 1$) in the fitted model to improve model fit.

Because overall abundance differed among zones, we compared overall species richness along the gradient with rarefied species richness. We rarefied species by randomly sampling 95 individuals using the rarefy function in “Vegan” (Oksanen et al., 2019). To test for differences in mean coccinellid species richness along the gradient we used a LMM following the same procedure described for mean abundance data. Species richness data did not require transformation. Finally, we calculated overall coccinellid diversity in different zones using the Shannon–Wiener diversity index (H') in “Vegan” (Oksanen et al., 2019), and tested for mean variation along the gradient using LMM and Tukey post hoc test for pairwise comparisons.

2.6.4 | Variability of predictors along the rural to urban gradient

We analyzed variation in predictor variables (prey abundance, flower abundance, plant diversity, temperature, relative humidity, precipitation, percent coverage of crop vegetation, non-crop vegetation, and impervious surface, and land cover diversity) along the gradient. We used LMMs and included gardens within zones as a random effect to account for our nested study design.

2.6.5 | Local and landscape correlates of coccinellid abundance and species richness along the rural to urban gradient

To analyze the effect of local and landscape factors on abundance and richness we fitted LMMs to our data points from visual surveys. Local factors analyzed included flower abundance, prey abundance, plant diversity, garden size, temperature, and relative humidity. We calculated plant diversity using the Shannon–Wiener diversity index (H') in “Vegan” (Oksanen et al., 2019). Landscape factors included percentages of crop vegetation, non-crop vegetation, and impervious surface cover, and land cover diversity in the three buffers (0.5 km, 1 km, and 3 km). We used a modified version of the Shannon–Wiener index to calculate land cover diversity based on the percent cover of the different land cover types. In the model, we also included precipitation and seasons as predictors. Some data required rescaling, this was done by applying a log or $\log + 1$ transformation. Since the global model contained many predictor variables, we first checked for multicollinearity through variance inflation factors (VIF) using the “vif” function in

the CAR package (Fox & Weisberg, 2019). We removed predictors sequentially until only those with $VIF < 3$ remained in the model. Abundance data were transformed ($\log + 1$) to improve model fit. We then subjected the global model to model selection with the “dredge” function in the MuMIn package (Bartoń, 2019) and selected the model with the lowest corrected Akaike information criterion (AICc) as the best model. The same procedure was repeated to analyze species richness data. We tested potential spatial autocorrelation of the model residuals with spatial correlograms using the “correlog” function in the “ncf” package (Bjørnstad, 2020) and Moran’s I statistic using the “morantest” function in the “spdep” package (Bivand & Wong, 2018).

3 | RESULTS

3.1 | Overall coccinellid abundance and species richness

We collected 980 coccinellids representing 40 morphospecies (Table 1). The greatest abundance (N) and number of species (S) were obtained through visual surveys ($N = 508$, $S = 36$), followed by sticky traps ($N = 444$, $S = 26$), and pan traps ($N = 28$, $S = 14$; Table S3). Overall, rural, suburban, and urban gardens harbored 32, 28, and 19 species, respectively. We found 15 species shared by all zones and detected 21 species absent from the urban zone (Table 1). Ten species were exclusive to rural gardens and six were exclusive to suburban gardens.

3.2 | Coccinellid species composition in zones of the rural-urban gradient

The NMDS showed that urban and rural gardens formed tight clusters (Figure 2). Each of the suburban gardens had distinct species composition, and suburban gardens were not clustered (Figure 2). Species composition differed along the rural to urban gradient (PERMANOVA, pseudo $F = 1.61$, $p = .03$). Within group, multivariate dispersion was non-significant ($F = 1.09$, n.s.).

3.3 | Are urban coccinellid assemblages a subset of rural assemblages?

Coccinellid species composition structure among gardens and among zones of the rural to urban gradient was not nested (Figure 3a, b). Observed NODF ($N_{obs} = 32.2$) for gardens did not differ from expected NODF ($N_{exp} = 34.01$, Z -value = -2.01 , $p = .07$). The same pattern was observed for zones of the gradient ($N_{obs} = 43.9$, $N_{exp} = 44.7$, Z -value = -1.20 , $p = .26$). We observed that the spatial turnover component (species replacement, $\beta_{sim} = 0.66$) contributed most to the overall beta diversity in gardens ($\beta_{sor} = 0.75$), while nestedness

TABLE 1 Species of coccinellids in private domestic gardens and their respective abundance along a rural to urban gradient in southeastern Quintana Roo, Mexico. Morphospecies were delineated through an integrative approach (see Catzim et al., 2022). Total abundances representing pooled number of individuals from three different collecting methods and abundances from the visual search method are presented

Tribe	Morphospecies	Abbreviation	Pooled data				Visual search			
			R	SU	U	Total	R	SU	U	Total
Subfamily Microweiseinae										
Serangiinni	<i>Delphastus catalinae</i> ^a	De_c	1	3	4	8	1	3	3	7
	<i>Delphastus pusillus</i>	De_p	5	17	24	46	3	13	10	26
	<i>Delphastus</i> sp.	De	1	0	0	1	1	0	0	1
Subfamily Coccinellinae										
Azyini	<i>Azya orbigera orbigera</i>	Az_oo	9	83	15	107	8	80	15	103
Brachiacanthini	<i>Brachiacantha bistrispustulata</i>	Br_b	13	2	0	15	10	2	0	12
	<i>Brachiacantha</i> sp.	Br	1	0	0	1	1	0	0	1
Chilocorini	<i>Chilocorus cacti</i>	Ch_c	5	2	2	9	5	2	2	9
	<i>Chilocorus nigrita</i> ^a	Ch_n	2	2	31	35	0	2	29	31
	<i>Exochomus insatiabilis</i>	Ex_i	0	40	10	50	0	38	10	48
	<i>Exochomus</i> sp.	Ex	1	0	0	1	1	0	0	1
Chnoodini	<i>Exoplectra</i> sp.	Exo	1	0	0	1	1	0	0	1
Coccinellini	<i>Cycloneda sanguinea sanguinea</i>	Cy_ss	9	10	51	70	9	9	42	60
	<i>Olla v.nigrum</i>	O_vn	5	0	1	6	5	0	1	6
	<i>Psyllobora vigintimaculata</i>	Ps_v	4	1	0	5	1	0	0	1
Diomini	<i>Diomus roseicollis</i>	Di_r	8	37	29	74	3	18	14	35
	<i>Diomus</i> sp. 1	Di_1	23	13	6	42	2	2	1	5
	<i>Diomus</i> sp. 2	Di_2	14	68	71	153	0	6	4	10
	<i>Diomus</i> sp. 3	Di_3	0	1	0	1	0	1	0	1
	<i>Diomus</i> sp. 4	Di_4	1	0	0	1	0	0	0	0
	<i>Diomus</i> sp. 5	Di_5	0	1	0	1	0	1	0	1
	<i>Diomus</i> sp. 6	Di_6	0	1	0	1	0	1	0	1
	<i>Diomus</i> sp. 7	Di_7	7	1	0	8	7	0	0	7
	<i>Diomus</i> sp. 8	Di_8	0	1	1	2	0	1	0	1
Hyperaspidiini	<i>Hyperaspis globula</i>	Hy_g	2	6	2	10	1	6	2	9
Scymnillini	<i>Zagloba hystrix</i>	Za_h	10	6	0	16	9	5	0	14
	<i>Zagloba satana</i>	Za_s	6	3	1	10	4	0	0	4
Scymnini	<i>Scymnus (Pullus) pulvinatus</i>	Sc_p	25	30	15	70	6	25	3	34
	<i>Scymnus (Pullus)</i> sp.	Sc	0	1	0	1	0	0	0	0
	<i>Nephaspis indus</i>	Ne_i	8	10	39	57	0	0	2	2
	<i>Nephaspis</i> sp. 1	Ne_1	1	0	0	1	0	0	0	0
	<i>Nephaspis</i> sp. 2	Ne_2	1	0	0	1	1	0	0	1
	<i>Nephus (Scymnobius)</i> sp. 1	Nep_1	2	0	0	2	2	0	0	2
	<i>Nephus (Scymnobius)</i> sp. 2	Nep_2	10	0	0	10	3	0	0	3
	<i>Nephus (Scymnobius)</i> sp. 3	Nep_3	1	0	1	2	0	0	1	1
	<i>Nephus (Scymnobius)</i> sp. 4	Nep_4	0	1	0	1	0	1	0	1
	<i>Nephus (Scymnobius)</i> sp. 5	Nep_5	3	18	0	21	1	10	0	11
Stethorini	<i>Stethorus punctum picipes</i>	St_pp	27	49	39	115	8	23	17	48
	Unidentified sp. 1	Un_1	0	1	0	1	0	1	0	1
	Unidentified sp. 2	Un_2	5	16	2	23	2	7	0	9
	Unidentified sp. 3	Un_3	1	0	0	1	0	0	0	0
Total			212	424	344	980	95	257	156	508

Note: Abbreviations: R, rural; SU, suburban; U, urban.

^aExotic.

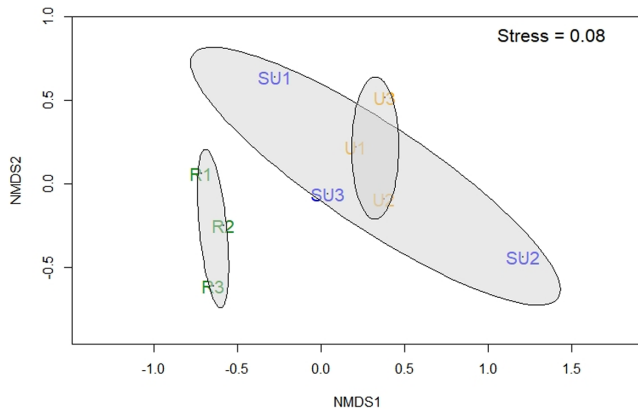


FIGURE 2 Two dimensions NMDS ordination plot based on the Bray-Curtis dissimilarity matrix of coccinellid community in 9 gardens along a rural to urban gradient in southern Quintana Roo. R1–R3: rural gardens; SU1–SU3: suburban gardens; U1–U3: urban gardens. Stress type 1, weak ties. Two convergent solutions found after 20 tries

contribution was smaller (species loss, $\beta_{\text{sne}} = 0.10$). Variation in species composition between zones was attributed mostly to species replacement ($\beta_{\text{sim}} = 0.37$, $\beta_{\text{sne}} = 0.10$, $\beta_{\text{sor}} = 0.48$).

3.4 | Coccinellid abundance, species richness, and diversity along the rural–urban gradient

Overall abundance in visual surveys was twice as high in the suburban zone than in the rural area (Figure 4a), yet mean abundance did not vary between zones (Wald, $\chi^2 = 3.44$, $p = .18$; Figure 4b). Rarefied curves showed that the number of species decreased along the gradient; with 11 more species in the rural compared with the urban zone (25 vs. 14; Figure 4c). Yet, mean richness did not vary between zones (Wald, $\chi^2 = 1.13$, $p = .57$; Figure 4d). Overall diversity decreased along the rural to urban gradient (rural, $H' = 2.91$; suburban, $H' = 2.35$; urban, $H' = 2.21$). Mean diversity varied along the gradient (Wald, $\chi^2 = 81.4$, $p < .001$); gardens in the suburban (Tukey post hoc, $Z = -8.93$, $p < .001$) and urban (Tukey post hoc, $Z = -3.50$, $p = .001$) zones were less diverse than those in the rural zone. The urban zone supported higher diversity than the suburban zone (Tukey post hoc, $Z = -5.50$, $p < .001$).

3.5 | Variability of predictor variables along the gradient

Prey abundance, flower abundance, temperature, relative humidity, and precipitation did not vary along the rural to urban gradient (Tables S4 and S5). Plant diversity increased (Wald, $\chi^2 = 9.60$, $p < .001$) and garden size decreased (Wald, $\chi^2 = 563.9$, $p < .001$) toward the urban zone. Plant diversity was very variable, particularly in gardens located in the suburban zone (Table S1). Percent cover of crop vegetation, non-crop vegetation, impervious surface, and land cover diversity within buffer zones (0.5 km, 1 km, and 3 km) also varied significantly (Tables S4 and S5).

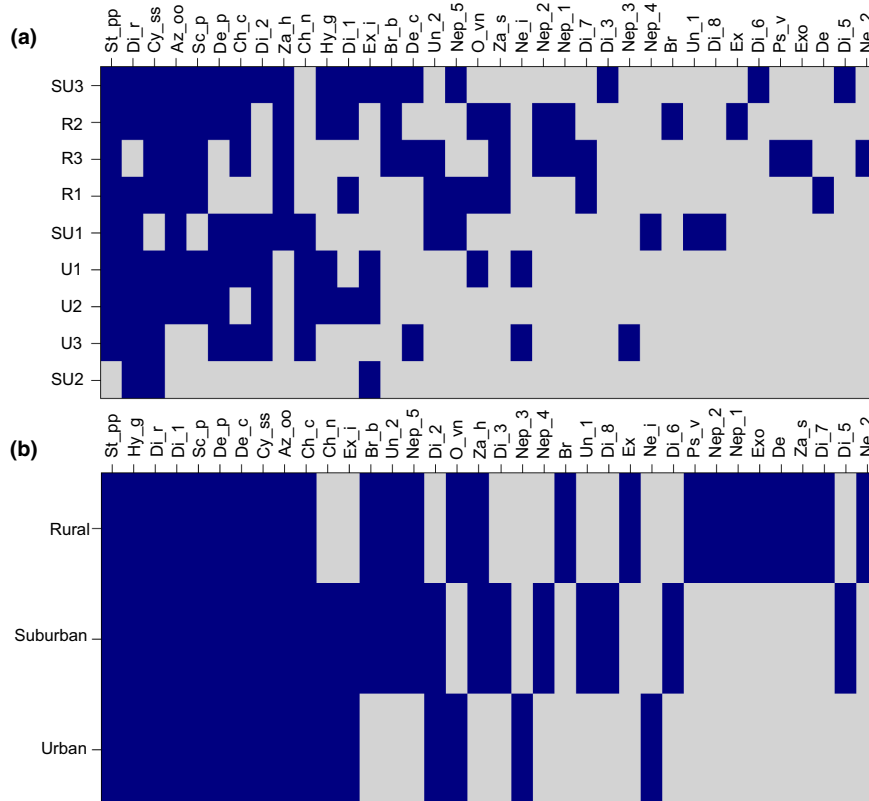
3.6 | Local and landscape correlates of coccinellid species richness and abundance

The global model after elimination of collinear factors included prey abundance, flower abundance, plant diversity, garden size, relative humidity, temperature, precipitation, crop vegetation within 3 km, non-crop vegetation within 3 km, impervious surface within 3 km, land cover diversity within 3 km, and season as predictors. After model selection, the best model that explained the variation in abundance along the gradient included prey abundance and plant diversity (Table 2, Table S6). Abundance was positively correlated with prey abundance (Wald, $\chi^2 = 12.77$, $p < .001$; Figure 5a) and negatively correlated with plant diversity (Wald, $\chi^2 = 5.46$, $p < .019$; Figure 5b). The best model that explained the variation in richness along the gradient included plant diversity and temperature (Table 2, Table S6); species richness positively correlated with temperature (Wald, $\chi^2 = 9.94$, $p < .01$), but correlated negatively with plant diversity (Wald, $\chi^2 = 4.04$, $p < .05$; Figure 5c, d). There was no significant evidence for spatial autocorrelation (abundance data, Moran's $I = -1.46$, $p = .93$; richness data, Moran's $I = -1.70$, $p = .96$). Landscape factors and seasonality did not influence abundance or species richness.

4 | DISCUSSION

Our first research question addresses whether coccinellid species composition changes along the rural to urban gradient, and our study documents, for the first time, strong differences in tropical zones. This corroborates several temperate studies documenting effects of urbanization gradients on other arthropods, such as carabid beetles (Magura & Lövei, 2021), spiders (Alaruiikka et al., 2002; Magura et al., 2010), butterflies (Bergerot et al., 2011), bees and hoverflies (Bates et al., 2011), and studies on coccinellid abundance and diversity in temperate and subtropical regions (e.g., Egerer, Arel, et al., 2017; Gardiner et al., 2021; Grez et al., 2019). In general, urbanization effects on arthropods vary widely; some taxa display marked compositional changes along the gradient while others remain unchanged. We found a clear separation of rural and urban gardens, each grouped accordingly in multidimensional space based on the species composition (Figure 2). According to our data, 14 of 36 coccinellid species (rarefied number of species) occurred in the urban zone; thus 61% of species were filtered out of this zone. Environmental changes due to urbanization constitute a strong filter on species traits (Magura & Lövei, 2021; Piano et al., 2017) restricting urban species pools to only those species that tolerate urban conditions. Some species absent from the urban zone were found exclusively in the rural zone; these species could be considered urban avoiders and are likely most sensitive to anthropogenic disturbances (Blair & Launer, 1997). Egerer et al. (2018) argue that a decrease in coccinellid richness and abundance in urban sites, ultimately driving assemblage composition, can be explained by the proportion of native species in the community. Native species are less likely to tolerate disturbances created by urbanization, and significant changes can

FIGURE 3 Nestedness plots of coccinellid species in southern Quintana Roo based on presence (blue) and absence (gray) data obtained through visual search. (a) Nestedness plot of the species assemblage between gardens and, (b) Nestedness plot of species assemblages between zones of the rural to urban gradient. R1–R3: rural gardens; SU1–SU3: suburban gardens; U1–U3: urban gardens. Morphospecies abbreviations according to Table 1



be expected along a rural to urban gradient in assemblages where native species are predominant. In our study, of those coccinellids identified to species, most are native to North America, except of *Chilocorus nigrita* and *Delphastus catalinae*. It is likely that most, if not all, other morphospecies we found are native to the region, because the coccinellid fauna has been poorly explored. Interestingly, both *D. catalinae* and *C. nigrita* were present in all zones but were more abundant in the urban zone: 43% of the individuals of *D. catalinae* and 94% of *C. nigrita* were collected in the urban zone with specimens of *C. nigrita* representing 19% of the total abundance of coccinellids in the urban zone. The fact that exotic species were found mainly in the urban zone further corroborates that urbanization promotes the establishment of non-native species (Fitch et al., 2019; McKinney, 2006). In some temperate countries, for example, coccinellid species composition has changed from being all native to increasingly dominated by exotic species (e.g., Bahlai et al., 2014; Gardiner et al., 2009; Harmon et al., 2007). We, however, did not observe overall numerical dominance of exotic species in the coccinellid community. As the first study on coccinellid diversity in the region, this may provide foundational knowledge for future studies monitoring exotic species in the community, in a region with accelerated urbanization.

Our second research question addresses the possible nested structure of coccinellid assemblages along the rural to urban gradient. We hypothesized that species-poor sites would be a subset of species-rich sites. Contrary to our expectations, we did not find nestedness along the gradient. Instead, species replacement was the major driver of changes in species composition along the gradient. As mentioned by Baselga (2010), distinguishing between components of beta diversity has conservation implications for deciding whether

to prioritize conservation of sites with the highest species richness (when strong nestedness is present) or designate conservation efforts to a larger number of sites. Herein, the rural zone had the most recorded species, with 10 exclusive species, but the suburban zone, despite lower richness, harbored six species not found in the rural zone (Table 1). The urban zone did not host exclusive species, but two species, *Exochomus insatiabilis* and *Diomus* sp. 8, found in this zone were absent from the rural zone. The great majority of species recorded exclusively in one zone were found in negligible numbers; more sampling is needed to determine whether those species can be considered as being resident species at a site or not. The presence of rare species in coccinellid communities is not uncommon; communities usually consist of few dominant species, several common species, and rare species (Honek et al., 2017).

Our third research question addressed whether coccinellid abundance, species richness, and diversity changes along the rural to urban gradient. Mean abundance did not vary along the urbanization gradient, but overall abundance was highest in suburban gardens. This can be attributed to the high abundance of two species, *Azya orbiger orbiger* and *Exochomus insatiabilis* which contributed to 46% of the overall abundance in this zone. These species were frequently observed on heavily prey-infested plants; hence, this spike in abundance in suburban gardens is not necessarily due to zone, but rather influenced by periods of high prey infestation in plants of certain gardens (Table S7). Likewise, mean species richness did not vary along the gradient, but overall richness was highest in the rural zone. Both non-significant and significant differences in richness of arthropods have been reported between zones along a rural to urban gradient (e.g., Alaruikka et al., 2002; Magura et al., 2004, 2010; Papastefanou

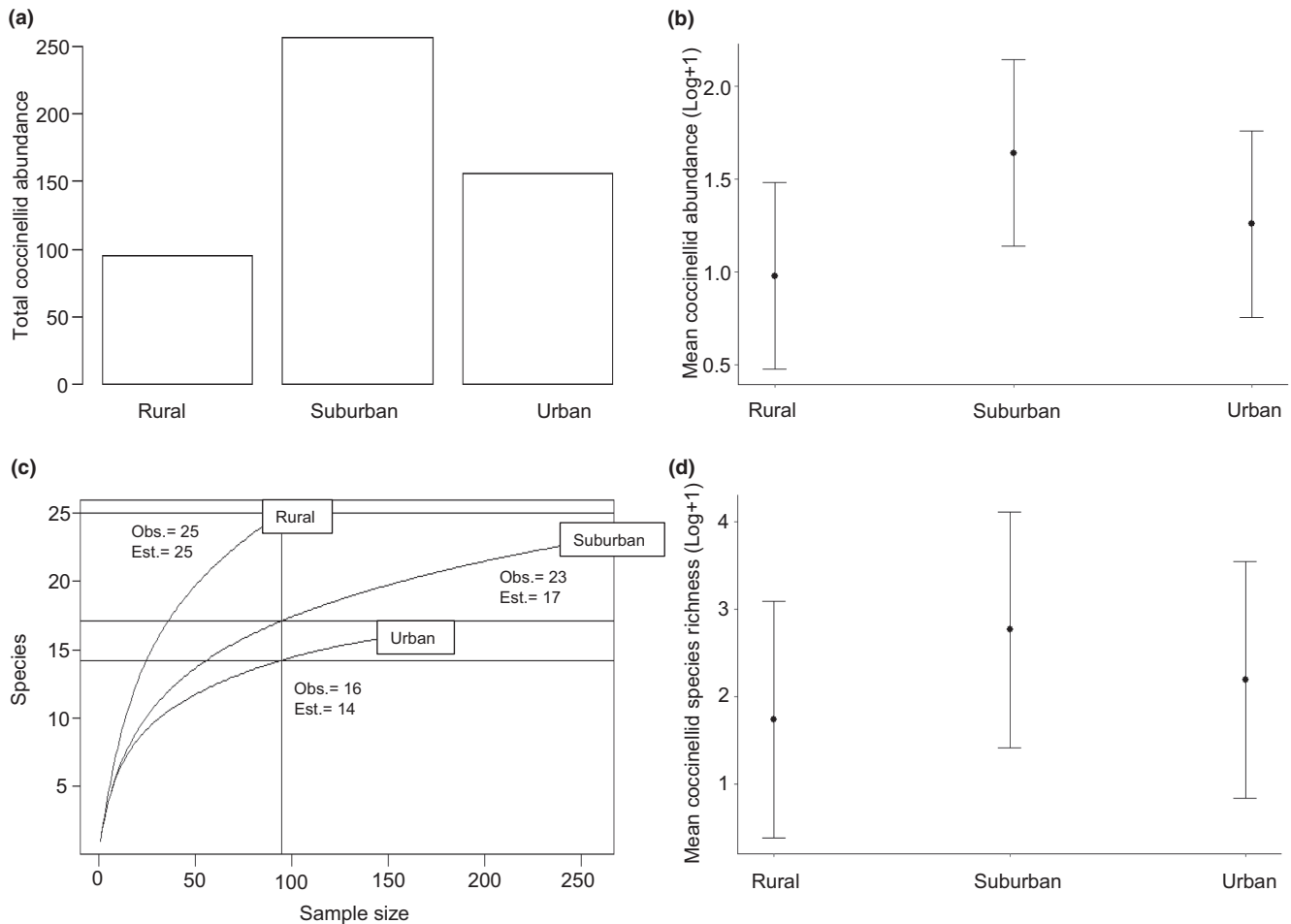


FIGURE 4 Coccinellid abundance and species richness in gardens along a rural to urban gradient in southern Quintana Roo. (a) Overall coccinellid abundance; (b) Estimated mean abundance \pm standard error obtained through LMM; (c) Rarefied number of coccinellid species in zones along the rural to urban gradient; (d) Estimated mean \pm standard error of coccinellids species richness obtained through LMM. LMMs were fitted considering data points of the visual survey only

TABLE 2 Summary of models that best predicted coccinellid abundance and species richness along the rural to urban gradient. Linear Mixed-effect Models with garden as random effect were fitted to data points from visual surveys. Significant predictors according to Wald χ^2 test are in bold

Variable response	Predictors	Estimate	Std. Error	Df	t	p	2.5% CI	97.5% CI
Abundance	(Intercept)	2.41	0.70	8.46	3.43	.001	1.03	3.79
	Prey abundance (log transformed)	0.13	0.04	107	3.57	<.001	0.06	0.20
	Plant diversity	-0.53	0.23	7.30	-2.34	.019	-0.97	-0.08
Richness	(Intercept)	0.91	0.75	15.2	1.22	.22	-0.55	2.38
	Plant diversity	-0.41	0.21	7.00	-2.01	.04	-0.81	-0.01
	Temperature	0.04	0.01	119	3.15	.002	0.02	0.07

et al., 2015); however, several studies do document declines in arthropod richness with urbanization (e.g., Bates et al., 2011; Egerer et al., 2018; Fenoglio et al., 2020; Ishitani et al., 2003; Piano et al., 2020; Sadler et al., 2006; Weller & Ganzhorn, 2004). We observed that coccinellids in urban gardens represented only 39% (rarefied) of the species in the overall community; but both the small number of gardens sampled and high spatial species replacement may account for the lack of difference in mean species richness between zones.

More studies are needed to understand how urbanization affects the physical and biotic environment for coccinellids in the tropics. In general, insect abundance tends to increase in city greenspaces relative to less transformed landscapes due to higher abundance of synanthropic generalist species and resource concentration (Faeth et al., 2011; Shochat et al., 2006). Contrary to our prediction, suburban gardens, with moderate disturbance levels, were not more diverse and our data do not support the intermediate disturbance

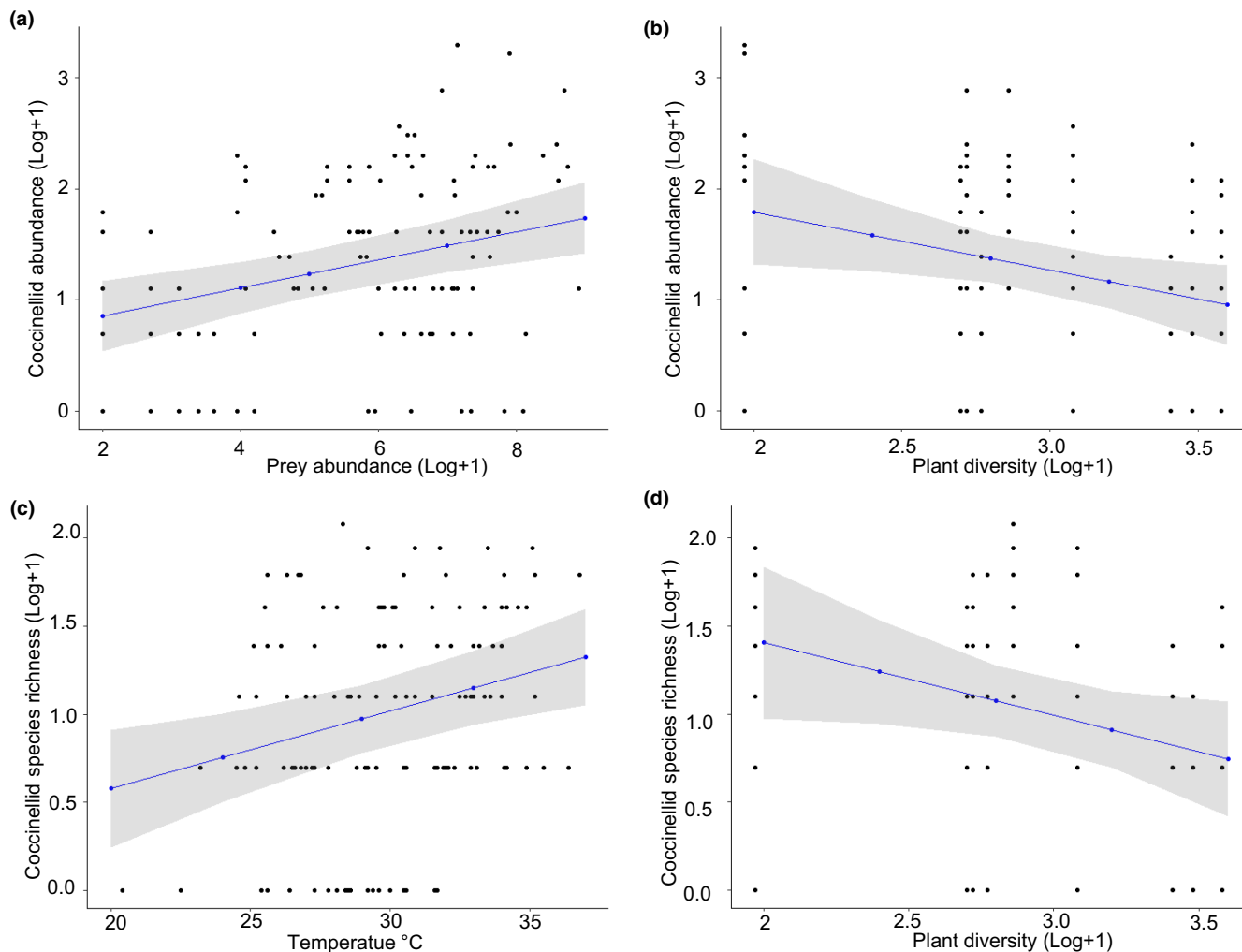


FIGURE 5 Significant predictors of coccinellid abundance and richness determined with Linear Mixed-Effects Models. Estimates and prediction lines are shown in blue and the confidence interval (95%) in gray. LMMs were fitted considering data points of the visual survey only

hypothesis (Connell, 1978). This supports other analyses showing that even within a taxonomic group, individual species respond differently to urbanization gradient (Magura & Lövei, 2021).

Our fourth research question addressed the local and landscape correlates of coccinellid species richness and abundance. Overall, only local factors were important correlates of coccinellid species richness and abundance. Previous studies report influences of both or just local or landscape factors but differ in the spatial extent at which urbanization was assessed, and in the climatic range of areas under study (Egerer, Bichier, et al., 2017; Egerer et al., 2018; Grez et al., 2019). For example, our results are at odds with those of Grez et al. (2019) who found that local variables were not important predictors of coccinellids in urban green spaces in Santiago, Chile, which experiences a Mediterranean type of climate. Similarly, no relationship was found between local vegetation variables, aphid prey abundance, and exotic coccinellid abundance; however, local variables were predictive of native coccinellid distribution in vacant land in Cleveland (Parker et al., 2020). We observed a positive correlation between prey abundance and coccinellid abundance. An increase in prey availability meets one of the requirements for predaceous coccinellids to

oviposit and correlates with increased abundance (Nedvěd & Honěk, 2012). Plant diversity correlated negatively with both coccinellid species richness and abundance, which may be linked to the presence of several plants with few or no flowers in some gardens; some coccinellids use pollen as alternative food sources to complete development (Lundgren, 2009). Moreover, some gardens with high plant diversity contained plants that do not host coccinellid prey; hence, a cascade effect could explain the negative correlation observed. Temperature correlated positively with coccinellid species richness along the gradient. Temperature influences coccinellid longevity, reproduction, growth, and development (Nedvěd & Honěk, 2012), all of which can influence coccinellid presence.

In both crop fields and city landscape studies, the configuration and diversity of land use surrounding studied areas predict coccinellid abundance and diversity, yet the strength and importance of landscape variables is context dependent, varying as a function of the spatial scale considered, local variables (Egerer, Arel, et al., 2017; Egerer et al., 2018), and even trophic guilds (Maisonhaute & Lucas, 2011; Parker et al., 2020). For example, in urban landscapes, gardens surrounded by less natural area had higher coccinellid abundance

and richness (Egerer, Bichier, et al., 2017), while percent natural vegetation boosted native coccinellid abundance and diversity in alfalfa crop fields (Grez et al., 2021). In addition, contrasting regional (geographical) responses to urbanization have been found when comparing coccinellid assemblages between temperate cities (Egerer et al., 2018). In our study, landscape variables did not affect coccinellid abundance or richness. This may be due to a limited number of study sites, the urbanization history of the city studied which ultimately determines the distinctiveness of the urban environment (see Parker, 2015), and/or the resolution of the land cover data. As signaled in other studies, resolution of available satellite images does not allow to differentiate small green spaces in highly heterogeneous urban environments (Egerer, Arel, et al., 2017; Egerer, Bichier, et al., 2017); such green areas may provide further connectivity across the landscape matrix (Parker et al., 2020). Future research should study how landscape factors influence coccinellid assemblages in the tropics, including studies addressing life history strategies or feeding guilds.

5 | CONCLUSION

This study contributes to the scarce literature regarding changes in coccinellid species composition, abundance, species richness, and diversity along a rural to urban gradient in tropical regions. We demonstrated that coccinellid species composition changes along the urbanization gradient, and that urbanization filters out several species which can be found in the rural and suburban areas. The conservation of coccinellid species from all zones of the rural to urban gradient seems equally important, as significant spatial species turnover was detected. This replacement of species along the gradient can, in part, explain why mean species richness was unaffected. The present study also provides further evidence that gardens in highly urbanized areas can represent valuable refuges for coccinellids. Our findings represent an opportunity to address coccinellid conservation in urban green spaces in the tropics.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTIONS

VVC and GP-L conceived and designed the study. VVC collected data. VVC, GP-L, and SMP analyzed data. YH and AG-A provided advice and necessary resources. GP-L led draft writing with all authors contributing to the final version.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the ZENODO digital repository. <https://doi.org/10.5281/zenodo.6383249> (Catzim et al., 2022).

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REFERENCES

- Alaruikka, D., Kotze, D. J., Matveinen, K., & Niemelä, J. (2002). Carabid beetle and spider assemblages along a forested urban-rural gradient in southern Finland. *Journal of Insect Conservation*, 6, 195–206. <https://doi.org/10.1023/A:1024432830064>
- Almeida-Neto, M., Guimaraes, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117, 1227–1239. <https://doi.org/10.1111/j.0030-1299.2008.16644.x>
- Alyokhin, A., & Sewell, G. (2004). Changes in a lady beetle community following the establishment of three alien species. *Biological Invasions*, 6, 463–471. <https://doi.org/10.1023/B:BINV.0000041554.14539.74>
- Bahlai, C. A., Colunga-García, M., Gage, S. H., & Landis, D. A. (2014). The role of exotic ladybeetles in the decline of native ladybeetle populations: evidence from long-term monitoring. *Biological Invasions*, 17, 1005–1024. <https://doi.org/10.1007/s10530-014-0772-4>
- Bartoń, K. (2019). *MuMIn: Multi-Model Inference*. R package version 1.43.6. Retrieved from <https://CRAN.R-project.org/package=MuMIn>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieux, F., & Logez, M. (2021). *betapart: Partitioning beta diversity into turnover and nestedness Components*. R package version 1.5.4. <https://CRAN.R-project.org/package=betapart>
- Bates, A. J., Sadler, J. P., Fairbrass, A. J., Falk, S. J., Hale, J. D., & Matthews, T. J. (2011). Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *PLoS One*, 6(8), e23459. <https://doi.org/10.1371/journal.pone.0023459>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bergerot, B., Fontaine, B., Julliard, R., & Baguette, M. (2011). Landscape variables impact the structure and composition of butterfly assemblages along an urbanization gradient. *Landscape Ecology*, 26, 83–94. <https://doi.org/10.1007/s10980-010-9537-3>
- Bivand, R. S., & Wong, D. W. S. (2018). Comparing implementations of global and local indicators of spatial association. *TEST*, 27(3), 716–748. <https://doi.org/10.1007/s11749-018-0599-x>
- Bjørnstad, O. N. (2020). *ncf: Spatial Covariance Functions*. R package version 1.2-9. <https://CRAN.R-project.org/package=ncf>
- Blair, R. B., & Launer, A. E. (1997). Butterfly diversity and human land use: Species assemblages along an urban gradient. *Biological*

- Conservation*, 3207(96), 113–125. [https://doi.org/10.1016/S0006-3207\(96\)00056-0](https://doi.org/10.1016/S0006-3207(96)00056-0)
- Catzim, V. V., Elías-Gutiérrez, M., & Pérez-Lachaud, G. (2022). Contribution to the lady beetle fauna of the Yucatan Peninsula and integrative taxonomy for species delimitation. *Systematics and Biodiversity*, 20(1), 1–16. <https://doi.org/10.1080/14772000.2021.2017060>
- Comont, R. F., Roy, H. E., Harrington, R., Shortall, C. R., & Purse, B. V. (2014). Ecological correlates of local extinction and colonisation in the British ladybird beetles (Coleoptera: Coccinellidae). *Biological Invasions*, 16, 1805–1817. <https://doi.org/10.1007/s10530-013-0628-3>
- Comont, R. F., Roy, H. E., Lewis, O. T., Harrington, R., Shortall, C. R., & Purse, B. V. (2012). Using biological traits to explain ladybird distribution patterns. *Journal of Biogeography*, 39(10), 1772–1781. <https://doi.org/10.1111/j.1365-2699.2012.02734.x>
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199(4335), 1302–1310. <https://doi.org/10.1126/science.199.4335.1302>
- Cortina Villar, S., Mendoza, P. M., & Orneva-Himmelberger, Y. (1999). Cambios en el uso del suelo y deforestación en el sur de los estados de Campeche y Quintana Roo, México. *Investigaciones Geográficas*, 1(38), 41–56. <https://doi.org/10.14350/riig.59077>
- Egerer, M. H., Arel, C., Ootshi, M. D., Quistberg, R. D., Bichier, P., & Philpott, S. M. (2017). Urban arthropods respond variably to changes in landscape context and spatial scale. *Journal of Urban Ecology*, 3(1), 1–10. <https://doi.org/10.1093/jue/jux001>
- Egerer, M. H., Bichier, P., & Philpott, S. M. (2017). Landscape and local habitat correlates of lady beetle abundance and species richness in urban agriculture. *Annals of the Entomological Society of America*, 110(1), 97–103. <https://doi.org/10.1093/aesa/saw063>
- Egerer, M. H., Li, K., & Ong, T. W. Y. (2018). Context matters: Contrasting ladybird beetle responses to urban environments across two US regions. *Sustainability*, 10(6), 1829. <https://doi.org/10.3390/su10061829>
- Faeth, S. H., Bang, C., & Saari, S. (2011). Urban biodiversity: Patterns and mechanisms. *Annals of the New York Academy of Sciences*, 1223(1), 69–81. <https://doi.org/10.1111/j.1749-6632.2010.05925.x>
- Fenoglio, M. S., Rossetti, M. R., & Videla, M. (2020). Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. *Global Ecology and Biogeography*, 28(8), 1412–1429. <https://doi.org/10.1111/geb.13107>
- Fitch, G., Wilson, C. J., Glaum, P., Vaidya, C., Simao, M. C., & Jamieson, M. A. (2019). Does urbanization favour exotic bee species? Implications for the conservation of native bees in cities. *Biology Letters*, 15(12), 20190574. <https://doi.org/10.1098/rsbl.2019.0574>
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression [R package car version 3.0-7] (Third edit)*. Sage. Retrieved from <https://socialsciences.mcmaster.ca/jfox/Books/Companion>
- García, E. (1973). *Modificaciones al sistema de clasificación climática de Köppen*. Instituto de Geografía, Universidad Nacional Autónoma de México.
- Gardiner, M. M., Landis, D. A., Gratton, C., Schmidt, N., O'Neal, M., Mueller, E., Chacon, J., Heimpel, G. E., & Difonzo, C. D. (2009). Landscape composition influences patterns of native and exotic lady beetle abundance. *Diversity and Distributions*, 15(4), 554–564. <https://doi.org/10.1111/j.1472-4642.2009.00563.x>
- Gardiner, M. M., Perry, K. I., Riley, C. B., Turo, K. J., Delgado de la Flor, Y. A., & Sivakoff, F. S. (2021). Community science data suggests that urbanization and forest habitat loss threaten aphidophagous native lady beetles. *Ecology and Evolution*, 11(6), 2761–2774. <https://doi.org/10.1002/ece3.7229>
- Gardiner, M. M., Prajzner, S. P., Burkman, C. E., Albro, S., & Grewal, P. S. (2014). Vacant land conversion to community gardens: Influences on generalist arthropod predators and biocontrol services in urban greenspaces. *Urban Ecosystems*, 17(1), 101–122. <https://doi.org/10.1007/s11252-013-0303-6>
- González, G., & Větrovec, J. (2021). New species and records of Neotropical ladybirds (Coleoptera: Coccinellidae). *Revista Chilena De Entomología*, 47(2), 331–374. <https://doi.org/10.35249/rche.47.2.21.19>
- Gordon, R. D. (1985). The Coccinellidae (Coleoptera) of America North of Mexico. *Journal of the New York Entomological Society*, 93(1), 1–912.
- Grez A. A., Zaviezo T., Casanoves F., Oberti R., & Plischoff P. (2021). The positive association between natural vegetation, native coccinellids and functional diversity of aphidophagous coccinellid communities in alfalfa. *Insect Conservation and Diversity*, 14(4), 464–475. <https://doi.org/10.1111/icad.12473>
- Greza, A. A., Zaviezo, T., Gardiner, M. M., & Alaniz, A. J. (2019). Urbanization filters coccinellids composition and functional trait distributions in greenspaces across greater Santiago, Chile. *Urban Forestry & Urban Greening*, 38, 337–345. <https://doi.org/10.1653/024.097.040910.1016/j.ufug.2019.01.002>
- Hagen, K. S. (1962). Biology and ecology of predaceous coccinellidae. *Annual Review of Entomology*, 7(1), 289–326. <https://doi.org/10.1146/annurev.en.07.010162.001445>
- Harmon, J. P., Stephens, E., & Losey, J. (2007). The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. *Journal of Insect Conservation*, 11(1), 85–94. <https://doi.org/10.1007/s10841-006-9021-1>
- Hodek, I., Honek, A., & Van Emden, H. F. (Eds.). (2012). *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. Wiley-Blackwell.
- Honek, A., Dixon, A. F., Soares, A. O., Skuhrovec, J., & Martinkova, Z. (2017). Spatial and temporal changes in the abundance and composition of ladybird (Coleoptera: Coccinellidae) communities. *Current Opinion in Insect Science*, 20, 61–67. <https://doi.org/10.1016/j.cois.2017.04.001>
- Honek, A., Martinkova, Z., & Dixon, A. F. G. (2015). Detecting seasonal variation in composition of adult Coccinellidae communities. *Ecological Entomology*, 40(5), 543–552. <https://doi.org/10.1111/een.12225>
- Iperti, G. (1999). Biodiversity of predaceous Coccinellidae in relation to bioindication and economic importance. *Ecosystems and Environment*, 74(1–3), 323–342. [https://doi.org/10.1016/S0167-8809\(99\)00041-9](https://doi.org/10.1016/S0167-8809(99)00041-9)
- Ishitani, M., Kotze, D. J., & Niemelä, J. (2003). Changes in carabid beetle assemblages across an urban-rural gradient in Japan. *Ecography*, 26(4), 481–489. <https://doi.org/10.1034/j.1600-0587.2003.03436.x>
- Islebe, G. A., Sánchez-Sánchez, O., Valdéz-Hernández, M., & Weissenberger, H. (2015). Distribution of vegetation types. In G. A. Islebe, J. L. León-Cortés, S. Calmé, & B. Schmook (Eds.), *Biodiversity and conservation of the Yucatán Peninsula* (pp. 39–53). Springer.
- Liere, H., Egerer, M. H., & Philpott, S. M. (2019). Environmental and spatial filtering of ladybird beetle community composition and functional traits in urban landscapes. *Journal of Urban Ecology*, 5(1), 1–12. <https://doi.org/10.1093/jue/juz014>
- Lundgren, J. G. (2009). Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. *Biological Control*, 51(2), 294–305. <https://doi.org/10.1016/j.biocontrol.2009.05.016>
- Magura, T., Horváth, R., & Tóthmérész, B. (2010). Effects of urbanization on ground-dwelling spiders in forest patches, in Hungary. *Landscape Ecology*, 25(4), 621–629. <https://doi.org/10.1007/s10980-009-9445-6>
- Magura, T., & Lövei, G. L. (2021). Consequences of urban living: Urbanization and ground beetles. *Current Landscape Ecology Reports*, 6(1), 9–21. <https://doi.org/10.1007/S40823-020-00060-X>
- Magura, T., Tóthmérész, B., & Molnár, T. (2004). Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. *Landscape Ecology*, 19, 747–759. <https://doi.org/10.1007/s10980-005-1128-4>
- Maisonhaute, J.-É., & Lucas, É. (2011). Influence of landscape structure on the functional groups of an aphidophagous guild: Active-searching

- predators, furtive predators and parasitoids. *European Journal of Environmental Sciences*, 1(1), 41–50. <https://doi.org/10.14712/23361964.2015.64>
- Masetti, A., Magagnoli, S., Lami, F., Lanzoni, A., & Burgio, G. (2018). Long term changes in the communities of native ladybirds in Northern Italy: Impact of the invasive species *Harmonia axyridis* (Pallas). *BioControl*, 63(5), 665–675. <https://doi.org/10.1007/s10526-018-9891-7>
- McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *BioScience*, 52(10), 883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)
- McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127, 247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>
- McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, 11, 161–176. <https://doi.org/10.1007/s11252-007-0045-4>
- Nedvěď, O., & Honěk, A. (2012). Life history and development. In I. Hodek, H. F. van Emden, & A. Honěk (Eds.), *Ecology and behaviour of the ladybird beetles (Coccinellidae)* (pp. 54–109). Wiley-Blackwell.
- Nestor-Arriola, J. I., & Toledo-Hernández, V. H. (2019). Contribution to the knowledge of the *dentipes* group of the genus *Brachiacantha* (Coleoptera: Coccinellidae). *Zootaxa*, 4701, 537–552. <https://doi.org/10.11646/zootaxa.4701.6.3>
- Niemelä, J., & Kotze, D. J. (2009). Carabid beetle assemblages along urban to rural gradients: A review. *Landscape and Urban Planning*, 92(2), 65–71. <https://doi.org/10.1016/j.landurbplan.2009.05.016>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E. & Wagner, H. (2019). *Vegan: Community ecology package. R package version 2.5-6*. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Papastefanou, G., Panayiotou, E., Mylonas, M., & Simaiakis, S. M. (2015). Centipede assemblages along an urbanization gradient in the city of Heraklion, Crete (Greece). In I. H. Tuf, & K. Tajovský (Eds.), *Proceedings of the 16th International Congress of Myriapodology* (pp. 163–179). ZooKeys. doi:<https://doi.org/10.3897/zookeys.510.8414>
- Parker, D. M., Turo, K. J., Delgado de la flor, Y. A., & Gardiner, M. M. (2020). Landscape context influences the abundance and richness of native lady beetles occupying urban vacant land. *Urban Ecosystems*, 23, 1299–1310. <https://doi.org/10.1007/s11252-020-01000-7>
- Parker, S. S. (2015). Incorporating critical elements of city distinctiveness into urban biodiversity conservation. *Biodiversity and Conservation*, 24, 683–700. <https://doi.org/10.1007/s10531-014-0832-1>
- Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., Lens, L., Merckx, T., Mertens, D., van Kerckvoorde, M., De Meester, L., & Hendrickx, F. (2017). Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, 23(7), 2554–2564. <https://doi.org/10.1111/gcb.13606>
- Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Bäckeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hanashiro, F. T. T., Higuti, J., Lens, L., ... Hendrickx, F. (2020). Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, 26(3), 1196–1211. <https://doi.org/10.1111/gcb.14934>
- Rocha, E. A., Souza, E. N. F., Bleakley, L. A. D., Burley, C., Mott, J. L., Rue-Glutting, G., & Fellowes, M. D. E. (2018). Influence of urbanisation and plants on the diversity and abundance of aphids and their ladybird and hoverfly predators in domestic gardens. *European Journal of Entomology*, 115, 140–149. <https://doi.org/10.14411/eje.2018.013>
- Rodríguez-Vélez, J. M. (2018). New species of *Exochomus* (Coleoptera: Coccinellidae: Chilocorinae) from Mexico. *Revista Mexicana De Biodiversidad*, 89(3), 666–671. <https://doi.org/10.22201/ib.20078706e.2018.3.2445>
- RStudio Team (2020). *RStudio: Integrated Development for R*. RStudio Inc.
- Sadler, J. P., Small, E. C., Fiszpan, H., Telfer, M. G., & Niemelä, J. (2006). Investigating environmental variation and landscape characteristics of an urban – rural gradient using woodland carabid assemblages. *Journal of Biogeography*, 33(6), 1126–1138. <https://doi.org/10.1111/j.1365-2699.2006.01476.x>
- Seago, A. E., Giorgi, J. A., Li, J., & Ślipiński, A. (2011). Phylogeny, classification and evolution of ladybird beetles (Coleoptera: Coccinellidae) based on simultaneous analysis of molecular and morphological data. *Molecular Phylogenetics and Evolution*, 60(1), 137–151. <https://doi.org/10.1016/j.ympev.2011.03.015>
- SEDATU (2018). *Programa de desarrollo urbano de Chetumal-Calderitas-Subteniente López- Huay-Pix y Xul-Há. Municipio de Othón P. Blanco, Estado de Quintana Roo*. Retrieved from <http://www.opb.gob.mx>
- Sheldon, K. S. (2019). Climate change in the tropics: ecological and evolutionary responses at low latitudes. *Annual Review of Ecology, Evolution, and Systematics*, 50, 303–333. <https://doi.org/10.1146/annurev-ecolsys-110218-025005>
- Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution*, 21(4), 186–191. <https://doi.org/10.1016/j.tree.2005.11.019>
- Ślipiński, S. A., Leschen, R. A. B., & Lawrence, J. F. (2011). Order Coleoptera Linnaeus, 1758. In: Zhang, Z.-Q. (Ed.) *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa*, 3148(1), 203–208. doi:<https://doi.org/10.11646/zootaxa.3148.1.39>
- USGS (2018). *United States Geological Survey*. Retrieved from <https://earthexplorer.usgs.gov/>
- Weller, B., & Ganzhorn, J. U. (2004). Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. *Basic and Applied Ecology*, 5(2), 193–201. <https://doi.org/10.1078/1439-1791-00220>
- Woltz, J. M., & Landis, D. A. (2014). Coccinellid response to landscape composition and configuration. *Agricultural and Forest Entomology*, 16, 341–349. <https://doi.org/10.1111/afe.12064>
- Wootton, J. T. (1998). Effects of disturbance on species diversity: A multitrophic perspective. *American Naturalist*, 152(6), 803–825. <https://doi.org/10.1086/286210>

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