



# Local and landscape drivers of bird abundance, species richness, and trait composition in urban agroecosystems

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Published online: 6 February 2020

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## Abstract

Urban gardens, or spaces that include vegetables, fruit trees, and ornamental plants, can support bird species and communities by providing food and nesting habitat within urban landscapes. Yet, variation in management of gardens (e.g., garden size, number of tree and shrub species, ground cover) and the landscape (e.g., urban cover, landscape diversity) that surrounds them may alter communities within gardens. We examined how garden management and landscape features influence bird abundance, richness, species composition, and traits in 19 urban community gardens in the central coast of California. We found that bird abundance was higher in larger gardens and in gardens with more grass, and species richness was higher in larger gardens. Bird abundance also differed with garden ecoregion. Urban cover influenced bird species composition while bird trait distributions were influenced by urban cover, ecoregion, and grass cover. Gardens with more urban cover supported fewer insectivores, ground-nesters, and forest-associated birds, higher nesting height and more urban-associated bird species. Gardens in the ecoregion closer to the coast had more cliff nesters and more marsh-associated birds. Although urban cover and ecoregion were important for the composition and trait distribution of birds, manipulation of garden management and size may promote bird species richness, or abundance of functionally important birds in gardens.

**Keywords** Avian · Biodiversity · California · Community garden · Functional traits

## Introduction

As human populations expand and natural landscapes are destroyed by urban sprawl, bird communities are impacted by habitat loss and fragmentation (Enoksson et al. 1995; Mörtberg 2001). Effects of urban development on local bird communities are context-dependent yet several clear patterns have emerged. Habitat loss associated with continued development spurs declines in species richness, increases in abundance, and increases in the abundance of certain bird species to the detriment of others closer to urban centers (Owens and Bennett 2000; Ortega-Álvarez and MacGregor-Fors 2009;

Aronson et al. 2014). Moreover, structural changes to urban habitats such as nest box introduction, impervious surface, sealed area, building height, and electrical wiring also affect bird communities (Jokimäki 1999; MacGregor-Fors and Schondube 2011; Strohbach et al. 2013; Schütz and Schulze 2015; Silva et al. 2015; Threlfall et al. 2016; Evans et al. 2018) and bird trait and species composition (Ortega-Álvarez and MacGregor-Fors 2009; Barth et al. 2015). In particular, urban bird communities are highly homogenized with abundance skewed towards generalist, anthropophilic species over birds with less urban-adapted diet, social, nesting, and migratory requirements (Crooks et al. 2004; Kark et al. 2007; Ortega-Álvarez and MacGregor-Fors 2009) and fewer specialists overall (Devictor et al. 2007). Urban areas support fewer interior and ground-nesting birds in favor of those that nest in buildings (Marzluff 2001), and are generally associated with lower insectivore abundance (Bakermans and Rodewald 2006; Kark et al. 2007; Barth et al. 2015) due to environmental filtering of birds with specialist life history traits (Crocini et al. 2008) such as insect diets (Evans et al. 2018). Although urban bird communities can be less species rich and more homogenized, urban green spaces are extremely important breeding habitats (Han et al. 2019) and can support

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s11252-020-00934-2>) contains supplementary material, which is available to authorized users.

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higher breeding success of insectivorous birds if management practices, such as plant choice, support arthropod prey (Narango et al. 2017). However, urban cover can also negatively affect bird reproductive success and egg production due to higher brood parasitism and fewer nesting attempts in developed areas (Rodewald and Shustack 2008; Coogan et al. 2018). Given that urban areas form part of the permanent landscape, understanding how to shift management of urban habitats to best support high bird abundance, species, and functional richness is highly warranted.

Urbanization inherently modifies the environment for birds, but the negative effects of urban sprawl and development may be offset by maintaining green spaces (e.g., city parks, urban community gardens) that may support even greater habitat and avian functional group diversity than that of semi-natural areas (Oliveira Hagen et al. 2017). Urban green spaces provide habitat for birds by provisioning resources and connecting habitat networks at the landscape scale (Rudd et al. 2002) thereby increasing the overall quality of the urban matrix for avian communities (Andersson and Colding 2014). Urban green spaces also provide economic, socio-cultural and ecological services including locally-based food supply, noise mitigation, climate regulation, and pollination which can reduce the ecological footprints of cities and enhance quality of life for humans (Gómez-Baggethun and Barton 2013). Depending on management, urban green spaces may support higher or lower abundance and diversity of urban birds and promote greater species evenness. For instance, bird abundance and richness in urban green spaces increase with shrub species richness (Paker et al. 2014), native plant biomass (Day 1995; Reis et al. 2012), vegetative cover (Daniels and Kirkpatrick 2006; Threlfall et al. 2016), local habitat quality (Chamberlain et al. 2004), higher canopy cover (Beissinger and Osborne 1982), weed growth (DeGraaf and Wentworth 1986), more natural habitat in the landscape (Chamberlain et al. 2004; Dale 2018), and higher microhabitat heterogeneity (Nielsen et al. 2014). The impacts of local habitat and landscape changes, however, appear to be largely species- or functional group-specific Day 1995; Jokimäki 1999; Chamberlain et al. 2004; Daniels and Kirkpatrick 2006) and are poorly understood in the context of urban agriculture. Community gardens, or spaces that include vegetables, fruit trees, and ornamental plants, experience quick turnover in plant composition, ground cover, and vegetation structure, and could be easily adapted to benefit bird biodiversity (Philpott and Bichier 2017).

Conservation of birds in urban habitats may also be valuable to humans in cities because birds provide ecosystem services. First, in addition to their inherent biodiversity value, urban birds offset the disconnect with nature reported by people in highly urbanized areas through their appeal to birdwatchers and citizen scientists who are motivated by their love of flight, sport, nature, and an intrinsic fascination with

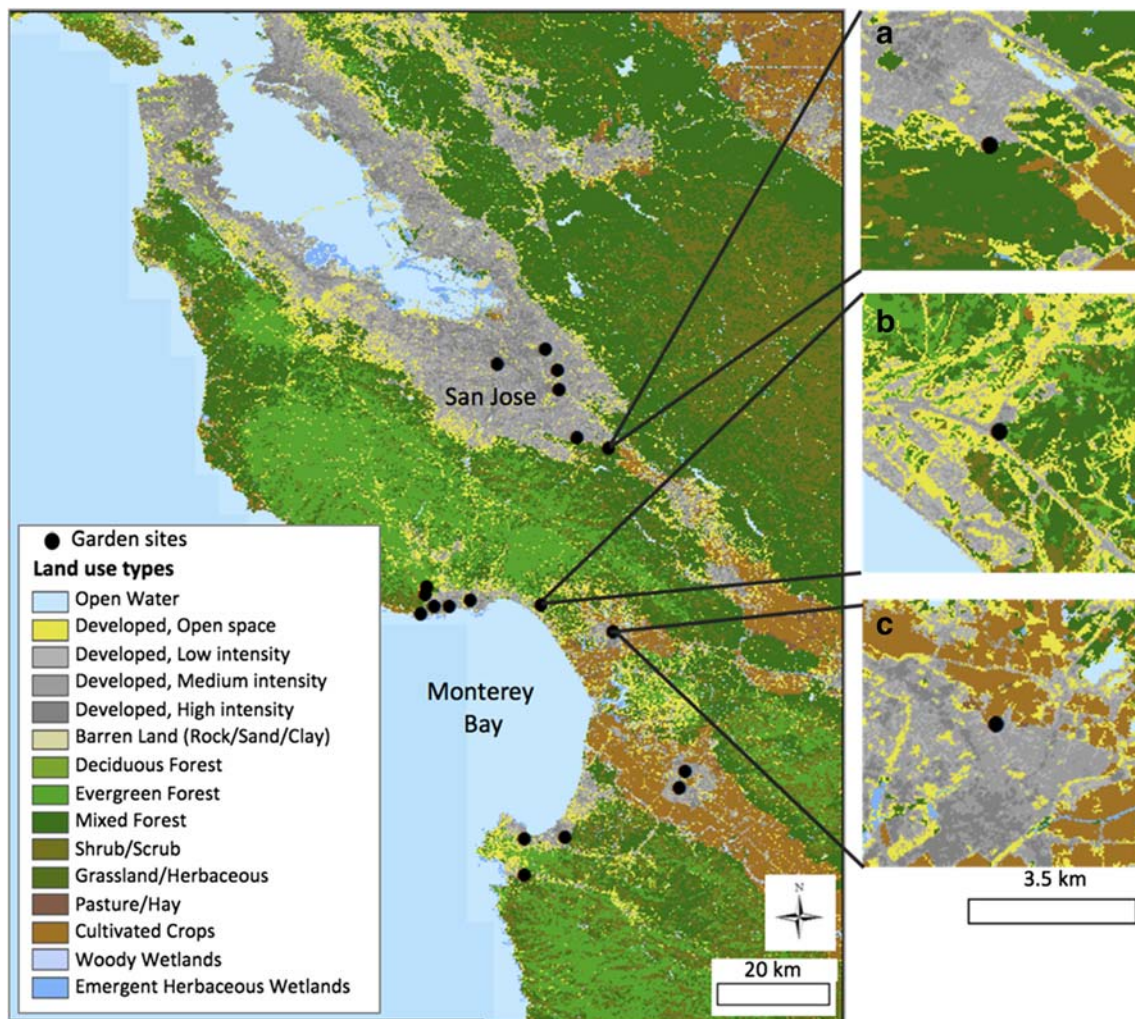
birds and their aesthetic qualities (Kellert 1985; Goddard et al. 2010; Reynolds et al. 2017). Second, in the urban environment, birds provide ecosystem services by acting as pollinators, scavengers, seed dispersers, pest control agents, nutrient depositors, and ecosystem engineers by generating products that contribute to ecological functioning (Whelan et al. 2008; Fujita and Koike 2009). In particular, insectivorous birds control pests in an array of agricultural habitats (Mooney et al. 2010), and the effectiveness of pest control provided by birds may be dependent on both species richness (Van Bael et al. 2008) and functional richness of the avian community (Philpott et al. 2009). Thus, urban bird communities in urban agroecosystems are potentially important to gardeners for the crucial pest control services they provide (Sekerçioğlu 2006; Philpott et al. 2009).

We focus on understanding which local habitat and landscape characteristics of urban agroecosystems (e.g., community gardens, or spaces that include vegetables, fruit trees, and ornamental plants) influence bird communities in the central coast of California. Specifically, we asked 1) Which local habitat and landscape features of community gardens influence abundance and species richness of urban birds? and 2) Which local habitat and landscape features of community gardens influence bird species composition and species trait composition? Our aim was to examine whether and how urban gardens can be managed to boost abundance, species richness and birds with traits that may support ecosystem services, such as pest control, in urban agroecosystems.

## Methods

### Study system and site characteristics

We studied bird communities in urban gardens in the California central coast region between May and September 2015. We chose 19 gardens in Monterey ( $N=6$ ), Santa Cruz ( $N=7$ ), and Santa Clara ( $N=6$ ) Counties (Fig. 1). Gardens are distributed within two California ecoregions – defined as areas that support similar ecosystems and environmental resources – the Monterey Bay Plains and Terraces and the Bay Terraces/Lower Santa Clara Valley. According to the description by Griffith et al. (2016), the Monterey Bay Plains and Terraces ecoregion (including all Monterey and Santa Cruz County gardens) has marine-influenced weather with frequent morning fog in the summer, higher precipitation, cooler temperatures than surrounding areas, and plant communities including Coast live oak (*Quercus agrifolia*) and California oatgrass (*Danthonia californica*), coastal scrub and sage, and agriculture (e.g., lettuce, artichokes, strawberries). The Bay Terraces/Lower Santa Clara Valley ecoregion (including all Santa Clara gardens) is a largely urbanized area immediately south of the San Francisco Bay, with little remaining native vegetation



**Fig. 1** Map of urban garden study sites in the central coast of California. Inset panels highlight gardens surrounded by relatively higher amounts of natural habitat (a), open space (b) and agriculture (c). Map layers come from the National Landcover Database (Homer et al. 2015)

(Griffith et al. 2016). The two ecoregions also differ in mean summer temperatures with  $\sim 4.5$  °C hotter temperatures in the Bay Terraces/Lower Santa Clara Valley (MH Egerer, *unpublished data*). All gardens are community gardens managed collectively or in individual allotments (plots), and range in size from 444 m<sup>2</sup> to 15,525 m<sup>2</sup>. Each garden contained vegetable crops and ornamental flowering plants and had been in production for between 4 and 46 years at the time bird surveys were conducted. Gardens were separated by a minimum of 2 km.

At the center of each garden, we established a 20 × 20 m plot within which we sampled local vegetation and ground cover characteristics five times across the sampling season between 16 - 18 June, 7–11 July, 2–14 August, 1–2 September, and 21–23 September 2015. We sampled canopy cover with a concave spherical densiometer at the center of each plot, and 10 m to the N, S, E, and W of the center. We counted the number of trees and shrubs (e.g., woody plants), the number of tree and shrub species, and the number of trees

and shrubs in flower. We selected four 1 × 1 m plots within the 20 × 20 m plots using a stratified random sampling approach with one plot each within four 5 m × 20 m strips inside the sampling area. In the 1 × 1 m plots, we identified all herbaceous plants (except grass) to morphospecies. We measured the height of the tallest herbaceous vegetation, and estimated the percent ground cover from a) bare ground, b) grass, c) herbaceous plants, d) leaf litter, and e) mulch or wood chips. We measured the size of each garden and noted the ecoregion and number of years during which cultivation had taken place. Values for all variables were averaged across sample periods except herbaceous plant richness which was cumulative over the summer. Overall, we took data on 14 local vegetation and ground cover variables in each garden.

We used a geographic information system (GIS) to assess land-cover types surrounding each garden. We used land-cover data from the 2011 National Land Cover Database (NLCD, 30 m resolution) (Homer et al. 2015) and calculated the percentage of land-cover types within



200 m, 300 m, 400 m, 500 m, 600 m, 700 m, 800 m, 900 m, 1000 m, 2000 m, 3000 m, 4000 m, and 5000 m of the center of each garden. We chose these spatial extents to cover a range from typical breeding territory size for the birds we encountered to several times a daily dispersal distance for these species (Jackson and Fahrig 2015). We created four land-cover categories: 1) natural (including deciduous, evergreen, and mixed forests, dwarf scrub, shrub/scrub, and grassland/herbaceous), 2) open (including lawn grass, park, and golf courses), 3) urban (including low, medium, and high intensity developed land), and 4) agriculture (including pasture/hay and cultivated crop area). Other land-cover types covered <5% of the surrounding landscape and were not included. We used the *vegan* package in R (Oksanen et al. 2018) to calculate landscape diversity (e.g., modified Shannon-Wiener diversity index ( $H'$ )) for each garden at each spatial scale (McGarigal et al. 2002; Bennett and Gratton 2012). Thus we calculated a total of five landscape variables at each of 13 spatial scales for the analysis.

### Bird surveys

All bird surveys were conducted by one observer (PB) with 10-min point counts during daylight hours (7:15 AM - 7:00 PM) approximately every 3 weeks between 12 June - 23 September 2015. The observer stood at the center of the garden and recorded all birds seen or heard within 30 m. Any birds seen or heard within 30 m but confirmed to be outside of the garden were not included. Each site was visited four times across the survey period with approximately 3 weeks between each visit. Each site was visited during different times of day (i.e., morning, afternoon, evening) across sample periods to reduce bias in survey time. The observer waited silently for 5 min after set up at gardens for birds to acclimatize to observer presence.

### Bird trait classification

We categorized traits of all birds seen or heard in the gardens according to three traits related to diet and foraging (feeding guild, foraging strata, foraging strategy), two traits related to nesting (nest location, nest height), as well as data for bird mass (g), migratory status, and preferred habitat type (Table S1). We extracted information for the different traits from three sources: Birder's Handbook (Ehrlich et al. 1988), The Sibley Guide to Birds (Sibley 2014), and The Cornell Lab of Ornithology (2018) (Table 1). For the one bird species not listed in Ehrlich et al. (1988), Eurasian Collared Dove, *Streptopelia decaocto*, we used other sources for trait information.

### Data analysis

We measured a large number of local and landscape predictors and used three techniques to select variables included in the final analysis. First, we created two vegetation indices to summarize woody vegetation and herbaceous vegetation characteristics (as in Philpott et al. 2008). For the woody vegetation complexity index (VCI woody) we scaled all values for canopy cover, number of trees and shrubs, number of tree and shrub species, and number of tree and shrub species in flower to a scale from 0 to 1 (with 1 being the highest value measured across all sites and 0 the lowest value measured across all sites). Then we averaged scaled variable values to create the VCI woody metric. For the herbaceous vegetation complexity index (VCI herb), we scaled all values for number of herbaceous plant species, height of the tallest herbaceous vegetation, percent herbaceous plant cover to a scale from 0 to 1 (with 1 being the highest value measured across all sites and 0 the lowest value measured across all sites). Then we averaged scaled variable values to create the VCI herb metric. Second, we ran one Pearson's correlation for all local-scale variables – VCI woody, VCI herb, percent cover from mulch, bare ground, grass, and leaf litter, garden size, and garden age (Table S2) and a second Pearson's correlation for landscape-scale variables (Table S3) to select non-correlated variables. Garden size was correlated with garden age, VCI herb was correlated with percent bare ground and percent leaf litter cover, and mulch cover was correlated with percent bare ground. Thus, we chose to include garden size, VCI woody, VCI herb, percent mulch cover, and percent grass cover in subsequent analysis. At the landscape scale, urban, natural, open cover, and  $H'$  were correlated at most spatial scales. We chose to include urban cover as our variable of interest because this variable most often had the highest average Pearson correlation coefficients with the other three variables. Agriculture cover was not correlated with other landscape variables, but we did not include this variable as there were few gardens with >5% agriculture cover at any spatial scale (Table S4). Third, to ensure that we still did not have collinearity among the selected variables (ecoregion, garden size, VCI woody, VCI herb, mulch cover, grass cover, and percent urban) we checked the variable inflation factor (VIF) with the 'vif' function in the *car* package version 3.0–2 (Fox and Weisberg 2011). All VIF scores were below 2.03.

To examine which local and landscape factors drive abundance and richness of all birds encountered, we used generalized linear models (GLMs) with the *glm* function in R (R Development Core Team 2018). We included total bird abundance and total bird species richness as response variables. For each dependent variable, we used a negative binomial distribution as this provided the best fit (e.g., relatively equal residual deviance and df values and non-significant asymptotic chi-square tests for goodness of fit). To select which spatial extent

**Table 1** Bird traits, trait values, numbers of species and percentages of bird individuals with each trait, and sources of trait information for birds observed within urban gardens in the California central coast

Trait	Trait values	No. of species	Percent of individuals	Source(s)	Notes
Feeding guild	Insectivore	24	25.23%	Ehrlich et al. (1988); Cornell Lab of Ornithology (2018)	We used breeding season diet info. to mirror survey period and used broadest diet info provided.
	Granivore	13	42.20%		
	Omnivore	7	23.39%		
	Nectarivore	2	9.16%		
Foraging strata	Ground forager	21	66.87%	Cornell Lab of Ornithology (2018)	NA
	Tree/ shrub forager	11	22.00%		
	Tree forager	7	9.16%		
	Aerial forager	5	1.84%		
	Ground/ shrub forager	2	0.12%		
Foraging strategy	Ground glean	21	68.38%	Ehrlich et al. (1988); Cornell Lab of Ornithology (2018)	Where sources differed, we used terminology of Ehrlich et al. (1988)
	Foliage glean	15	17.13%		
	Aerial glean	5	1.8%		
	Hawking	2	3.27%		
	Hover and glean	2	9.16%		
	Bark glean	1	0.20%		
Nest location	Trees	16	47.36%	Ehrlich et al. (1988); Cornell Lab of Ornithology (2018)	Where sources differed, we used more recent Cornell Lab of Ornithology (2018) data
	Cavities	9	19.26%		
	Shrubs	9	22.29%		
	Ground	7	5.93%		
	Buildings	3	4.17%		
	Banks	1	0.65%		
	Cliffs	1	0.32%		
Nest Height	Continuous from 0 to 11 m	NA	NA	Ehrlich et al. (1988)	Where range was provided, we used the midpoint of range
Bird mass (g)	Continuous from 3 to 450 g	NA	NA	Sibley (2014)	NA
Migratory status	Resident	32	96.15%	Sibley (2014)	NA
	Migrant	14	3.84%		
Preferred habitat type	Open woodland	15	27.93%	Cornell Lab of Ornithology (2018)	NA
	Forest	9	5.44%		
	Scrub	8	16.52%		
	Urban	7	46.01%		
	Grassland	3	7.36%		
	Marsh	1	2.33%		
	Lakes and ponds	2	3.68%		
	Riparian	1	0.65%		

to use for the percent urban cover, we ran the global model ( $y \sim \text{ecoregion} + \text{garden size} + \text{VCI woody} + \text{VCI herb} + \text{mulch cover} + \text{grass cover} + \text{percent urban}$ ) with urban cover for each of the 13 spatial scales for each dependent variable and compared the AIC scores for each model (Table S5). For bird species richness, urban cover within 700 m provided the best fit, and for bird abundance, 900 m provided the best fit. Yet, AIC scores did not vary more than 0.81 across all spatial scales for any dependent variable, thus we chose to use 700 m as the landscape scale for both analyses. Finally, we compared model fit while including garden size and natural

log-transformed values of garden size. Transformed values improved the model fit according to AIC scores for all dependent variables, and thus we used LN garden size in final models. For GLMs, we tested all combinations of the 7 selected explanatory variables with the ‘glmulti’ package (Calcagno and de Mazancourt 2010). We selected the top model based on the AICc values. If other models were within 2 AICc points of the best model, we averaged all models within 2 AICc points with the ‘MuMIn’ package (Barton 2012) and report conditional averages for significant model factors. We graphed all significant local and landscape predictors of dependent

variables with the ‘visreg’ package in R; where averaged models are reported, we extracted graphs from top models including the same variables included in the final averaged model (Breheny and Burchett 2013).

To explore the importance of local and landscape variables for predicting patterns of bird species composition, we used a Permutation Analysis of Variance (PERMANOVA) that allowed us to test the significance of specific predictor variables on the species dissimilarity matrix. We ran the PERMANOVA with the *adonis2* function in ‘vegan’. We used Bray-Curtis similarity and included all local and landscape variables used in the GLM analysis.

To examine relationships between bird traits and local and landscape features of gardens, we used a combined RLQ and fourth-corner analysis with the ‘ade4’ package in R (Dray and Dufour 2007). The RLQ method allowed us to examine a covariance matrix between bird traits and local and landscape factors as mediated by bird species abundances (Dolédec et al. 1996; Dray et al. 2003) and the fourth-corner method allowed us to measure and test multiple associations between bird traits and local and landscape variables one at a time (Dray and Legendre 2008; Dray et al. 2014). We created three matrices: R (local and landscape factors; the same included in GLM analysis), Q (bird traits), and L matrix (bird abundance). Then, we performed a correspondence analysis (CA) to the L matrix and principal component analysis (PCA) to the R and Q matrix. Then we used two models to evaluate if local and landscape features influence the distribution of bird traits (model 2; Dray et al. 2014), and if traits influence the composition of bird species found in gardens with certain local and landscape features (model 4; Dray et al. 2014). Combined examination of models 2 and 4 allowed us to evaluate whether relationships between bird traits and local and landscape factors were significant. We created an RLQ biplot to assess relationships between species traits and local and landscape factors, and then determined the significance of each trait-factor relationship using the fourth corner analysis of the R, L, and Q matrices. We transformed bird abundance with a Hollinger transformation (Legendre and Gallagher 2001) and included those local and landscape factors included in the GLM analysis. Monte-Carlo permutations (9999) tested for correlations between quantitative variables, producing correlation coefficients and individual *p*-values; we used the ‘D2’ correlation coefficient to test for associations between quantitative and categorical variables separately (Dray et al. 2014).

## Results

### Bird abundance and species richness

We recorded a total of 2445 individuals across 46 bird species in the urban gardens (Fig. S1). The six most common birds

observed represented nearly 55% of all individuals recorded and included the House Finch (*Haemorrhous mexicanus*) (21.84%), House Sparrow (*Passer domesticus*) (11.82%), Anna’s Hummingbird (*Calypte anna*) (8.75%), Bushtit (*Psaltiriparus minimus*) (6.34%), and California Towhee (*Melospiza crissalis*) (5.97%). Nearly 30% of all bird species were rare and were recorded only once (10 species) or twice (3 species). Species recorded twice were the Lincoln’s Sparrow (*Melospiza lincolni*), Purple Finch (*Haemorrhous purpureus*), and Steller’s Jay (*Cyanocitta stelleri*) and species recorded only once were the Band-tailed Pigeon (*Patagioenas fasciata*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Common Yellowthroat (*Geothlypis trichas*), Lark Sparrow (*Chondestes grammacus*), Pine Siskin (*Spinus pinus*), Tree Swallow (*Tachycineta bicolor*), Western Kingbird (*Tyrannus verticalis*), Western Tanager (*Piranga ludoviciana*), Wilson’s Warbler (*Cardelina pusila*), and Yellow Warbler (*Setophaga petechia*) (Fig. S1).

Bird abundance responded to only local features of gardens, as well as garden ecoregion. The model that best predicted increases in bird abundance was a model averaged across the top four models that included garden size, ecoregion, grass cover, and mulch cover (Table 2, Table S6). Larger gardens with more grass cover supported more bird individuals (Fig. 2ab, Table 2) while gardens in the Lower Santa Clara Valley ecoregion supported more birds than those in the Monterey Bay Plains ecoregion (Fig. 2c, Table 2). Mulch cover, although included in the averaged top models, did not significantly predict changes in bird abundance. The model that best predicted bird species richness was the top model and included only garden size as a predictor variable (Table S6). Bird species richness was higher in larger gardens (Fig. 2d, Table 2). Because ecoregion was a significant predictor of bird abundance, we ran univariate analysis of variance to examine whether any local or landscape factors varied with ecoregion. For most factors (size, grass cover, mulch cover, VCI herb, and urban cover within 700 m) there were no differences between ecoregions ( $P > 0.5$ , Table S7) but VCI woody was significantly higher in the Monterey Bay Plains ecoregion than in the Lower Santa Clara Valley ecoregion ( $F_{1,17} = 5.261$ ,  $P = 0.035$ , Table S7).

### Bird composition and traits

The gardens supported birds with a diverse array of body sizes, migratory patterns, mass, habitat association, and feeding, foraging, and nesting strategies (Table 1).

The PERMANOVA revealed shifts in bird species composition with increases in urban cover within 700 m, but no other factors influenced bird species composition (Fig. 3, Table 3).

The fourth-corner correlation matrix revealed significant correlations between increases in urban cover within 700 m and nesting location (fewer ground nesters),

**Table 2** Model output from GLM models examining local and landscape correlates of bird abundance and bird species richness, and number of insect-feeding bird functional groups

Dependent variable	Best or Average model	Factor	Relative importance	No. of models included	Estimate	SE	Z or t <sup>a</sup>	P
No. of birds	Average	LN garden size	0.67	2	0.381	0.177	2.003	0.045
		Ecoregion (MB Plains)	0.37	3	−0.749	0.276	2.504	0.012
		Grass 1 m	0.37	3	0.112	0.044	2.375	0.018
		Mulch 1 m	0.1	2	0.011	0.008	1.376	0.169
No. of bird species	Best	LN garden size	NA	NA	0.228	0.078	2.945	0.009

<sup>a</sup> Z is included for no. of birds (for an average GLM model) and t is included for no. of bird species (with one best GLM model)

nesting height (lower), and habitat preference (i.e., fewer forest associated birds and more urban associated birds) (Fig. 3a, Table S8). The combined RLQ and fourth-corner analysis revealed that overall, local and landscape features of gardens did not influence the distribution of bird species (model 2,  $P=0.416$ ) and that bird traits did not influence the composition of species found in sites with certain local and landscape features (model 4,  $P=0.169$ ) (Table S9). But individual factors still related to changes in certain bird traits. The first trait axis (AxcQ1) was driven by differences in urban cover where gardens with less urban cover had more insectivores, more ground nesters, lower nesting heights, more forest-associated birds, and fewer urban-associated birds (Fig. 3a, b). The second trait axis (AxcQ2) was driven by

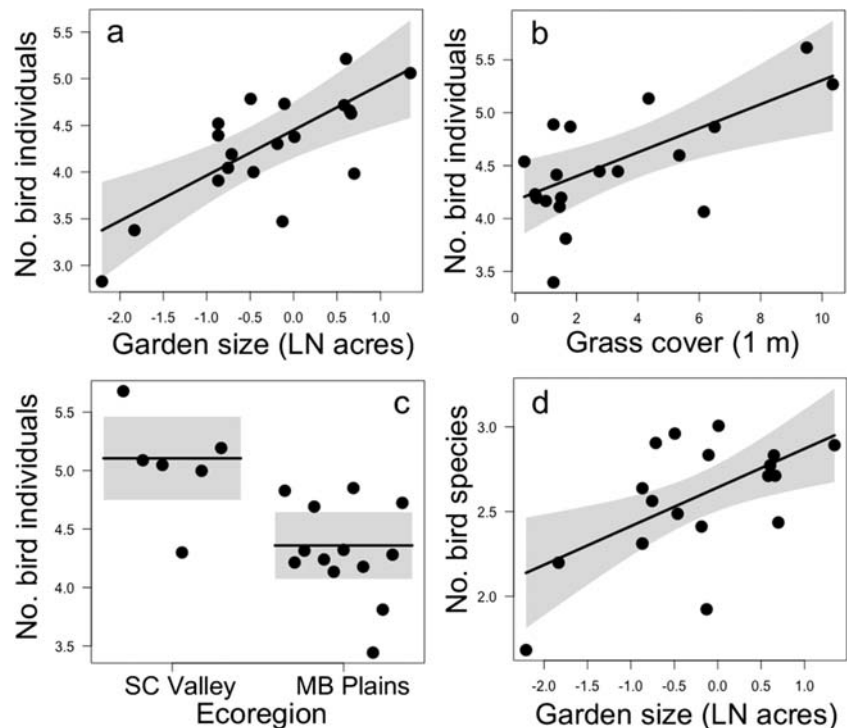
differences in ecoregion and grass cover where gardens in the Lower Santa Clara Valley and with less grass cover had fewer cliff-nesting birds and fewer marsh-associated birds (Fig. 3a, b).

## Discussion

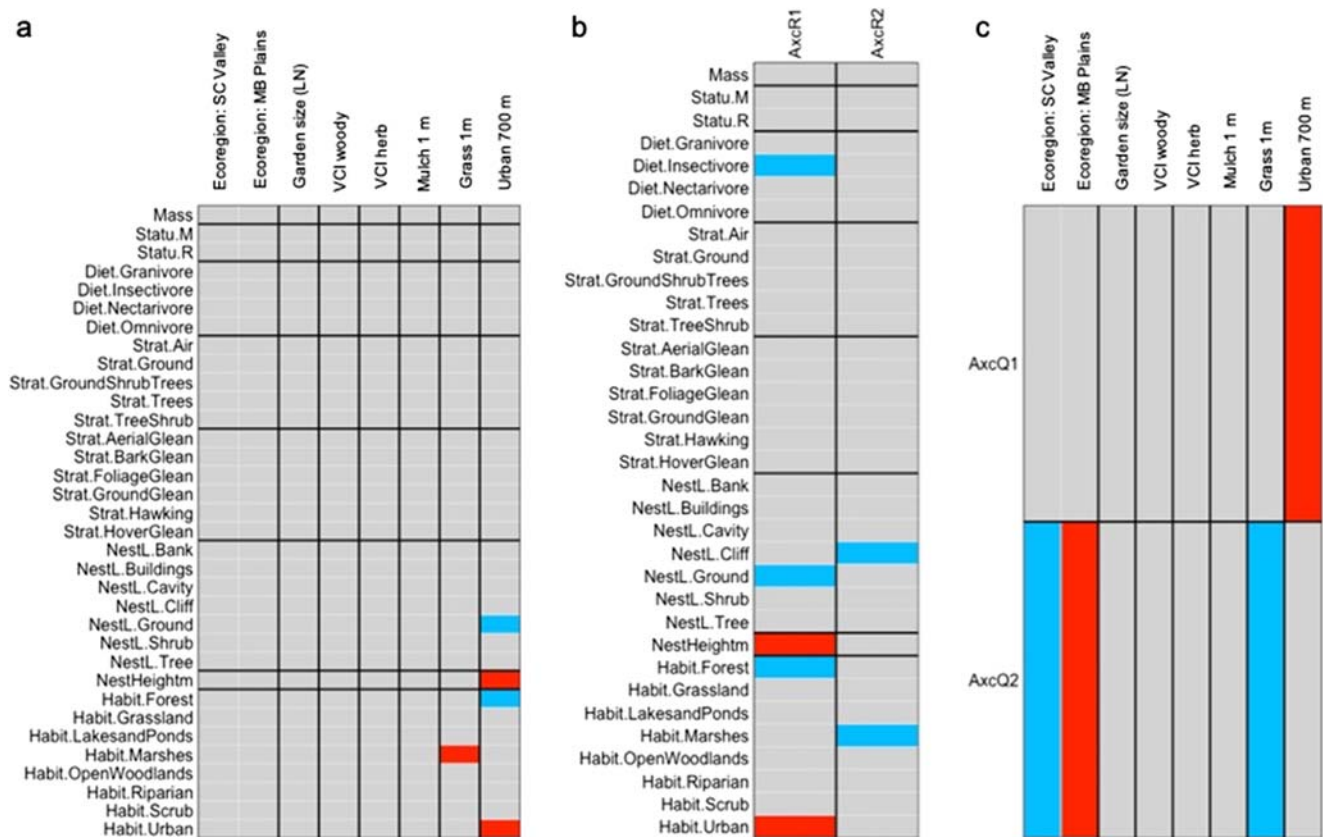
### Bird abundance and species richness

Of all local and landscape features examined, we found that grass cover, garden size, and ecoregion influenced bird abundance and garden size influenced bird species richness. Garden size may be important for a few reasons. First, larger urban green spaces have been found to promote bird

**Fig. 2** Local and landscape drivers of bird abundance (a–c) and bird species richness (d) in urban community gardens in the central coast of California. Graphs show results of GLM models comparing local and landscape drivers of bird abundance and richness. All relationships are significant ( $P < 0.05$ ) and grey bands show 95% confidence bands







**Fig. 3** Results of a fourth-corner test and combined fourth-corner and RLQ analyses to test for associations between local and landscape features of urban community gardens and bird traits. Colored squares show significant associations at the  $P < 0.05$  level (red = positive; blue = negative); gray squares represent non-significant associations. Black lines separate different variables; white lines separate different modalities for categorical variables. Panel **a** shows a correlation table of the bivariate associations between each trait with each factor and bird trait, panel **b** shows

the correlation table between the first two RLQ axes for local and landscape features (AxR1/AxR2) and bird traits, and panel **c** shows the correlation table between the first two RLQ axes for traits (AxQ1 and AxQ2) and local and landscape features of gardens. Trait variables are as follows: Statu = migratory status with M as migratory and R as resident; Strat (upper rows) = foraging strata; Strat (lower rows) = foraging strategy; NestL = nest location; and Habit = associated habitat

abundance and species richness due to higher general resource availability and higher abundance of trees and shrubs that come with larger spaces (Jokimäki 1999; Crooks et al. 2004; Strohbach et al. 2013; Schütz and Schulze 2015). Others have found that larger urban habitat fragments tend to support

**Table 3** Results of PERMANOVA examining the influence of local and landscape features of urban community gardens on bird species composition

Factor	df	R <sup>2</sup>	F	P
Ecoregion	1	0.048	0.828	0.642
LN garden size	1	0.047	0.813	0.640
VCI herb	1	0.040	0.682	0.775
VCI woody	1	0.044	0.756	0.716
Mulch 1 m	1	0.035	0.600	0.843
Grass 1 m	1	0.034	0.577	0.863
Urban 700 m	1	0.112	1.914	0.045

higher bird abundance (Crooks et al. 2004), a higher probability of occurrence for more species (Chamberlain et al. 2004), and higher bird species richness (Jokimäki 1999; Dale 2018). Most of the grass observed in our study was dried grass in between plots or grass growing in weedy garden plots, rather than highly manicured lawns; so grass cover could be considered an indicator of “messy” gardens with less discrete bounds between plots. These “messy” gardens may have higher plant species richness, higher abundance of certain arthropod prey for insect-feeding birds, and higher structural complexity that could provide more diverse habitat, resources, and protection for garden birds (Evans et al. 2009). Alternatively, grass cover could have affected detectability of the birds. At least one study from suburban areas demonstrated that weed growth and lawn cover both increased habitat complexity and provided prey insects for birds (DeGraaf and Wentworth 1986). At the landscape scale, ecoregion had a significant positive impact on bird abundance in the Lower Santa Clara Valley ecoregion. Among the local and landscape



factors included in our analysis, only vegetation complexity of woody plants differed by ecoregion and was lower in the Lower Santa Clara Valley. In other urban studies, increases in tree abundance and canopy cover promoted bird abundance and richness by providing additional food and nesting resources, especially for opportunistic and cavity-nesting birds (Beissinger and Osborne 1982; Mörtberg 2001; Sandström et al. 2006; Ikin et al. 2012; Threlfall et al. 2016). Thus, ecoregion changes could be in part due to differences in woody vegetation. Moreover, although urban cover within 700 m of study sites did not differ between the two ecoregions, the Lower Santa Clara Valley area is much more urbanized as a whole (Fig. 1) and the ecoregions differ in various ways not specifically measured in this study (e.g., rainfall, temperature, fog, remnant natural vegetation). But temperature, precipitation and vegetation structure are all frequently used for modeling species distributions of birds at both continental and regional scales (Stralberg et al. 2009). Therefore, temperature and rainfall differences by ecoregion may contribute to differences in bird abundance patterns.

### Bird composition, traits, and functional richness

Our landscape factor—urban cover—influenced both species and trait composition of birds in the gardens while grass cover and ecoregion together affected trait composition. Urban cover around gardens shaped bird species composition by lowering the abundance of insectivores, ground-nesters, and forest-associated birds and by bolstering the abundance of urban-associated birds and birds with higher nesting heights. Generally, our results are consistent with findings that ground-nesting birds become rare (DeGraaf and Wentworth 1986; Kark et al. 2007; Ikin et al. 2012; Dale 2018), and birds adapted to urban environments tend to thrive (Sandström et al. 2006; Kark et al. 2007) as vegetative complexity is replaced by concrete structures in urban areas. The significance of grass cover and the negative impact of higher urban cover on ground-nesting birds observed in our study has been previously documented and the stated mechanism was higher predation of ground-nesting birds by generalist predators in sites with less vegetative cover (Jokimäki and Huhta 2000). Given that nesting height has been found to decrease with higher levels of urbanization (Reale and Blair 2005), higher nesting heights for the species recorded within the gardens of our study is either indicative of fewer ground nesters (removing the lowest heights from species averages) or could be indicative of greater nesting habitat quality in the gardens than in the surrounding urban landscape. Consistent with what others have found in studies of urban birds, there were fewer insectivores in more urban areas (Andersson and Colding 2014; Evans et al. 2018). This could be attributed to lower insect biomass found in urban green spaces with shorter grass (Ambardar et al. 2018) and to management decisions at the

garden scale that influence insect prey availability such as pesticide application, composting, and personal preference for less manicured gardens with greater plant diversity (Jaganmohan et al. 2013). Grass cover and gardens in the Monterey Bay Plains were associated with more cliff-nesting birds and more marsh-associated birds whose abundance could be driven by adaptation to built features in the urban landscape. For instance, cliff-nesting birds may nest in tall buildings that replicate cliff environments and marsh-associated birds may use drainage impoundments and flood lines in urban areas in lieu of as naturally-occurring marshes (Symes et al. 2017). As the Monterey Bay plains is located along the coast, higher presence of more embankments and wetlands may have supported our marsh-associated species (Red-winged Blackbird) and our cliff-dwelling species (Cliff Swallow), with spillover into the garden habitats. In sum, these results about changes in bird traits generally underscore the importance of maintaining habitat fragments and reducing urban sprawl to support bird communities in urban areas (DeGraaf and Wentworth 1986; Crooks et al. 2004; Kark et al. 2007).

### Management implications

Urban agroecosystems such as community gardens present a unique opportunity for people in cities to support biodiversity (Savard et al. 2000). In general, urban green spaces can act as habitat refuges by providing nesting and food resources for urban birds (Haq 2011) and connecting other city green spaces with larger habitat areas such as expansive parks or adjacent natural landscapes (Rudd et al. 2002). With these refuges in place, urban birds can navigate through sprawling cities where resources are limited for non-generalist species (Crooks et al. 2004). Nonetheless, birds with certain traits (e.g., insectivorous diets, birds that prefer forest habitats, and ground foragers) are consistently threatened by urban sprawl and developed landcover (Sandström et al. 2006; Kark et al. 2007; Ikin et al. 2012; Evans et al. 2018). Our study provides some evidence that more ‘messy’ gardens (with higher grass cover) may support higher bird abundance. Likewise, others have found that including more native plants in urban backyard gardens can promote insectivorous birds by increasing prey abundance (Narango et al. 2017). We also found some evidence that gardens in ecoregions with less developed areas contained gardens with more woody plants and supported more birds. Based on our results, we would recommend planting larger gardens with more scattered grass cover in order to increase microhabitat heterogeneity and support bird abundance and richness, especially for insectivores and ground-nesting birds in urban areas. Because of the detrimental effects of urban cover increases, developed areas devoid of pre-existing habitat should be prioritized to achieve maximal benefits to biodiversity.

**Acknowledgements** We thank H. Cohen, M. Egerer, M. Otoshi, and R. Quistberg for assistance with vegetation and landscape data collection. A. Lucatero, M. Egerer, and anonymous reviewers provided helpful comments on the manuscript. We thank all community gardens for allowing us to conduct research: Aptos Community Garden, Beach Flats Community Garden, Berryessa Community Garden, Center for Agroecology and Sustainable Food Systems, Chinatown Community Garden, Coyote Creek Community Garden, El Jardín at Emma Prusch Park, The Forge at Santa Clara University, Giving Garden at Faith Lutheran Church, Homeless Garden Project, La Colina Community Garden, Laguna Seca Community Garden, The Live Oak Grange, Mearth at Carmel Valley Middle School, Mi Jardín Verde at All Saints' Episcopal Church, Our Green Thumb Garden at Monterey Institute for International Studies, Salinas Community Garden at St. George's Episcopal Church, Trescony Community Garden. Funding for this project was provided by the University of California, Santa Cruz New Faculty Research Grant to SMP, Ruth & Alfred Heller Chair in Agroecology, UC LEADS Program, UCSC Stem Diversity Programs, and USDA-NIFA grant #2016-67019-25185 to SMP, H Liere, B Lin, and S Jha.

## References

- Ambardar M, Dunn PO, Whittingham LA (2018) Reproductive and foraging success of the eastern bluebird (*Sialia sialis*) in relation to vegetation height. *Wilson J Ornithol* 130:362–370
- Andersson E, Colding J (2014) Understanding how built urban form influences biodiversity. *Urban For Urban Green* 13:221–226
- Aronson MF, La Sorte FA, Nilon CH et al (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc Roy Soc B Biol Sci* 281:20133330
- Bakermans MH, Rodewald AD (2006) Scale-dependent habitat use of Acadian Flycatcher (*Empidonax virescens*) in Central Ohio. *Auk* 123:368–382
- Barth B, FitzGibbon S, Wilson R (2015) New urban developments that retain more remnant trees have greater bird diversity. *Landscape Urban Plan* 136:122–129
- Barton K (2012) MuMin: multi-model inference. R package version 1.5.2. Available from <http://CRAN.R-project.org/package=MuMin>
- Beissinger SR, Osborne DR (1982) Effects of urbanization on avian community organization. *Condor* 84:75–83
- Bennett A, Gratton C (2012) Local and landscape scale variables impact parasitoid assemblages across an urbanization gradient. *Landscape Urban Plan* 104:26–33
- Breheny P, Burchett W (2013) Visualization of regression models using visreg. *R J* 9:56–71
- Calcagno V, de Mazancourt C (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. *J Stat Softw* 34:1–29
- Chamberlain DE, Cannon AR, Toms MP (2004) Associations of garden birds with gradients in garden habitat and local habitat. *Ecography* 27:589–600
- Coogan SC, Raubenheimer D, Zantis SP, Machovsky-Capuska GE (2018) Multidimensional nutritional ecology and urban birds. *Ecosphere* 9:e02177
- Cornell Lab of Ornithology (2018) <http://www.birds.cornell.edu/netcommunity/page.aspx?pid=1636>. Accessed 18 July 2018
- Croci S, Butet A, Clergeau P (2008) Does urbanization filter birds on the basis of their biological traits. *Condor* 110:223–240
- Crooks KR, Suarez AV, Bolger DT (2004) Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biol Conserv* 115:451–462
- Dale S (2018) Urban bird community composition influenced by size of urban green spaces, presence of native forest, and urbanization. *Urban Ecosyst* 21:1–14
- Daniels GD, Kirkpatrick JB (2006) Does variation in garden characteristics influence the conservation of birds in suburbia? *Biol Conserv* 133:326–335
- Day TD (1995) Bird species composition and abundance in relation to native plants in urban gardens, Hamilton, New Zealand. *Notornis* 42:172–186
- DeGraaf RM, Wentworth JM (1986) Avian guild structure and habitat associations in suburban bird communities. *Urban Ecol* 9:399–412
- Devictor V, Julliard R, Couvet D, Lee A, Jiguet F (2007) Functional homogenization effect of urbanization on bird communities. *Conserv Biol* 21:741–751
- Dolédéc S, Chessel D, Ter Braak CJF, Champely S (1996) Matching species traits to environmental variables: a new three-table ordination method. *Environ Ecol Stat* 3:143–166
- Dray S, Dufour A-B (2007) The ade4 package: implementing the duality diagram for ecologists. *J Stat Softw* 22:1–20
- Dray S, Legendre P (2008) Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology* 89:3400–3412
- Dray S, Chessel D, Thioulouse J (2003) Co-inertia analysis and the linking of ecological data tables. *Ecology* 84:3078–3089
- Dray S, Choler P, Dolédéc S, Peres-Neto PR, Thuiller W, Pavoine S, ter Braak CJ (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95:14–21
- Ehrlich P, Dobkin D, Wheye D (1988) *The Birder's handbook*. Simon and Schuster, New York
- Enoksson B, Angelstam P, Larsson K (1995) Deciduous forest and resident birds – the problem of fragmentation within a coniferous forest landscape. *Landsc Ecol* 10:267–275
- Evans KL, Newson SE, Gaston KJ (2009) Habitat influences on urban avian assemblages. *Ibis* 151:19–39
- Evans BS, Reitsma R, Hurlbert AH, Marra PP (2018) Environmental filtering of avian communities along a rural-to-urban gradient in greater Washington, DC, USA. *Ecosphere* 9:e02402
- Fox J, Weisberg S (2011) *An R companion to applied regression*. Second. Sage, Thousand Oaks
- Fujita M, Koike F (2009) Landscape effects on ecosystems: birds as active vectors of nutrient transport to fragmented urban forests versus forest-dominated landscapes. *Ecosystems* 12:391–400
- Goddard MA, Dougill AJ, Benton TG (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends Ecol Evol* 25:90–98
- Gómez-Baggethun E, Barton DN (2013) Classifying and valuing ecosystem services for urban planning. *Ecol Econ* 86:235–245
- Griffith GE, Omernik JM, Smith DW, Cook TD, Tallyn E, Moseley K, Johnson CB (2016) *Ecoregions of California*. No. 2016-1021. US Geological Survey
- Han Y, Bai J, Zhang Z, Wu T, Chen P, Sun G, Miao L, Xu Z, Yu L, Zhu C, Zhao D, Ge G, Ruan L (2019) Nest site selection for five common birds and their coexistence in an urban habitat. *Sci Total Environ* 690:748–759
- Haq SMA (2011) Urban green spaces and an integrative approach to sustainable environment. *J Environ Prot* 2:601–608
- Homer C, Dewitz J, Yang L et al (2015) Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogramm Eng Rem S* 81:345–354
- Ikin K, Knight E, Lindenmayer DB, Fischer J, Manning AD (2012) Linking bird species traits to vegetation characteristics in a future

- urban development zone: implications for urban planning. *Urban Ecosyst* 15:961–977
- Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? *Glob Ecol Biogeogr* 24:52–63
- Jaganmohan M, Vailshery L, Nagendra H (2013) Patterns of insect abundance and distribution in urban domestic gardens in Bangalore, India. *Diversity* 5:767–778
- Jokimäki J (1999) Occurrence of breeding bird species in urban parks: effects of park structure and broad-scale variables. *Urban Ecosyst* 3: 21–34
- Jokimäki J, Huhta E (2000) Artificial nest predation and abundance of birds along an urban gradient. *Condor* 102:838–847
- Kark S, Iwaniuk A, Schalintzek A, Banker E (2007) Living in the city: can anyone become an ‘urban exploiter’? *J Biogeogr* 34:638–651
- Kellert SR (1985) Birdwatching in American society. *Leisure Sci* 7:343–360
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- MacGregor-Fors I, Schondube JE (2011) Gray vs. green urbanization: relative importance of urban features for urban bird communities. *Basic Appl Ecol* 12:372–381
- Marzluff JM (2001) Worldwide urbanization and its effects on birds. In: *Avian ecology and conservation in an urbanizing world*. Springer, pp 19–47
- McGarigal K, Cushman S, Neel M, Ene E (2002) FRAGSTATS v3: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- Mooney K, Gruner D, Barber N, Van Bael S, Philpott S, Greenberg R (2010) Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *Proc Natl Acad Sci U S A* 107:7335–7340
- Mörtberg UM (2001) Resident bird species in urban forest remnants: landscape and habitat perspectives. *Landsc Ecol* 16:193–203
- Narango DL, Tallamy DW, Marra PP (2017) Native plants improve breeding and foraging habitat for an insectivorous bird. *Biol Conserv* 213:42–50
- Nielsen AB, Van Den Bosch M, Maruthaveeran S, Van Den Bosch CK (2014) Species richness in urban parks and its drivers: a review of empirical evidence. *Urban Ecosyst* 17:305–327
- Oksanen J et al (2018) Vegan: community ecology package. R package version 2.3–4 (<http://CRAN.R-project.org/package=vegan>). Accessed 8 July 2018
- Oliveira Hagen E, Hagen O, Ibáñez-Álamo JD, Petchey OL, Evans KL (2017) Impacts of urban areas and their characteristics on avian functional diversity. *Front Ecol Evol* 5:84
- Ortega-Álvarez R, MacGregor-Fors I (2009) Living in the big city: effects of urban land-use on bird community structure, diversity, and composition. *Landscape Urban Plan* 90:189–195
- Owens IPF, Bennett PM (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc Natl Acad Sci U S A* 97:12144–12148
- Paker Y, Yom-Tov Y, Alon-Mozes T, Bamea A (2014) The effect of plant richness and urban garden structure on bird species richness, diversity and community structure. *Landscape Urban Plan* 122:186–195
- Philpott SM, Bichier P (2017) Local and landscape drivers of predation services in urban gardens. *Ecol Appl* 27:966–976
- Philpott SM, Arendt WJ, Armbrecht I, Bichier P, Diestch TV, Gordon C, Greenberg R, Perfecto I, Reynoso-Santos R, Soto-Pinto L, Tejeda-Cruz C, Williams-Linera G, Valenzuela J, Zolotoff JM (2008) Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conserv Biol* 22:1093–1105
- Philpott SM, Soong O, Lowenstein JH, Pulido AL, Lopez DT, Flynn DFB, DeClerck F (2009) Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. *Ecol Appl* 19:1858–1867
- R Development Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051–07–0, URL: <http://www.R-project.org/>
- Reale JA, Blair RB (2005) Nesting success and life-history attributes of bird communities along an urbanization gradient. *Urban Habitats* 3: 1–24
- Reis E, López-Iborra GM, Pinheiro RT (2012) Changes in bird species richness through different levels of urbanization: implications for biodiversity conservation and garden design in Central Brazil. *Landscape Urban Plan* 107:31–42
- Reynolds SJ, Galbraith JA, Smith JA, Jones DN (2017) Garden bird feeding: insights and prospects from a north-south comparison of this global urban phenomenon. *Front Ecol Evol* 5:Article 24
- Rodewald AD, Shustack DP (2008) Urban flight: understanding individual and population-level responses of Nearctic–Neotropical migratory birds to urbanization. *J Anim Ecol* 77:83–91
- Rudd H, Vala J, Schaefer V (2002) Importance of backyard habitat in a comprehensive biodiversity conservation strategy: a connectivity analysis of urban green spaces. *Restor Ecol* 10:368–375
- Sandström UG, Angelstam P, Mikusiński G (2006) Ecological diversity of birds in relation to the structure of urban green space. *Landscape Urban Plan* 77:39–53
- Savard JPL, Clergeau P, Mennechez G (2000) Biodiversity concepts and urban ecosystems. *Landscape Urban Plan* 48:131–142
- Schütz C, Schulze C (2015) Functional diversity of urban bird communities: effects of landscape composition, green space area and vegetation cover. *Ecol Evol* 5:5230–5239
- Sekerçioğlu CH (2006) Increasing awareness of avian ecological function. *Trends Ecol Evol* 21:464–471
- Sibley D (2014) The Sibley guide to birds. Alfred A Knopf, New York
- Silva CP, Garcia CE, Estay SA, Barbosa O (2015) Bird richness and abundance in response to urban form in a Latin American city: Valdivia, Chile as a case study. *PLoS One* 10:e0138120
- Stralberg D, Jongsomjit D, Howell C, Snyder M, Alexander J, Wiens J, Root T (2009) Re-shuffling of species with climate disruption: a no-analog future for California birds? *PLoS One* 4:e6825
- Strohbach MW, Lerman SB, Warren PS (2013) Are small greening areas enhancing bird diversity? Insights from community-driven greening projects in Boston. *Landscape Urban Plan* 114:69–79
- Symes CT, Roller K, Howes C, Lockwood G, van Rensburg BJ (2017) Grassland to urban forest in 150 years: avifaunal response in an African metropolis. In: Murgui E, Hedblom M (eds) *Ecology and conservation of birds in urban environments*. Springer, Cham, pp 309–341
- Threlfall C, Williams N, Hahs A, Livesley S (2016) Approaches to urban vegetation management and the impacts on urban bird and bat assemblages. *Landscape Urban Plan* 153:28–39
- Van Bael SA, Philpott S, Greenberg R, Bichier P, Barber N, Mooney K, Gruner D (2008) Birds as predators in tropical agroforestry systems. *Ecology* 89:928–934
- Whelan CJ, Wenny DG, Marquis RJ (2008) Ecosystem services provided by birds. *Ann N Y Acad Sci* 1134:25–60