Are invasive House Sparrows a nuisance for native avifauna when scarce?

Michelle García-Arroyo[1], Diego Santiago-Alarcón[2], Javier Quesada[3] & Ian MacGregor-Fors[1]

1 Red de Ambiente y Sustentabilidad, Instituto de Ecología, A. C., Carretera antigua a Coatepec 351, El Haya, 91073 Xalapa, Veracruz, Mexico

2 Red de Ecología y Conservación de Vertebrados, Instituto de
Ecología, A. C., Carretera antigua a Coatepec 351, El Haya,
91073 Xalapa, Veracruz, Mexico

3 Department of Vertebrates, Natural Sciences Museum of Barcelona, Parc de la Ciutadella s/n, 08003 Barcelona, Catalonia, Spain

Correspondenc author: Ian MacGregor-Fors

ian.macgregor@inecol.mx; macgregor.ian@gmail.com

Abstract

Biological invasions are the second most important cause of species extinction. Aided by processes such as transportation and urbanization, exotic species can establish and spread to new locations, causing changes in the function and structure of ecosystems. The House Sparrow is a widespread and highly abundant landbird associated to human presence. Previous studies performed in urban landscapes have suggested that this species could be acting, in synergy with urbanization, as a potential threat to native urban avian assemblages. In this study we assessed the relationship between House Sparrow density and native bird species richness in a region where the sparrows are scarce and sparsely distributed. We surveyed bird assemblages in and around four small-sized human settlements, considering three conditions in relation to House Sparrow presence: urban invaded, urban non-invaded, and non-urban non-invaded. To assess the potential detrimental role of House Sparrows on native bird species richness, we measured, additionally to sparrow densities, 20 predictor variables that describe vegetation structure and complexity, as well as urban infrastructure and human activities across four seasons of 1 year. Our results show that maximum shrub height was positively related to bird species richness, built cover was negatively associated with it, and House Sparrow invaded sites were related to a significant decrease of bird species richness, with increasing richness loss when more sparrows were present. Thus, we here provide evidence that urban areas can act in synergy with the presence of House Sparrows (even in low densities) in the urban-related species richness decline pattern.

Keywords:

Biological invasions, Bird density, Passer domesticus, Species composition, Species richness, Urban ecology

Introduction

Biological invasions are considered one of the main drivers of species extinctions, altering species richness and composition of native communities at different spatiotemporal scales (Bellard et al. 2016). When the individuals of exotic species establish and colonize new locations, successful biological invasions occur (Blackburn et al. 2011) and may alter local environmental processes and the structure of local native communities (e.g., nutrient cycles, trophic networks, fire and erosion regimes; Pyšek et al. 2012; Ricciardi et al. 2013; Simberloff et al. 2013). Although invasive birds are abundant across the globe (Blackburn et al. 2009), the magnitude and variability of their impact on native assemblages remains poorly understood (Kumschick and Nentwig 2010). It is notable that three avian species have been included in the list of 100 worst invasive alien species (Lowe et al. 2000; but see Kumschick et al. 2016): Common Myna (Acridotheres tristis), Red-vented Bulbul (Pycnonotus cafer; but see Thibault et al.2018), and European Starling (Sturnus vulgaris). These three species alone have been responsible for massive damages to crops and infrastructure, but also for spreading diseases, and displacing native avifauna through predation and competition for nest cavities (Fisher and Wiebe 2005; Harper et al. 2005; Tindall et al. 2007; Grarock et al. 2012).

Cities are key components for avian invasions, not only as hubs for the deliberate trading of pets, but also by promoting the establishment and spread of diverse bird species in highly predictable systems (Vitousek et al. 1997; Sax and Brown 2000; Shochat 2004; Shochat et al.2010). The filtering of regional avifaunas in urban settings generally results in depauperate avian assemblages, especially in heavily urbanized conditions, a niche that has been heavily exploited by generalists, often exotic and/or invasive species (Chace and Walsh 2006; Aronson et al. 2014; La Sorte et al. 2018). Given that many of these generalist urban exploiters are prone to experience population explosions in urban areas, they frequently dominate urban bird assemblages (Sol et al. 2014).

Urban invasive birds have been accounted for economic losses due to damages to buildings and other urban structures (Pimentel et al. 2001, 2005; Booy et al. 2017), as well as the spread of diseases on a global scale (Pedersen et al. 2006). However, there is a lack of agreement on the ecological impacts that invasive birds pose on native species (Linz et al.2007; Strubbe and Matthysen 2007; MacGregor-Fors et al.2010, 2011; Mori et al. 2017; González-Oreja et al. 2018; Luna et al. 2018). One of the most widespread urban-related invasive bird species is the House

Sparrow (*Passer domesticus*), a species considered to be native to Eurasia and North Africa and that has been associated with humans for 10,000 years, since the appearance of agricultural practices (Anderson 2006; Sætre et al. 2012). This sparrow has been either intentionally or unintentionally introduced by humans in Australia, New Zealand, North America, South America, and South Africa (Anderson 2006). Regarding its North American invasion, it was successfully introduced to Northeastern United States in the 1850s and arrived to Mexico around the 1910s, establishing numerous and dense populations that expanded across the country in following decades, reaching Mexico City by 1930 (Wagner 1959). House Sparrow populations resulting from these invasion events have continued their range expansion southward to Central America (Anderson 2006).

House Sparrows are ecologically and physiologically plastic, with an extensive array of nesting habits (Kimball 1997; Nhlane 2000; Peach et al. 2008; Hoi et al. 2011), foraging behaviors, and dietary breadth (Guillory and Deshotels 1981; Kalmus 1984; Flux and Thompson 1986; Anderson 2006). Although its main food sources are seeds, it has an omnivorous diet in urban environments, ranging from nectar, fruits, insects, and even discarded human food leftovers (Stidolph 1974; Gavett and Wakeley 1986; Clergeau 1990; Moulton and Ferris 1991; Leveau 2008; MacGregor-Fors et al. 2020). Behaviorally, the House Sparrow is aggressive with both its conspecifics and heterospecifics, often competing for nesting cavities and food resources (Kalinoski 1975; Gowaty 1984; Radunzel et al. 1997; Anderson 2006). It is also known to be an important source of pathogens (Rappole and Hubálek 2003; e.g., avian pox and malaria, West Nile Virus; Anderson 2006; Delgado-V and French 2012). Albeit the undeniable success of House Sparrows in North America, population declines have been recorded in the past decades along urban-agricultural landscapes of Western Europe (Summers-Smith 2003).

Previous studies have shown negative relationships between the presence and abundance of House Sparrows and other native land birds. For instance, in a Central Western Mexico medium-size city, avian assemblages dominated by House Sparrows had lower bird species richness (MacGregor-Fors et al. 2010). In another study performed in Mexico City, the abundance of some native bird species showed to be negatively related with the presence and abundance of House Sparrows (i.e., Berylline Hummingbird–*Amazilia beryllina*, Black-headed Grosbeak–*Pheucticus melanocephalus*), with lower average abundance per point count ranging from 40% to 300% decreases (Ortega-Álvarez and MacGregor-Fors 2010). Moreover, the abundance of rare native birds was negatively associated with sites used by House Sparrows for roosting and breeding, such as lamp poles in a west-central Mexican city (MacGregor-Fors and Schondube 2011). Yet, results of a recent study performed in urban greenspaces of three Mexican cities suggest that House Sparrows are not related with declines in native species richness (González-Oreja et al. 2018). Based on all of the above, we consider that there is enough correlative evidence to acknowledge that House Sparrows can represent a potential competitor able to displace native species (Schondube et al. 2009).

In this study we assessed the relationship between House Sparrow density and native bird species richness in scenarios where sparrows are scarce and sparsely distributed. It is notable that these conditions, where House Sparrows are not hyper-abundant differ to those of previous studies focused on the potential effects to native avifauna, where sparrow densities are high (MacGregor-Fors et al. 2010; Ortega-Álvarez and MacGregor-Fors 2010). Thus, we surveyed bird assemblages in and around four small-sized human settlements in Central Veracruz (Mexico), where House Sparrows are present in low numbers, considering three different conditions: urban invaded, urban non-invaded, and non-urban non-invaded. Based on contrasting results related to the potential negative relationship between House Sparrows and native bird species richness, we tested the following hypotheses: (1) low densities of House Sparrows are associated with a lower bird species richness and composition, holding the pattern of previous studies evidencing the negative relationship regardless of sparrows' densities, and (2) low densities of House Sparrows do not relate to bird species richness nor its composition, and thus do not represent a nuisance for native avifauna when present in low densities.

Methods

Study area

We conducted this study in four human settlements from Central Veracruz: Xico, Teocelo, San Marcos de León, and Colonia Úrsulo Galván (referred to as Xico, Teocelo, San Marcos, and Úrsulo Galván hereafter; Table 1). The largest settlement in the region is Xico, with an extension of 2 km2 and a population of ~18,650 inhabitants (INEGI 2010), followed by Teocelo (1 km2, ~9950 inhabitants; INEGI 2010), San Marcos (0.7 km2, ~7250 inhabitants; INEGI 2010), and Úrsulo Galván (0.14 km2, ~1700 inhabitants; INEGI 2010). The studied settlements have similar urban infrastructure (mainly composed of one to two story houses, few commercial areas, few buildings with over four stories) and are embedded in a landscape with similar characteristics (hilly topography, presence of multiple water streams, and similar climate; INAFED 2010). It is notable that the study region was originally covered, in general, by tropical montane cloud forest, which has been partially replaced over the last century by shade coffee plantations, cattle ranches, and urban centers (Williams-Linera 2007; García-Franco et al. 2008).

Study design and field surveys

We followed a survey design that allowed us to assess the relationship between the presence and abundance of House Sparrows and native bird species richness, considering two dichotomies: (1) House Sparrow invaded / House Sparrow non-invaded sites and (2) built up environments (referred to as urban hereafter) / non-built sites (*sensu* MacGregor-Fors2010). Given that House Sparrows are absent outside urban areas in the region, we considered three survey conditions: (1) urban House Sparrow invaded (UI), (2) urban House Sparrow non-invaded (UNI), and (3) non-urban House Sparrow noninvaded (NUNI). Due to differing sizes of the studied settlements and the presence and distribution of House Sparrows within them, our design was unbalanced, with a total of 110 survey sites (Table 1, Fig. 1).

MG-A performed 5-min point counts (25 m limited radius) from sunrise to 11:00 h, recording all birds seen or heard at each survey site in four seasons: spring, summer, fall, and winter (i.e., April 2016, July 2016, October 2016, January 2017). MG-A measured the exact distance from point-count locations to each recorded bird individual with a rangefinder (Bushnell Yardage Pro Sport 450). We established point counts at least 150 m apart from each other to be considered as independent sampling units (Ralph et al. 1996; Bibby et al. 2000; Huff et al. 2000).

Predictor variables

We measured 20 predictor variables within the same 25 m radius area in which birds were counted, once every surveyed season, to describe the environmental characteristics of each survey site. To describe vegetation structure and complexity, we recorded: (1) tree richness (morphospecies), (2) tree cover (%), (3) number of trees, (4) maximum tree height (m), (5) maximum diameter at breast height of trees (DBH) (cm), (6) shrub richness (morphospecies),

(7) shrub cover (%), (8) maximum shrub height (m), (9) herbaceous plant richness (morphospecies), (10) herbaceous plant cover (%), and (11) maximum herbaceous plant height (m). To describe urban infrastructure and human activities, we recorded: (1) number of buildings, (2) maximum building height (m), (3) minimum building height (m), (4) number of light and electric poles, (5) number of cables, (6) number of windows, (7) passing cars per minute, and (8) number of pedestrians per minute. Additionally, we quantified built cover (%) in the 25 m radius survey area using satellite images from 2016 on Google Earth Pro (2018).

Data analysis

We computed the statistical expectation of species richness for each condition using rarefaction procedures with EstimateS, which allows statistical comparisons among treatments through the repeated re-sampling of all pooled samples based on their recorded abundances (Gotelli and Colwell 2001; Colwell 2013). For comparisons among conditions we contrasted the 84% confidence intervals of the computed statistical expectations and considered statistical differences with $\alpha = 0.05$ when confidence intervals did not overlap (following MacGregor-Fors and Payton 2013). We used 84% confidence intervals as 95% confidence intervals fail to indicate statistical differences with $\alpha = 0.05$ (MacGregor-Fors and Payton 2013). Given that sampling effort varied among conditions, we used a factor of extrapolation of 2.5 for the smallest sample (i.e., UI) to robustly contrast its species richness calculations with the other two conditions at the same sampling effort (i.e., UNI, NUNI) (Gotelli and Colwell 2001; Colwell 2013).

We performed a multivariate Bray-Curtis cluster analysis (i.e., average linkage) using the package ‘vegan’ in R (Oksanen et al. 2016; R Development Core Team 2018) to describe similarities in bird assemblage composition among the studied conditions. Taking into account the 20 measured predictor variables and to avoid statistical issues related with multi-collinearity, we identified moderate-to-highly correlated variables (i.e., $r > 0.5$, $P < 0.05$), keeping those with highest variance. We used the remaining variables, including House Sparrow abundance per point count, in a generalized additive model (GAM) to explore their relationship with bird species richness. We used a GAM given that, as a variant of generalized linear models, additive models have different error structures and link functions able to provide a better fit for different types of variables, also allowing the use of non-parametric ‘smoothers’ (fitting procedure where the form of the curve is not predetermined but estimated through data; Wang 2014) to describe non-linear relationships (Crawley 2013). If House Sparrow abundances showed a significant relationship with species richness, we conducted a t-test to assess differences in built cover between sites with and without House Sparrow records.

To allow comparisons with results of previous studies in Mexico, we report the number of House Sparrows per point count, as well as estimated distance-corrected House Sparrow densities by season using Distance 6.2 (Thomas et al. 2010). Distance computes densities (ind/ha) based on the detection probability of individuals at increasing distances from the observer, as well as standardizing detection rates along concentric surveyed areas (Buckland et al. 2001).

Results

Over the course of four seasons (i.e., spring, summer, fall, winter) we recorded a total of 89 bird species of 29 families (Table S1 in Online Resource 1), of which 55% were recorded uniquely at the NUNI condition. In particular, we recorded 84 bird species at the NUNI condition, 36 at the UNI condition, and 20 at the UI condition. Nearly 25% of the recorded species are reported in the literature to be associated with wellvegetated areas, all of which we recorded at the NUNI condition, one of them also recorded at the UNI condition (i.e., Black-throated Green Warbler–*Setophaga virens*), and two at the UI condition (i.e., Magnolia Warbler–*Setophaga magnolia*, Rusty Sparrow–*Aimophila rufescens*) (Table S1 in Online Resource 1). Bird species richness at the UI condition was significantly lower when compared to that of the NUNI condition during almost all the year (summer, fall, winter) and compared to the UNI condition during summer (Table 2). Regarding species composition, the cluster analysis revealed that the UI condition shared less species with UNI and NUNI conditions, thus having a different assemblage composition across seasons (β = 0.13; Fig. 2).

Results of the GAM show that bird species richness was significantly related with season (Table 3). After taking into account the smoothing adjustment for the numerical variables (i.e., shrub richness, maximum shrub height, built cover, House Sparrow abundances, passing cars per minute), we identified that the relationship between maximum shrub height and bird species richness was positive (Fig. 3a), the one with built cover was negative (Fig. 3b), and the one with House Sparrow abundances showed three different scenarios (i.e., 0 individuals, 1–5 individuals, 6–12 individuals; Fig. 3c). Due to the complexity of the interpretation of such trichotomy, we calculated the statistical expectation of bird species richness for each scenario, finding a significant decrease in bird species richness as the number of House Sparrows increased (Fig. 3c). It is notable that we did not find differences for built cover values in sites with and without House Sparrow records (t25 = −0.77, p = 0.45; Fig. 4), showing that such decrease in species richness was not given by urbanization intensity.

The number of House Sparrows per point count was of 0.6 individuals during spring, 0.49 in summer, 0.45 in fall, and 0.4 in winter. Regarding distance-corrected densities, we recorded the highest House Sparrow density during winter (12.6 ind/ha 84% CI: 3.5–45.4), followed by spring (5.4 ind/ha 84% CI:2.8–10.4), summer (2.5 ind/ha 84% CI: 1.2–4.8) and fall (2.3 ind/ha 84% CI: 1.0–5.0).

Discussion

The House Sparrow is a widespread and highly abundant landbird associated to humans (Aronson et al. 2014; Sol et al. 2014) that could be acting in synergy with urbanization as a potential threat to native avian assemblages, even when present in low numbers (MacGregor-Fors et al. 2010; Loss et al. 2015). Results of this study showed that vegetation elements are positively associated with bird species richness, meanwhile heavily urbanized areas are negatively related to it. Furthermore, sites with House Sparrows presence had lower bird species richness than non-invaded and non-urban areas. Also, the assemblages of invaded urbanized areas were more similar among themselves compared to those of noninvaded and non-urban areas. Altogether, our findings suggest the existence of different dynamics among bird species within urban areas where invasive sparrows are present, having an effect on both the number and composition of bird species.

Seasonality was related to an increase in bird species richness given by the amount of Neotropical-Nearctic migrants recorded in winter. It is noteworthy that our study area is located within one of the most important Neotropical Nearctic bird migration routes (Ruelas-Inzunza et al. 2005). The positive relationship between maximum height of shrubs and bird species richness agrees with previous studies assessing avian ecology along urban-agricultural landscapes (Ortega-Álvarez and MacGregor-Fors 2009; Faggi and Caula 2017). This variable, as proxy of vegetation at each site, highlights the importance of structural stratification of vegetation for birds both in non-urban and urban areas (Cueto and de Casenave 1999; Napoletano et al. 2017). Built cover was negatively associated with bird species richness, which also agrees with previous studies assessing avian assemblages in cities (MacGregor-Fors and Schondube 2011; Luck et al. 2013; Schneider and Miller 2014; Faggi and Caula 2017). Actually, this relationship was not surprising, as urbanization has been directly linked to a decrease in bird species richness due to the loss of a wide variety of food resources, breeding sites, and additional factors inherent to urbanization (e.g., cat predation, window collision, parasitism; Santiago-Alarcon and Delgado-V 2017), among other causes (Emlen 1974; Chace and Walsh 2006).

Finally, House Sparrow numbers had a gradual negative effect on bird species richness, where sites having no sparrows (NUNI, UNI) showing significantly more bird species compared to sites with sparrows. Specifically, urban invaded areas (UI), with 1–5 House Sparrows had significantly more bird species than sites with 6–12 House Sparrows (Fig. 3). It is important to highlight that significant differences in bird species richness in sites where we recorded 1–5 and 6–12 House Sparrows were not related to built cover, as urbanized sites (invaded and non-invaded) had similar values (Fig. 4). Given that a possible confounding factor of the recorded relationship between House Sparrows and bird species richness could be the potential association with the presence and abundance of other urban-related species (i.e., Great-tailed Grackle– *Quiscalus mexicanus*, Rock Pigeon–*Columba livia*, Tropical Kingbird–*Tyrannus melancholicus*), we assessed potential correlations between the presence and abundance of the most frequently recorded species with House Sparrows data. However, we found no significant or strong correlations between House Sparrow abundance and the abundance of other common urban-associated species ($rS \leq |0.13|$, p-values <0.53; Table S2 in Online Resource 1). Therefore, our conclusion regarding the negative relationship between House Sparrows and native bird species richness holds true.

Altogether, our results add information to the scarce evidence that this invasive sparrow could be acting as a driver of native urban bird assemblages, even when present in low densities. It is important to note that House Sparrow numbers recorded in this study were much lower (i.e., 10–32 times lower in terms of relative abundance and 1.6–3 times lower in terms of density) than those reported in previous studies (i.e., ~20 ind/point count in MacGregor-Fors et al. 2010, 9.5–33.3 ind/ha in MacGregor-Fors et al. 2017; ~7 ind/point count in Ortega-Álvarez and

MacGregor-Fors 2011a). Yet, similar low densities are reported for some of the native populations of the House Sparrow (Šálek et al. 2015), where this species is considered at risk (Summers-Smith 2003; BirdLife International 2004; Shaw et al. 2008).

Previous evidence has suggested that not only House Sparrows could represent a threat to similar sized and smaller granivore species through direct antagonistic interactions (Schondube et al. 2009), but also to species from other guilds and sizes, such as hummingbirds (Ortega-Álvarez and MacGregor-Fors 2010), as well as species with similar nesting habits (e.g., bluebirds, swallows; Kalinoski 1975; pers. obs.). House Sparrow presence along with the threats of urbanization (e.g., introduced predators, pollution, habitat destruction; Santiago-Alarcon and Delgado-V 2017) and indirect interactions (Marzal et al. 2011, e.g., parasite transmission to native birds via both invasive [novel weapon hypothesis] and migratory species; Marzal et al. 2018) can be driving the observed patterns. Thus, our results support that House Sparrows can act synergistically in relation with urbanization in the species richness decline pattern (Chace and Walsh 2006; OrtegaÁlvarez and MacGregor-Fors 2011b, c; Aronson et al. 2014; Sol et al. 2014; MacGregor-Fors and García-Arroyo 2017).

We consider that further directions to test the effects of House Sparrows, in synergy with urbanization on native bird communities, require both laboratory and field experiments. In doing so, studies ought to consider balanced designs, taking into account diverse urban conditions (e.g., residential, industrial, commercial, greenspaces), including non-urban controls of different land uses (e.g., original vegetation, agricultural), and several House Sparrow abundance scenarios. Additionally, it is of the utmost importance to study House Sparrow intraspecific and interspecific interactions (e.g., feeding and nesting resources), as well as monitoring their populations in different spatiotemporal scales. Finally, and based on our field observations, we highlight the importance of the maintenance of vegetation cover and structure in urban areas, not only in large greenspaces but also in private gardens and along streets, with the aim of promoting the native avian assemblage diversity.

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References

Anderson TR (2006) Biology of the ubiquitous house sparrow: from genes to populations. Oxford University Press, Oxford; New York

Aronson MFJ, 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 R Soc B Biol Sci 281:20133330

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biol Lett 12:20150623

Bibby CJ, Burges ND, Hill DA, Mustoe SH (2000) Bird census techniques, 2nd edn. Academic Press Limited, London

BirdLife International (2004) Birds in the European Union: a status assessment. Birdlife International, Wageningen

Blackburn TM, Lockwood JL, Cassey P (2009) Avian invasions: the ecology and evolution of exotic birds. Oxford University Press, Oxford; New York

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Booy O, Cornwell L, Parrott D et al (2017) Impact of biological invasions on infrastructure. In: Vilà M, Hulme PE (eds) Impact of biological invasions on ecosystem services. Springer International Publishing, Cham, pp 235–247

Buckland ST, Anderson D, Burnham K et al (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74:46–69

Clergeau P (1990) Mixed flocks feeding with starlings: an experimental field study in Western Europe. Bird Behav 8:95–100

Colwell RK (2013) EstimateS: statistical estimation of species richness and shared species from samples. Version 9. Available in: http://purl. oclc.org/estimates. Accessed 16 Jan 2017

Crawley MJ (2013) The R book, 2nd edn. Wiley, Chichester

Cueto VR, de Casenave JL (1999) Determinants of bird species richness: role of climate and vegetation structure at a regional scale. J Biogeogr 26:487–492

Delgado-V CA, French K (2012) Parasite–bird interactions in urban areas: current evidence and emerging questions. Landsc Urban Plan 105:5–14

Emlen JT (1974) An urban bird community in Tucson, Arizona: derivation, structure, regulation. Condor 76:184

Faggi A, Caula S (2017) 'Green'or 'gray'? Infrastructure and bird ecology in urban Latin America. In: MacGregor-Fors I, Escobar-Ibáñez JF (eds) Avian ecology in Latin American cityscapes. Springer International Publishing, Cham, pp 79–97

Fisher RJ, Wiebe KL (2005) Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. Oecologia 147:744–753

Flux JEC, Thompson CF (1986) House Sparrows taking insects from car radiators. Notornis 33:190–191

García-Franco JG, Castillo-Campos G, Mehltreter K et al (2008) Composición florística de un bosque mesófilo del centro de Veracruz, México. Bol Soc Bot Méx 83:37–52

Gavett AP, Wakeley JS (1986) Diets of House Sparrows in urban and rural habitats. Wilson Bull 98:137–144

González-Oreja JA, Zuria I, Carbó-Ramírez P, Charre GM (2018) Using variation partitioning techniques to quantify the effects of invasive alien species on native urban bird assemblages. Biol Invasions

Google Earth Pro (2018) Version 7.3.1.4507. Central Veracruz, Mexico.DigitalGlobe 2018. In: http://www.earth.google.com

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Gowaty PA (1984) House Sparrows kill eastern bluebirds. J Field Ornithol 55:378–380

Grarock K, Tidemann CR, Wood J, Lindenmayer DB (2012) Is it benign or is it a pariah? Empirical evidence for the impact of the common myna (Acridotheres tristis) on Australian birds. PLoS One 7:e40622

Guillory HD, Deshotels JH (1981) House Sparrows flushing prey from trees and shrubs. Wilson Bull 93:554

Harper MJ, McCarthy MA, van der Ree R (2005) The use of nest boxes in urban natural vegetation remnants by vertebrate fauna. Wildl Res 32:509–516

Hoi H, Tost H, Griggio M (2011) The effect of breeding density and male quality on paternity-assurance behaviours in the House Sparrow, Passer domesticus. J Ethol 29:31–38

Huff MH, Bettinger KA, Ferguson HL, Brown MJ, Altman B (2000) A habitat-based point-count protocol for terrestrial birds, emphasizing Washington and Oregon. U.S.D.A., Forest Service, Pacific northwest Research Station. Gen. Tech. Rep. PNW-GTR-501, Portland

INAFED Instituto Nacional para el Federalismo y el Desarrollo Municipal (2010) Estado de Veracruz de Ignacio de la Llave. In: Enciclopedia de Los Municipios y Delegaciones de México. http:// www.inafed.gob.mx/work/enciclopedia/EMM30veracruz/index. html

INEGI Instituto Nacional de Estadística y Geografía (2010) Sistema para la consulta de las Síntesis Estadísticas Municipales 2010. In: http:// www.inegi.org.mx/est/contenidos/espanol/sistemas/sem10/default. htm

Kalinoski R (1975) Intraand interspecific aggression in House Finches and House Sparrows. Condor 77:375–384

Kalmus H (1984) Wall clinging: energy saving by the house sparrow Passer domesticus. Ibis 126:72–74

Kimball RT (1997) Male morphology and nest-site quality in House Sparrows. Wilson Bull 109:711–719

Kumschick S, Nentwig W (2010) Some alien birds have as severe an impact as the most effectual alien mammals in Europe. Biol Conserv 143:2757–2762

Kumschick S, Blackburn TM, Richardson DM (2016) Managing alien bird species: time to move beyond “100 of the worst” lists? Bird Conserv Int 26:154–163

La Sorte FA, Lepczyk CA, Aronson MFJ et al (2018) The phylogenetic and functional diversity of regional breeding bird assemblages is reduced and constrained through urbanization. Divers Distrib 24: 928–938

Leveau L (2008) Dynamics of nectarivory in the house sparrow in an urban environment. Ornitol Neotrop 19:275–281

Linz GM, Homan HJ, Gaulker SM et al (2007) European starlings: a review of an invasive species with far-reaching impacts. Manag Vertebr Invasive Species 24

Loss SR, Will T, Marra PP (2015) Direct mortality of birds from anthropogenic causes. Annu Rev Ecol Evol Syst 46:99–120

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database. The Invasive Species Specialist Group (ISSG), Auckland

Luck GW, Smallbone LT, Sheffield KJ (2013) Environmental and socioeconomic factors related to urban bird communities. Austral Ecol 38:111–120

Luna Á, Romero-Vidal P, Hiraldo F, Tella JL (2018) Cities favour the recent establishment and current spread of the Eurasian collared dove Streptopelia decaocto (Frivaldszky, 1838) in Dominican Republic. BioInvasions Rec 7:95–99

MacGregor-Fors I (2010) How to measure the urban-wildland ecotone: redefining 'peri-urban' areas. Ecol Res 25:883–887

MacGregor-Fors I, García-Arroyo M (2017) Who is who in the city? Bird species richness and composition in urban Latin America. In: MacGregor-Fors I, Escobar-Ibáñez JF (eds) Avian ecology in Latin American cityscapes. Springer International Publishing, Cham, pp 33–55

MacGregor-Fors I, Payton ME (2013) Contrasting diversity values: statistical inferences based on overlapping confidence intervals. PLoS One 8:e56794

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

MacGregor-Fors I, Morales-Pérez L, Quesada J, Schondube JE (2010) Relationship between the presence of House Sparrows (Passer domesticus) and Neotropical bird community structure and diversity. Biol Invasions 12:87–96

MacGregor-Fors I, Calderón-Parra R, Meléndez-Herrada A et al (2011) Pretty, but dangerous! Records of non-native monk parakeets (Myiopsitta monachus) in Mexico. Rev Mex Biodivers 82:1053–1056

MacGregor-Fors I, García-Arroyo M, Marín-Gómez OH, Quesada J (2020) On the meat scavenging behavior of House Sparrows (Passer domesticus). Wilson J Ornithol (in press)

MacGregor-Fors I, Quesada J, Lee JG-H, Yeh PJ (2017) Space invaders: house sparrow densities along three urban-agricultural landscapes. Avian Conserv Ecol 12:11

Marzal A, Ricklefs RE, Valkiūnas G et al (2011) Diversity, loss, and gain of malaria parasites in a globally invasive bird. PLoS One 6: e21905

Marzal A, Møller AP, Espinoza K et al (2018) Variation in malaria infection and immune defence in invasive and endemic house sparrows. Anim Conserv. 21:505–514

Mori E, Grandi G, Menchetti M et al (2017) Worldwide distribution of non–native Amazon parrots and temporal trends of their global trade. Anim Biodivers Conserv 40:49–62

Moulton MP, Ferris DK (1991) Summer diets of some introduced Hawaiian finches. Wilson Bull 103:286–292

Napoletano BM, Pijanowski BC, Dunning JBJ (2017) Influences of horizontal and vertical aspects of land cover and their interactions with regional factors on patterns of avian species-richness. Cogent Environ Sci 3:1296604

Nhlane MED (2000) The breeding biology of the House Sparrow Passer domesticus at Blantyre, Malawi. Ostrich 71:80–82

Oksanen J, Blanchet FG, Friendly M et al (2016) Vegan: community ecology package. R package version 2.4–1. https://CRAN.Rproject.org/package=vegan

Ortega-Álvarez R, MacGregor-Fors I (2009) Living in the big city: effects of urban land-use on bird community structure, diversity, and composition. Landsc Urban Plan 90:189–195

Ortega-Álvarez R, MacGregor-Fors I (2010) What matters most? Relative effect of urban habitat traits and hazards on urban park birds. Ornitol Neotrop 21:519–533

Ortega-Álvarez R, MacGregor-Fors I (2011a) Conociendo al Gorrión Casero: Variación de la abundancia de Passer domesticus en diferentes tipos de uso de suelo de la Ciudad de México. El Canto Centzontle 2:15–28

Ortega-Álvarez R, MacGregor-Fors I (2011b) Spreading the word: the ecology of urban birds outside the United States, Canada, and Western Europe. Auk 128:415–418

Ortega-Álvarez R, MacGregor-Fors I (2011c) Dusting-off the file: a review of knowledge on urban ornithology in Latin America. Landsc Urban Plan 101:1–10

Peach WJ, Vincent KE, Fowler JA, Grice PV (2008) Reproductive success of house sparrows along an urban gradient. Anim Conserv 11: 493–503

Pedersen K, Clark L, Andelt WF, Salman MD (2006) Prevalence of Shiga toxin–producing Escherichia coli and Salmonella enterica in rock pigeons captured in Fort Collins, Colorado. J Wildl Dis 42: 46–55

Pimentel D, McNair S, Janecka J et al (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. Agric Ecosyst Environ 84:1–20

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288

Pyšek P, Jarošík V, Hulme PE et al (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species’ traits and environment. Glob Chang Biol 18:1725–1737

R Development Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Radunzel LA, Muschitz DM, Bauldry VM, Arcese P (1997) A long-term study of the breeding success of eastern bluebirds by year and cavity type. J Field Ornithol 68:7–18

Ralph CJ, Geupel GR, Pyle P et al (1996) Handbook of field methods for monitoring landbirds. U.S.D.A., Forest Service, Pacific southwest Research Station. Gen. Tech. Rep. PSW-GTR-144, Albany

Rappole JH, Hubálek Z (2003) Migratory birds and West Nile virus. J Appl Microbiol 94:47–58

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr 83:263–282

Ruelas-Inzunza E, Hoffman SW, Goodrich LJ (2005) Stopover ecology of neotropical migrants in Central Veracruz, México. In: Bird conservation implementation and integration in the Americas: proceeding of the third International Partners in Flight Conference. U.S.D.A., Forest Service, Pacific southwest Research Station. Gen. Tech. Rep. PSW-GTR-191, Albany, pp 657–672

Sætre G-P, Riyahi S, Aliabadian M, Hermansen JS, Hogner S, Olsson U, Gonzalez Rojas MF, Sæther SA, Trier CN, Elgvin TO (2012) Single origin of human commensalism in the house sparrow. J Evol Biol 25:788–796

Šálek M, Riegert J, Grill S (2015) House Sparrows Passer domesticus and tree sparrows Passer montanus: fine-scale distribution, population densities, and habitat selection in a central European city. Acta Ornithol 50:221–232

Santiago-Alarcon D, Delgado-V CA (2017) Warning! Urban threats for birds in Latin America. In: MacGregor-Fors I, Escobar-Ibáñez JF (eds) Avian ecology in Latin American cityscapes. Springer International Publishing, Cham, pp 125–142

Sax DF, Brown JH (2000) The paradox of invasion. Glob Ecol Biogeogr 9:363–371

Schneider SC, Miller JR (2014) Response of avian communities to invasive vegetation in urban forest fragments. Condor 116:459–471

Schondube JE, Escobar A, Quesada J, MacGregor-Fors I (2009) The bigger the better? Competition among invasive and native bird species at urban feeders in a Neotropical area. World Conference on Biological Invasions and Ecosystem Functioning ICCE-CIIMAR, Porto, p 92

Shaw LM, Chamberlain D, Evans M (2008) The house sparrow Passer domesticus in urban areas: reviewing a possible link between postdecline distribution and human socioeconomic status. J Ornithol 149:293–299

Shochat E (2004) Credit or debit? Resource input changes population dynamics of city-slicker birds. Oikos 106:622–626

Shochat E, Lerman SB, Anderies JM et al (2010) Invasion, competition, and biodiversity loss in urban ecosystems. BioScience 60:199–208

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66

Sol D, González-Lagos C, Moreira D et al (2014) Urbanisation tolerance and the loss of avian diversity. Ecol Lett 17:942–950

Stidolph RHD (1974) The adaptable house sparrow. Notornis 21:88

Strubbe D, Matthysen E (2007) Invasive ring-necked parakeets Psittacula krameri in Belgium: habitat selection and impact on native birds. Ecography 30:578–588

Summers-Smith JD (2003) The decline of the house sparrow: a review. Br Birds 96:439–446

Thibault M, Vidal E, Potter MA et al (2018) The red-vented bulbul (Pycnonotus cafer): serious pest or understudied invader? Biol Invasions 20:121–136

Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JR, Marques TA, Burnham KP (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47:5–14

Tindall SD, Ralph CJ, Clout M (2007) Changes in bird abundance following common myna control on a New Zealand island. Pac Conserv Biol 13:202–212

Vitousek PM, D'Antonio CM, Loope LL et al (1997) Introduced species: a significant component of human-caused global change. N Z J Ecol 21:1–16

Wagner VHO (1959) Die Einwanderung des Haussperlings in Mexiko. Ethology 16:584–592

Wang J (2014) Encyclopedia of business analytics and optimization. IGI Goblal, Montclair

Williams-Linera G (2007) El bosque de niebla del centro de Veracruz: Ecología, historia y destino en tiempos de fragmentación y cambio climático. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad e Instituto de Ecología A. C., Xalapa, Ver

Table 1 Number and distribution of survey sites in the three conditions of the studied urban settlements. a urban House Sparrow invaded, b urban House Sparrow non-invaded, c non-urban House Sparrow non-invaded, d Elevation was retrieved from INEGI (2010)

Study region	Settlement size (km2)	UIa	UNIb	NUNIc	Latitude (N)	Longitude (W)	Elevation (m a.s.l.)
Xico	2	9	12	21	19° 25′ 21.72″	97° 0′ 33.48″	1320
Teocelo	1	1	19	20	19° 23′ 7.08″	96° 58′ 30″	1160
San Marcos	0.7	3	7	10	19° 25′ 22.8″	96° 57′ 59.04″	1100
Úrsulo Galván	0.14	0	4	4	19° 25′ 45.84″	96° 58′ 41.88″	1140

Table 2 Bird species richness (average ± 84% CI) across seasons in the surveyed conditions considering all studied settlements.

a urban House Sparrow invaded, b urban House Sparrow non-invaded, c non-urban House Sparrow non-invaded

	Season			
Condition	Spring	Summer	Fall	Winter
UI[a]	17.7 ± 4.3	10.7 ± 1.7	11.8 ± 4.4	14.5 ± 6.4
UNI[b]	19.9 ± 3.6	16.0 ± 3.5	12.4 ± 2.0	16.1 ± 3.2
NUNI[c]	25.5 ± 3.7	21.3 ± 3.5	25.6 ± 3.8	28.2 ± 3.6

Table 3 GAM considering predictor variables describing vegetation characteristics and urban infrastructure in relation with native bird species richness

Variable	DF	χ2	P
Season	3	24.03	<0.001
s (Built cover)	1	28.34	<0.001
s (Maximum shrub height)	1	9.13	0.002
s (House Sparrow abundances)	2	11.32	0.012
s (Shrub richness)	1	0.58	0.494
s (Passing cars per minute)	1	2.54	0.110

Fig. 1 Study areas and sampling locations. Map scales differ for graphical purposes. HS = House Sparrow.

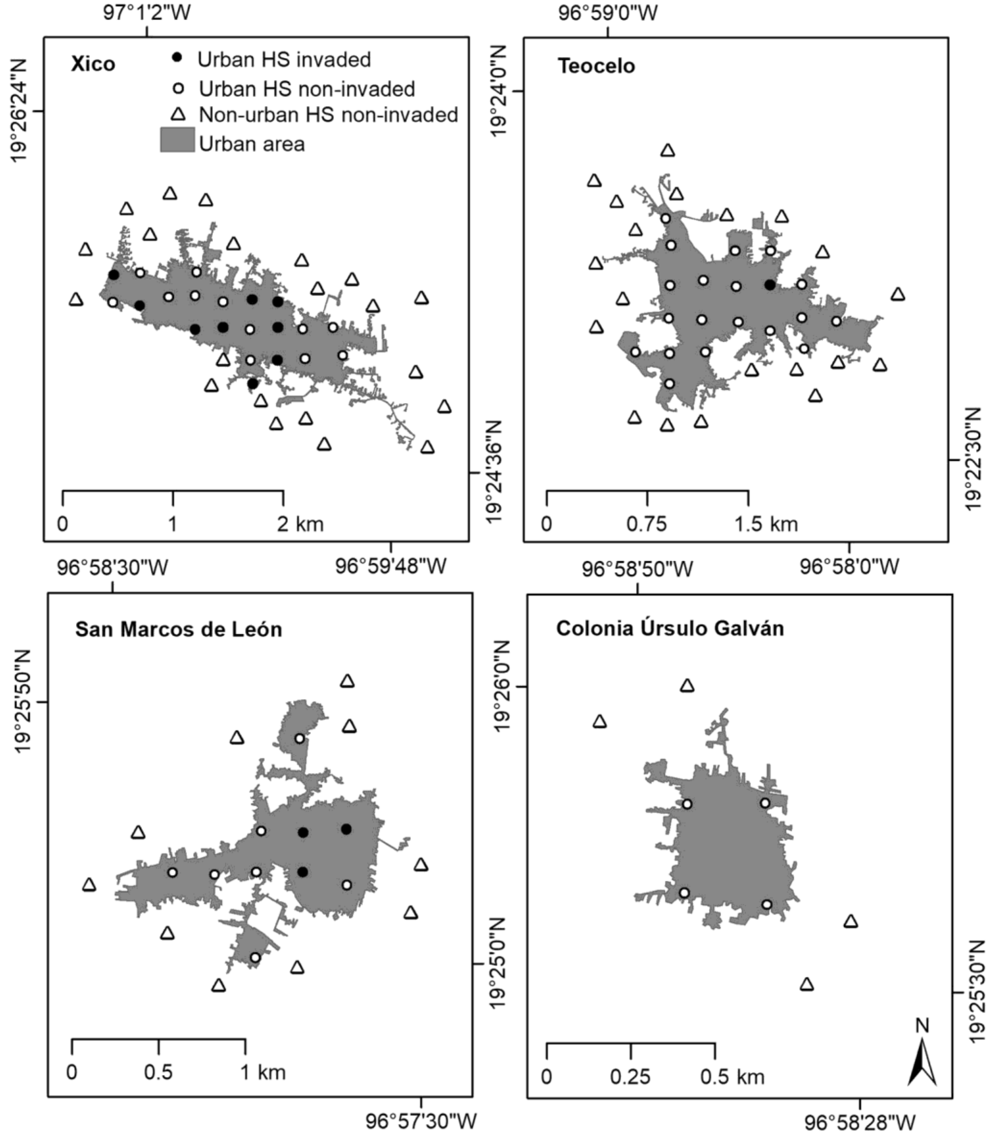

Fig. 2 Bray-Curtis group average link cluster showing avian assemblage composition patterns in the three studied conditions and seasons (UI = urban House Sparrow invaded; UNI = urban House Sparrow non- invaded; NUNI = non-urban House Sparrow non-invaded; numbers after study conditions represent seasons: 1 = spring, 2 = summer, 3 = fall, 4 = winter

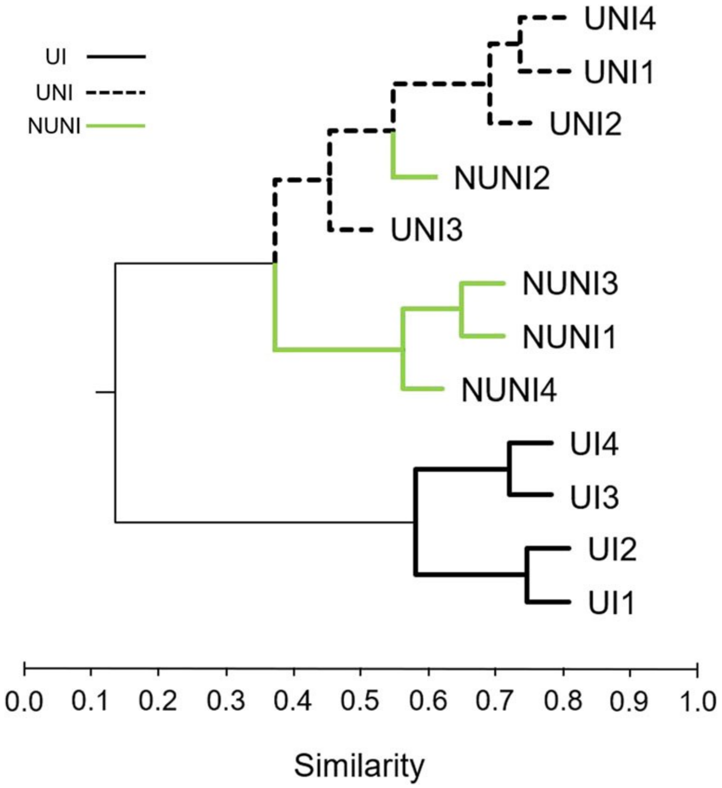

Fig. 3 In this graph we display variables that showed to be significantly related with bird species richness in the GAM. Panels a maximum shrub height and b built cover show the relationship with smoothened data, insets represent the best-fit for smoothened and observed values (positive for shrub height, negative for built cover). For c House Sparrow abundances, lower left panel corresponds to the best-fit adjustment, showing the three different scenarios of 0 individuals (red), 1–5 individuals (blue), and 6–12 individuals (black). Each scenario connects to its corresponding bird species richness in the lower right panel. Letters below the lower 84% CI bars stand for statistical significant differences. HS = House Sparrow.

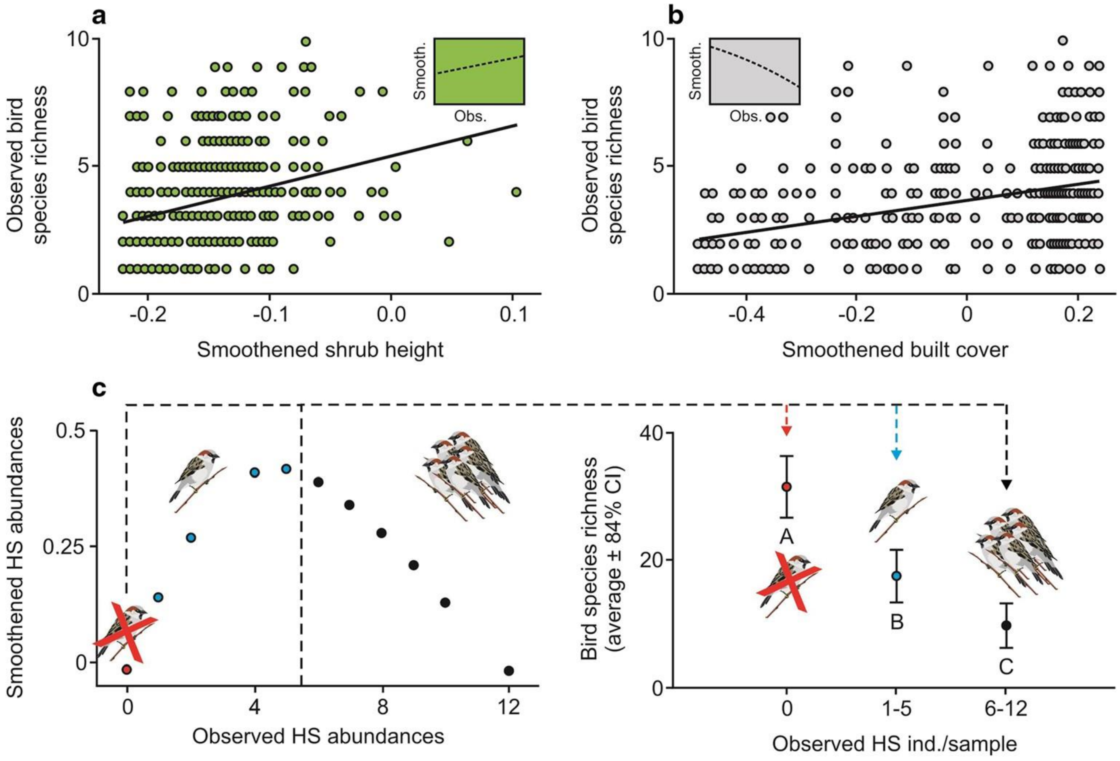

Fig. 4 Built cover at the studied conditions. Letters above error bars represent statistical differences