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Efectos de la urbanización sobre comunidades de aves neotropicales

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P R E S E N T A

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Por medio de la presente me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 9 de agosto del 2010, se acordó poner a su consideración el siguiente jurado para el examen de DOCTOR EN CIENCIAS del alumno **MACGREGOR FORS IAN** con número de cuenta **506021408**, con la tesis titulada: **"Efectos de la urbanización sobre comunidades de aves neotropicales"**, bajo la dirección del **Dr. Jorge Ernesto Schondube Friedewold**.

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ÍNDICE

RESUMEN

La urbanización es una de las actividades humanas que amenaza a la biodiversidad. Al sustituir hábitats no urbanos con estructuras urbanas y un juego de componentes vegetales distinto al que existía previo al cambio, el proceso de urbanización conlleva a la homogeneización de los hábitats. Estas modificaciones son generalmente intensas y de largo plazo, lo cual no permite que la sucesión ecológica se lleve a cabo. Así, con la centralización de fuentes de trabajo en zonas urbanas, la población humana pasó de ser básicamente rural a mayormente urbana en la última década, derivando en la expansión de zonas urbanas a lo largo y ancho del planeta. Estudios de ecología urbana han aportado una gran cantidad de información sobre los patrones de diversidad relacionados con la urbanización. Sin embargo, aun no comprendemos los mecanismos que generan los patrones registrados hasta la fecha. Así, en este proyecto de tesis me enfoqué en: (1) sintetizar gran parte del conocimiento que se tiene sobre el efecto que tiene la urbanización sobre las comunidades de aves (Capítulo II); describir el efecto que tiene la urbanización sobre las comunidades de aves migratorias (Capítulo VI); y (3) abordar, desde cuatro perspectivas, algunos de los mecanismos que son responsables de los patrones ecológicos de aves observados en zonas urbanas. Primero, determiné la respuesta de las comunidades de aves ante estadios tempranos de urbanización bajo diferentes contextos espaciales y con la ausencia/presencia de especies explotadoras de ambientes urbanos (Capítulo III). Segundo, evalué las relaciones que existen entre la presencia/abundancia de una especie de ave exótica y explotadora de ambientes urbanos (gorrión casero–*Passer domesticus*) y la diversidad de las comunidades de aves nativas (Capítulo IV). Tercero, me concentré en el efecto que tiene el tamaño de los asentamientos humanos sobre la diversidad, estructura y composición de las comunidades de aves, siguiendo un esquema de relación área-riqueza (Capítulo V). Cuarto, estudié la respuesta de las aves ante la estructura de hábitat de los sistemas urbanos, incluyendo los componentes urbanos, sociales, económicos y vegetales (Capítulo VII). Finalmente, resumí los hallazgos más importantes encontrados en los capítulos de esta tesis y subrayé las conclusiones generales en un apartado final (Capítulo VIII).

ABSTRACT

Urbanization is one of the human activities that severely threatens biodiversity. By substituting natural habitats with urban structures and different plant species, the process of urbanization leads to habitat homogenization. These modifications are usually intense and long-term, leaving no opportunity for ecological succession to occur. Financial and commercial centralization in urban areas has lead human population from being mainly rural to becoming mostly urban in the last decade, deriving in the expansion of urban areas worldwide. Urban ecology studies have contributed with information on the diversity patterns that take place within urban areas. However, little is known on the mechanisms that generate such patterns up to date. Thus, in this project, I focused on: (1) summing great part of the knowledge existing on the effect that urbanization has on bird communities (Chapter II); (2) describe the effect that urbanization has on migrant bird communities (Chapter VI; and (3) concentrating, from four perspectives, the mechanisms that are behind some of the recorded ecological patterns recorded for birds in urban areas. First, I determined the response of bird communities to early stages of urbanization in different spatial contexts and in the presence/absence of urban exploiter species (Chapter III). Second, I evaluated the relationships between the presence/abundance of an exotic urban exploiter bird species (House Sparrow–*Passer domesticus*) and native bird community diversity values (Chapter IV). Third, I concentrated on the effect that the size of human settlements has on bird diversity, structure, and composition, following a species-area approach (Chapter V). Fourth, I studied the response of bird to urban habitat structure, including urban infrastructure, socio-economy, and plant characteristics (Chapter VII). Finally, I summed the most relevant findings of this thesis and underlined the general conclusions in the final section (Chapter VIII).

Capítulo 1

Introducción

El crecimiento de la población humana en el último siglo ha generado una fuerte demanda por recursos y espacio. La manutención de una población mundial de más de seis mil millones de personas implica la alteración de hábitats naturales a gran escala (Pimentel *et al.* 1992, Lev-Yadun *et al.* 2000, Cohen 2003). Posterior a la revolución industrial, el modo de transformar la tierra experimentó cambios radicales (Vitousek *et al.* 1997) y la destrucción de los hábitats naturales con fines productivos (*e.g.,* agropecuarios, silvícolas) y/o de urbanización acentuó su efecto sobre la biodiversidad. De hecho, la urbanización es considerada como una de las causas principales de extinción de especies (Czech *et al.* 2000).

Actualmente, más de la mitad de la población humana mundial vive en zonas urbanas (Bierwagen 2007). En particular, México concentra cerca del 67% de su población total en zonas urbanas (Garza 2002). Debido a que los procesos de crecimiento urbano en México son desordenados (*e.g.,* Ciudad de Morelia; López *et al.* 2001), la expansión de sus ciudades representa una actividad insustentable. Así, la sobreexplotación de recursos naturales asociada con los procesos de urbanización se ha convertido en un problema para la conservación de la biodiversidad a nivel nacional (Rocha 2006).

El estudio de los efectos que tiene la urbanización sobre la biodiversidad ha incrementado considerablemente en las últimas décadas, utilizando principalmente a las aves como objeto de estudio (Mazluff *et al.* 2001, Chace y Walsh 2006). Los primeros estudios sobre el tema fueron llevados a cabo por Pitelka (1942) y Emlen (1974). El trabajo de Emlen (1974) conceptualizó a las ciudades como hábitats artificiales abiertos a la invasión y colonización de aquellas especies de aves que pudieran llegar a ellas, utilizar sus recursos y sobrevivir a sus amenazas. A partir de este trabajo pionero, los estudios de ecología de aves urbanas han establecido un patrón generalizado, en el que la riqueza de especies disminuye y la abundancia total de aves aumenta con la urbanización (Chace y Walsh 2006). Este patrón parece deberse a la exclusión de aves nativas por las características propias de la ciudad y al crecimiento poblacional explosivo de unas cuantas especies, generalmente exóticas, que son capaces de adaptarse a las condiciones urbanas (Blair 1996).

Se han identificado cinco factores que determinan la presencia y/o persistencia de las especies de aves dentro de los sistemas urbanos: (1) la presencia y el tamaño de parches de vegetación original dentro del área urbana (Emlen 1974, Gavareski 1976, Mills *et al.* 1989); (2) la competencia con especies exóticas pre-adaptadas a los ambientes urbanos (Major *et al.* 1996); (3) la abundancia de depredadores (Yahner 1996, Jokimäki y Huhta 2000, López-Flores *et al.* 2009); (4) la estructura y composición de la flora plantada en parques y jardines (MacGregor-Fors 2008, Ortega-Álvarez y MacGregor-Fors 2009); y (5) el suplemento antropogénico de recursos alimenticios (Shochat 2004). Aquellas especies de aves que logran persistir bajo condiciones urbanas han sido catalogadas como: (1) explotadoras de ambientes urbanos – aptas para aprovechar las condiciones generadas por los cambios provocados por la urbanización y capaces de explotar los recursos alimenticios generados por las actividades humanas; y (2) adaptables a ambientes urbanos – que aprovechan los recursos adicionales

aportados por el hombre en áreas con niveles bajos de urbanización (*e.g.,* vegetación densa en parques). Aquellas especies suceptibles al cambio de la estructura de la vegetación y del tipo de recursos disponibles en áreas urbanas, y que por tanto están ausentes o simplemente son visitantes ocasionales de las ciudades, son clasificadas como especies evasoras de ambientes urbanos (Blair 1996, McKinney 2002).

Aunque la mayoría de los estudios de ecología urbana se han desarrollado en el norte de Norteamérica (Estados Unidos y Canadá) y Europa (Marzluff *et al.* 2001, Chace y Walsh 2006), estudios en regiones tropicales (e.g., Australia, Latinoamérica) han aumentado considerablemente en las últimas décadas. Sin embargo, debido a que se pronostica un crecimiento acelerado tanto de la población humana, como de las zonas urbanas en los países tropicales, resulta imperativo realizar estudios que permitan identificar los efectos que tiene la urbanización sobre las comunidades de aves que habitan en sistemas urbanizados y comprender sus procesos (Clergeau *et al.* 1998, Jokimäki 1999, Marzluff *et al.* 2001, Turner 2003).

Más de 65 años de estudios ornitológicos en sistemas urbanos han aportado una gran cantidad de información sobre los patrones de diversidad relacionados con la urbanización (*e.g.,* Clergeau *et al.* 1998, Marzluff *et al.* 2001, Crooks *et al.* 2004, Simon *et al.* 2007). Sin embargo, es sumamente importante comprender los mecanismos que generan los patrones registrados hasta la fecha con la finalidad de mitigar el efecto que tiene la urbanización sobre la biodiversidad (Shochat *et al.* 2006). En este proyecto de tesis sinteticé gran parte del conocimiento existente sobre el efecto que tiene la urbanización sobre las comunidades de aves (Capítulo II), describí el efecto que tiene la urbanización sobre las comunidades de aves migratorias (Capítulo VI) y aborde, desde cuatro perspectivas, algunos de los mecanismos que son responsables de los patrones ecológicos de aves observados en zonas urbanas. Primero, determiné la respuesta de las comunidades de aves ante estadios tempranos de urbanización bajo diferentes contextos espaciales y con la ausencia/presencia de especies explotadoras de ambientes urbanos (Capítulo III). Segundo, evalué las relaciones que existen entre la presencia/abundancia de una especie de ave agresiva, exótica y explotadora de ambientes urbanos (gorrión casero–*Passer domesticus*) y la diversidad de las comunidades de aves nativas (Capítulo IV). Tercero, me concentré en el efecto que tiene el tamaño de los asentamientos humanos sobre la diversidad, estructura y composición de las comunidades de aves, siguiendo un esquema de relación área-riqueza (Capítulo V). Cuarto, estudié la respuesta de las aves ante la estructura de hábitat de los sistemas urbanos, incluyendo los componentes urbanos, sociales, económicos y vegetales (Capítulo VII). Finalmente, resumí los hallazgos más importantes encontrados en los capítulos de esta tesis y subrayé las conclusiones generales en un apartado final (Capítulo VIII).

Referencias

Bierwagen, B. G. 2007. Connectivity in urbanizing landscapes: The importance of habitat configuration, urban area size, and dispersal. Urban Ecosystems 10: 29–42.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6: 506–519.

Chace, J. F. y J. J. Walsh. 2006. Urban effects on native avifauna: A review. Landscape and Urban Planning 74: 46–69.

Clergeau, P., J. P. L. Savard, G. Mennechez y G. Falardeau. 1998. Bird abundance and diversity along an

urban-rural gradient: A comparative study between two cities on different continents. The Condor 100: 413–425.

Cohen, J. E. 2003. Human population: The next half century. Science 302: 1172–1175.

Crooks, K. R, A. V. Suarez y D. T. Bolger. 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biological Conservation 115: 451–462.

Czech, B., P. R. Krausman y P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. Bioscience 50: 593–601.

Emlen, J. T. 1974. An urban bird community in Tucson, Arizona: Derivation, structure, regulation. The Condor 76: 184–197.

Garza, G. 2002. Evolución de las ciudades mexicanas en el siglo XX. Datos, Hercho y Lugares 19: 7–16.

Gavareski, C. A. 1976. Relation of park size and vegetation to urban bird populations in Seattle, Washington. The Condor 78: 375–382.

Jokimäki, J. 1999. Occurrence of breeding bird species in urban parks: Effects of park structure and broad-scale variables. Urban Ecosystems 3: 21-34.

Jokimäki, J. y E. Huhta. 2000. Artificial nest predation and abundance of birds along an urban gradient. The Condor 102: 838–847.

Lev-Yadun, S., A. Gopher y S. Abbo. 2000. The cradle of agriculture. Science 288: 1602-1603.

MacGregor-Fors, I. 2008. Relation between habitat attributes and bird richness in a western Mexico suburb. Landscape and Urban Planning 84: 92-98.

Major, R., G. Gowing y C. Kendall. 1996. Nest predation in Australian urban environments and the role of the pied currawong Streptera graculina. Austral Ecology 21: 399-409.

Marzluff, J. M., Bowman R. & Donnely R.. 2001. A historical perspective on urban bird research: Trends, terms, and approaches. En Marzluff, J. M., R. Bowman y R. Donnely(eds): Avian conservation and ecology in an urbanizing world. Pp. 1–17. Kluwer Academic. Boston.

McKinney, M. L. 2002. Urbanization, biodiversity and conservation. Bioscience 52: 883-890.

Mills, G. S, J. B. Dunning y J. M. Bates. 1989. Effects of urbanization on breeding bird community structure in Southwestern desert habitats. The Condor 91: 416–428.

Ortega-Álvarez, R. e I. MacGregor-Fors. 2009. Living in the big city: Effects of urban land-use on bird community structure, diversity, and composition. Landscape and Urban Planning 90: 189-195.

Pimentel, D., U. Stachow, D. Takacs, H. Brubaker, A. Dumars, J. Meany, J. Oniel, D. Onsi y D. Corzilius. 1992. Conserving biological diversity in agricultural/forestry systems. Bioscience 42: 354-363.

Pitelka, F. A. 1942. High population of breeding birds within an artificial habitat. The Condor 44: 172-174.

Rocha, M. 2006. La situación ambiental del espacio megalopolitano de la ciudad de México. Economía Informa 339: 64–79.

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

Shochat, E., P. S. Warren y S. H. Faeth. 2006. Future directions in urban ecology. Trends in Ecology & Evolution 21: 661–662.

Simon, U., S. Kübler y J. Böhner. 2007. Analysis of breeding bird communities along an urban-rural gradient in Berlin, Germany, by Hasse Diagram Technique. Urban Ecosystems 10: 17–28.

Vitousek, P, H. Mooney, J. Lubchenco y J. Melillo. 1997. Human domination of Earth's ecosystems. Science 277: 494-499.

Yahner, R. H. 1996. Forest fragmentation, artificial nest studies, and predator abundance. Conservation Biology 10: 672-673.

Chapter 3

ON THE ECOLOGICAL QUALITY OF URBAN SYSTEMS: AN ORNITHOLOGICAL PERSPECTIVE

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1. WHY TO USE BIRDS AS TOOLS FOR MEASURING THE ECOLOGICAL QUALITY OF CITIES?

When you leave your home early in the morning, for work or school, the sunrise chorus of birds is usually ubiquitous. The main reason that enables you to enjoy this phenomenon inside a city is that birds are one of the few wildlife groups that assemble complex communities within urban areas. Due to the latter and to the fact that birds are generally conspicuous, diverse, and quickly respond to habitat changes, biologists that study urban ecosystems have focused greatly on this group to carry out their research. In this chapter, we attempt to summarize the knowledge on the factors that have been identified as important for maintaining diverse communities of urban-dwelling birds. We also pinpoint the relationship between these factors and the ecological quality of urban areas. Finally, we propose several urban management and planning activities that could assist on maintaining and promoting biodiversity within cities. At the same time, these activities could improve the ecological quality of the urban areas in which we live, leading to a win-win scenario.

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2. Birds and the City

When an area becomes urbanized, natural habitats are replaced with artificial structures that satisfy human-life requirements (Bradshaw, 2003). The establishment of these structures has drastic and long-term effects on the environment (Turner et al., 2004; McKinney, 2006). Thus, changing the attributes of the preexisting natural habitat urbanization represents a threat to the native biodiversity (Marzluff et al., 2001a; McKinney, 2008). However, each city comprises a unique and complex system, the essence of which is related to its specific attributes (Batty, 2008). Of these, the intensity of urbanization, quantified by measuring both built area and building density (Marzluff et al., 2001b), is one of the main factors affecting urban-dwelling wildlife.

Studies carried out all around the world have recorded both positive and negative effects of urbanization intensity on bird communities. As recorded by the great majority of urban ecologists, native resident bird species richness and abundance decrease in highly developed areas (Jokimäki and Suhonen, 1998; Jokimäki, 1999; Blair, 2004; Lim and Sodhi, 2004; Valiela and Martinetto, 2007; Shwartz et al., 2008). On the other hand, urbanization intensity has positive effects on the presence of a few urban-exploiter species, defined as those species with broad dietary requirements (mainly omnivorous and granivorous; Jokimäki and Suhonen, 1998; Lim and Sodhi, 2004; Kark et al., 2007), highly sociable and sedentary, with preferences for nesting in artificial structures, and able to expand their ranges throughout human-dominated landscapes (Blair, 1996; Kark et al., 2007). These characteristics make them capable to exploit the environmental changes generated by urbanization processes. Among the most widespread urban-exploiter species in North America, we find the House Sparrow (*Passer domesticus*), the Rock Pigeon (*Columba livia*), and the European Starling (*Sturnus vulgaris*). Obviously, 'urbanization intensity' encompasses a multi-factorial set of conditions and processes that are responsible for the recorded shifts in avian communities within urban areas. In the next two sections of this chapter ('Birds and Urban Habitats', and 'Birds and Humans') we steer through some of the main factors identified as drivers of bird diversity inside urban areas.

3. Birds and Urban Habitats

Urban areas comprise a unique combination of built structures, planted vegetation, and natural habitat remnants. Although these novel habitats are largely dissimilar from those that surround them, site-specific habitat characteristics within a city can have different effects on bird communities. In this section we review the relationships found between the 'artificial' and 'natural' components of urban environments and bird community diversity values.

3.1 The 'Artificial' Structure Component

The quantity of urbanized area within a city is closely related to the space available for the establishment of other 'natural' components. In this respect, the variable 'percent built' has been widely used to define discrete points along urban gradients (Marzluff et al., 2001b;

Hahs and McDonnell, 2006; Simon et al., 2007). Nevertheless, few studies have focused on the effects that the presence, type, or density of 'artificial' structures have on bird communities. One of the first urban ecologists that described directional relationships between urban 'artificial' structures and birds was John T. Emlen. Back in the 1970s, he described the urban bird community of Tucson, Arizona in the southwestern area of the United States of America, and pinpointed that 'house tops and particularly their superstructures such as air conditioning units and television aerials provide attractive song and resting perches [for birds]' (Emlen, 1974; pp. 188). Emlen (1974) also underlined the importance of perches located at different heights, such as fence tops, telephone poles, and wires.

In addition to Emlen's contribution, two characteristics of buildings have been related to avian ecological processes. First, the architectural style of buildings can determine if birds use them for nesting (DeGraff and Wentworth, 1986). Urban ecologists from Italy and the United States of America reported that 'ornate older buildings' encompass a higher number of nesting sites, and benefit those species that can exploit them (Johnsen and VanDruff, 1987; Sacchi et al., 2002). One clear example of this is the Rock Pigeon, an urban-exploiter species that exhibits highest abundances in areas with 'ornate older buildings' (Sacchi et al., 2002). Second, results from an urban ecology study carried out in west-central Mexico shows a positive relationship between total bird abundance and the maximum height of buildings. These results were principally explained by the abundance of two exotic bird species, the House Sparrow and the Rock Pigeon, that successfully exploit building facades and roofs for roosting and nesting (MacGregor-Fors et al., in press A).

3.2 The 'Natural' Vegetation Component

Green areas within a city, including urban forests, greenways, parks, and gardens offer many social and environmental benefits, such as recreation, landscaping, land-use buffering, and wildlife conservation (Furuseth and Altman, 1991; Schiller and Horn, 1997). Such green areas are characterized by the presence of vegetation components, independent of their structure and/or complexity, and are subject to different types and intensities of management activities (Grimm et al., 2003). A wide spectrum of urban green areas exists inside cities, ranging from simple single herb-stratum sport-fields, to complex urban forest remnants. Although urban green areas are diverse in kind, they generally have higher similarity to natural habitats than to highly-developed urban sites. Urban ecologists have widely focused their studies on natural and man-made vegetated areas inside cities (Collins et al., 2000; Marzluff et al., 2001a; Melles, 2005 Gavareski, 1976; Rosenberg et al., 1987; Schiller and Horn, 1997; Morneau et al., 1999; Fernández-Juricic and Jokimäki, 2001; Sandström et al., 2006). Empirical research focused on urban green areas have evaluated them by using landscape-geographic perspectives (e.g., size, form, aggregation), and by analyzing their structural components separately (e.g., trees, shrubs, herbaceous plants). Based on this clear division of study objectives, in this section we first review avian diversity patterns related to urban green areas size an location within a city, and second, we discuss the specific effect that each vegetation component has on birds.

3.2.1 Urban Green Areas

The diversity patterns of birds that use/inhabit urban green areas are consistent among studies (e.g., Jokimäki, 1999; Morneau et al., 1999; Crooks et al., 2004; Daniels and Kirkpatrick, 2006). Bird communities recorded in urban green areas are richer, and comprise a higher number of individuals than those from non-green urban sites. Independent studies have demonstrated that such increase of native bird species in urban green areas is the result of multiple factors. For example, the amount of urban area covered by vegetation in parks (Gavareski, 1976; Jokimäki, 1999; Morneau et al., 1999; Melles et al., 2003) and gardens (Daniels and Kirkpatrick, 2006) is positively related to both native breeding bird species richness and abundances (Clergeau et al., 1998; McKinney, 2002).

Aside from their size, other four characteristics of urban green areas have been identified as determinant for breeding bird species richness and abundances: (1) the origin of the green area (as natural or planted; Lim and Sodhi, 2004); (2) the structure and composition of the vegetation component (Gavareski, 1976; Fernández-Juricic et al., 2001; Marzluff and Ewing, 2001; McKinney, 2008); (3) the periodicity of the management they receive (Lim and Sodhi, 2004; Shwartz et al., 2008); and (4) the interconnectivity between urban green areas (Melles et al., 2003; Tan, 2006). The first three factors are related to the resources that urban green areas offer to birds. Because urban green areas are often re-populated with non-native plant species, their ecological relationships with native food resourses like insects, flowers, fruits, and seed are poor. Therefore, native bird species are not familiar with the novel set of resources. Also, birds are driven away from urban green areas due to the noise and constant habitat structure change (mainly on herbaceous plants and shrubs) that is caused by the regular management given to such green areas (Lim and Sodhi, 2004). On the other hand, the interconnection of urban green areas is an important geographical feature for the arrival and establishment of bird species in an urban area. The interconectivity among green areas opens the possibility for the incorporation of urban-sensitive bird species, by providing suitable habitat across corridors through complex green-networks (Tan, 2006; von Haaren and Reich, 2006).

Urban habitat characteristics identified as 'positive' for native breeding bird species tend to have negative relationships on urban-exploiter birds. Specifically, urban-exploiters are benefited by changes in the composition and structure of native vegetation, and by the presence of small-sized urban green areas. Also, because most urban-exploiter bird species are pre-adapted to urban conditions, they benefit from highly-developed homogeneous urban areas.

3.2.2 Vegetation components

3.2.2.1 The 'Tree' Component

Tree density is one of the vegetation variables that have been positively related to breeding bird species richness and abundances within cities (Emlen, 1974; Melles et al., 2003; Crooks et al., 2004; Lim and Sodhi, 2004). Also, tree density is positively related to invetebrate diversity (Smith et al., 2006), incorporating potential avian food resources. However, the relationship between tree density and bird diversity values vary depending if trees are native or exotic. Results from studies carried out in Tucson, Arizona (Mills et al., 1989), and Sidney, Australia (Parsons et al., 2006), suggest that exotic tree species are related

to decreases in native bird species richness, and increases in the number of generalist urban-exploiter bird species. On the other hand, the presence of native tree species is related to increases in native bird species richness (Emlen, 1974; Mills et al., 1989). These studies suggest that native bird species that could be driven away from the urban systems can find shelter in areas that include elements that are familiar to them. However, energy-rich exotic tree species, such as the Australian Silk Oak (*Grevillea robusta*), was identified as positive for bird species richness in a Mexican suburb (MacGregor-Fors, 2008).

In addition to the density and origin (native vs. exotic) of the tree species that are present in an urban green area, the number of tree species can also play an important role in shaping bird communities. Much of the food resources and vegetation structure heterogeneity that can be found in urban parks is related to the high vegetation diversity encountered within them, mostly in the form of tree species richness (Shwartz et al., 2008). This variable was positively related to breeding native bird species richness and abundances in a study that assessed bird diversity values along an urbanization gradient in Mexico City (Ortega-Álvarez and MacGregor-Fors, in press).

Additionally to these variables, tree height also seems to be an important factor affecting bird communities in urban environments around the world (Munyenyembe et al., 1989; Jokimäki, 1999; Daniels and Kirkpatrick, 2006; MacGregor-Fors, 2008). Because older trees are higher, tree height is related to the age of the urban green area. Also, higher trees provide a greater range of feeding, perching, resting, and nesting resources (MacGregor-Fors, 2008). Furthermore, even when these old high trees are ill or dying, they offer highly valuable resources for some urban adaptable cavity-nesters, such as owls, woodpeckers, and parrots (Shwartz et al., 2008; MacGregor-Fors pers. obs.) that usually are unable to breed inside cities that do not count with large old trees.

3.2.2.2 The 'Shrub' Component

While many urban ecologists have concentrated on tree canopy coverage as an ecological measurement of urban green areas (e.g., Moll, 1997), shrub density often provides information on the level of conservation and management of an urban green area (Jokimäki, 1999). Additionally, shrubs contribute importantly to the structure complexity of habitats inside cities. The presence and abundance of shrubs benefit both native and exotic bird species. On the one hand, a cover of large shrubs benefits urban-exploiter bird species richness (Daniels and Kirkpatrick, 2006; Ortega-Álvarez and MacGregor-Fors, in press). This phenomenon seems to be related to the fact that these species are highly gregarious and often exhibit communal nesting behavior, for which large shrubs are ideal (Kark et al., 2007). On the other hand, shrub cover has been related to the increase of species richness and abundance values for urban adaptable bird species (Melles et al., 2003; Daniels and Kirkpatrick, 2006). Empirical studies have showed three main benefits of the shrub component to native birds: (1) shrubs contribute with an important number of nesting sites (Jokimäki, 1999); (2) they can provide additional food resources, such as berries (Melles et al., 2003); and (3) they offer hiding cover for urban-dwelling birds, acting as shelter from predators and human disturbance (Fernández-Juricic et al., 2001).

3.2.2.3 The 'Herbaceous Plant' Component

Is common among cities to have large green areas dominated by grass that receive constant management . Good examples of this are lawns and sport-fields. Large extensions covered with managed herbaceous plants often generate decreases in native bird species richness (Gavareski, 1976; Mörtberg, 2001; Shwartz et al., 2008). Open green areas often lack trees and shrubs, afecting urban-adaptable species that them for foraging and nesting (DeGraff and Wentworth, 1986; Shwartz et al., 2008). However, some particular bird species benefit from large extensions of open green areas, such as exotic urban-exploiters (e.g., starlings), native generalists (e.g., cowbirds, grackles), and aerial insectivore bird species that use open spaces (e.g., tyrant flycatchers; Emlen, 1974; DeGraff and Wentworth, 1986; Mills et al., 1989).

By comparison, large urban areas covered with herbaceous plants that are not subjected to management have very different effects on birds. When herbaceous plants, both native and exotic, are left to grow, they tend to form environments similar to grasslands. These areas inside cities provide dense vegetation cover, perching sites, and food in the form of seeds and insects. Two studies carried out in cities of central and west-central Mexico found that areas with herbaceous plants with heights ranging from 0.3 to 4 m exhibited higher bird species richness and abundance values than urban sites with lower herbaceous plants (< 0.3 m; Ortega-Álvarez and MacGregor-Fors, in press; MacGregor-Fors et al., in press A). This result seems to be related to the absence of human management within abandoned lots, where habitat structure resembles those from shrubby grasslands, allowing the convergence of both native and exotic bird species (MacGregor-Fors et al., in press A).

4. BIRDS AND HUMANS

Within a city, physical, biological, and social factors interact to shape the urban ecosystem (Nilon et al., 2003). Although the social component of urban areas includes several complex variables such as gender, ethnic origin, education, income, and population density (Furuseth and Altman, 1991; Kinzig et al., 2005), most of these factors have been ignored in urban ecology studies. The few urban ecology studies that take into account the social component of urban ecosystems have mainly focused on the effects that population density and per capita income have on birds (e.g., Hope et al., 2003; Melles, 2005; Shaw et al., 2008; MacGregor-Fors et al., in press A). Some clear ecological patterns have been found by these studies: (1) bird species richness (specifically of frugivorous species) are positively related to low human population density (Lim and Sodhi, 2004); (2) the presence and abundance of insectivorous and carnivorous bird species is negatively related to high human population densities (Lim and Sodhi, 2004); (3) the abundance of generalist urban-exploiter bird species is positively related to high human population densities (Jokimäki and Suhonen, 1998; Lim and Sodhi, 2004); (4) urban wealthy neighborhoods have abundant and rich native bird communities; and (5) low-income districts encompass poorer and less abundant bird communities (Melles, 2005; Fuller et al., 2008). Based on these results, we can conclude that wealthy neighborhoods with low human densities offer better environmental conditions for native urban-dwelling birds.

Bird distribution patterns inside cities are clearly related to two main socioeconomical associated factors: (1) the lack of vegetation components in highly developed and populated urban areas (Melles, 2005); and (2) the intensity and frequency of human caused disturbance) in highly populated urban areas (e.g., density of pedestrians, car traffic, land-use change, percent built; Martinuzzi et al., 2007; MacGregor-Fors and Schondube pers. obs.). This affects urban-dwelling bird communities in two ways: (1) the number of pedestrians has negative effects on native urban-adaptable bird species, and positive effects on the abundance of exotic urban-exploiter species (Miller et al., 2001; Ortega-Álvarez and MacGregor-Fors, in press; MacGregor-Fors et al., in press A); and (2) the number of cars also affects bird communities, with highly transited streets, roads, and/or boulevards exhibiting lower bird species richness than streets with low traffic (Ortega-Álvarez and MacGregor-Fors, in press; MacGregor-Fors et al., in press A). Interestingly, one study carried out in Spain showed that larger bird species are less tolerant to the presence and abundance of humans (Fernández-Juricic et al., 2001). This phenomenon could act as an important ecological force molding the type of urban-adaptable bird species that can succeed in urban areas with different levels of human activity.

Other environmental agents affecting both birds and humans that dwell within cities include noise, pollution, and the dispersal of diseases by animal vectors. Urban noise, generally caused by vehicles, causes stress-related psychosocial symptoms in humans (Gidlöf-Gunnarsson and Öhrström, 2007) and can difficult the communication among birds for their year-round and reproductive activities (Slabbekoorn and Peet, 2003). Water and air pollution can drastically affect both human (Wu et al., 1999; WHO, 2000) and bird health (Eeva et al., 1998). High density of some human-related fauna, such as dog, cats, rats, mice, and birds can act as disease vectors for humans and wildlife (e.g., rabies, West Nile virus, avian flu), and can also affect avian predation rates (Matthews et al., 1999; Woods et al., 2003; Baker et al., 2005; López-Flores et al., in press). These factors can result in higher stress levels for both humans and birds dwelling within cities (Cappon, 1977; Partecke et al., 2006; Chávez-Zichinelli pers. com.).

While most human activities inside cities affect birds negatively, a positive and important factor shaping bird communities within urban settlements is the human-based input of food resources. These food resources can be provided by people both voluntarily (e.g., bird feeders), or involuntarily (e.g., litter). Because the input of human-based food resources that are important for birds is large and continuous in urban ecosystems, those species that can feed on them have a permanent food income, and therefore can 'live on their credit' (Shochat, 2004).

Several studies have documented that bird-feeders can affect the local distribution and abundance of bird species, benefiting specially those that are mainly granivorous (Emlen, 1974; Chace and Walsh, 2006; Daniels and Kirkpatrick, 2006; Gaston et al., 2007; Fuller et al., 2008). However, three negative aspects have been related to the presence and abundance of bird-feeders within an urban area. First, because birds congregate near feeders, different bird predators are attracted to them, making feeder-consumers highly vulnerable to predation (Kristan et al., 2003). Second, bird feeders favor the presence of urban-exploiter bird species that can exclude potential native visitors (Daniels and Kirkpatrick, 2006; MacGregor-Fors et al., in press B). Third, feeders can act as sites where diseases and parasites are passed among feeding individuals, which could have further avian population health issues (Dhondt et al., 1998; USGS, 2007).

5. Birds as Ecological Quality Thermostats

In this chapter we have reviewed urban ornithology knowledge to understand how urban conditions and resources affect urban-dwelling birds. But, why should these information concern urban planners and managers, or even a regular urban citizen? The information presented earlier in this chapter shows that avian life-quality resembles our concept of life-quality. While the information on the ecological quality of urban systems provided by birds could seem obvious, and some people could argue that we do not need birds as tools to measure the ecological quality of an area within a city, we believe that birds offer special insights on the identification of both conspicuous and inconspicuous factors affecting the quality of life inside cities. This 'urban avian alarm system' can be employed using single bird species or entire bird communities.

One of the main factors that make birds useful as bio-indicators is that they are a diverse group. Some species are highly sensitive to simple changes, while others are highly resistant to a great variety of disturbance types and intensities. Two excellent examples of these extremes are the Island Canary (*Serinus canaria*) and the House Sparrow. Island Canaries were used by miners in the past to test out air quality within mines due to their high sensitivity to methane and carbon dioxide. When a canary died for exposure to these gases, the miners were still able to exit the area before being affected by them. Similarly to the Island Canary, several species of native birds are sensitive to air quality inside cities, and their population trends could be used as indicators of air pollution levels, acting as 'urban mine-canaries'. Two examples of this are the Cedar Waxwing (*Bombycilla cedrorum*) and the American Robin (*Turdus migratorius*), which fell dead due to the high air pollution levels recorded in Mexico City in 1987 and 2004 (de Anda-Tenorio, 2004). Opposite to such habitat perturbation sensitivity, the House Sparrow, an ubiquitous species in urban systems, survives and reproduces under the most intense levels of urbanization. The presence and abundance of this species in a site indicates some level of disturbance, regardless of the area's apparent good environmental condition (MacGregor-Fors et al. in press B).

The use of entire bird communities for detecting changes in the urban system generally helps on the identification of changes in broad habitat structure (see Chace and Walsh, 2006 and references therein). This approach is helpful when no detailed information is available on the behavior of particular species. However, if precise information of the habitat variables that individual bird species pursue along the studied urban area is available, the presence/absence, arrival, or disappearance of one single species can be quite revealing. Thus, studying the particular biological, physical, and social preferences of urban-exploiter and urban-adaptable bird species throughout urbanization gradients could help us to identify inconspicuous changes in habitat and environmental conditions along urban systems.

Urban systems are quite different from natural habitats, and thus birds could be one of the few charismatic animal groups urban citizens could use to relate to nature. Some urban-exploiter bird species, such as the Rock Pigeon or the House Sparrow, are the only 'wild animals' identified by urban citizens. We believe that having contact with native fauna is relevant for urban people . The contact with several native bird species can increase people's

11

interest on native biodiversity, resulting in citizens that are concerned on the environmental issues of their cities.

6. Planning Towards Healthier Cities

Urban areas are complex systems, and understanding them requires the integration of their biological, physical, sociological, economical, and historical components (Pickett et al., 1997; Nilon et al., 2003). Indeed, urban planners and managers need better information on the factors that can assist in mitigating the negative impacts of urbanization and its processes (Clergeau et al., 2001; MacGregor-Fors, 2008). For this, in this last section we discuss several recommendations to improve urban management and planning activities based on the information generated by urban ornithological studies. Carrying out these actions may increase the ecological complexity of cities, and therefore assist on both the maintenance and promotion of biodiversity within urban areas, as well as improving the ecological quality of the urban areas we live in.

6.1 Controlling Land-Use Changes Within the Region of a City

If we want to live in cities with high biodiversity values and high ecological quality, we need to focus on controlling land-use change at two levels: (1) inside the city limits, preserving the actual green areas and promoting the transformation of 'non-functional' urban 'artificial' spaces into new urban green areas; and (2) outside the city limits, controlling the way in which cities are sprawling. New urbanizing activities should include natural wildland networks that allow the communication between areas surrounding the city and the new urbanized areas.

6.2 Increasing the Ecological Value of Urban Vegetation

Increasing the quality of urban vegetation inside and outside green areas involve both urban management and planning actions. First, native plant species that provide both beautification and environmental resources to support complex wildlife communities need to be evaluated. Plant species should be carefully chosen in order to be coherent with the environmental conditions of the city so as not to appear 'out of place' as in the case of dense and exuberant green areas found in arid urban systems (Grimm et al., 2003), and should need little or null management or resource input throughout their development. Second, existent urban green areas should be managed to increase the complexity of their vegetation structure using the appropriate plant species (Ortega-Álvarez and MacGregor-Fors, in press). Third, when urbanization processes do not consider the conservation of natural habitats, new urban green areas should be established using the evaluated plant species (preferably native ones), including some fast growing species with the aim of having green areas with complex vegetation structure in the short-to mid-term (MacGregor-Fors, 2008). On this point, it is

important to underline the relevance of the size of urban green areas. Based on urban ornithology research that have directly evaluated the effect of the size of parks (e.g., Gavareski, 1976; Jokimäki, 1999; Morneau et al., 1999), we suggest avoiding parks smaller than 1 ha (2.47 acres), and recommend establishing large parks and/or urban preserves from 20 to 100 ha (49.42 to 247.10 acres). These green areas can be established outside the city boundaries, allowing a less damaging and more organized urban growth.

Unfortunately, urban green areas are not evenly distributed throughout cities. In general, wealthy neighborhoods include better ecological conditions than those found in economically poorer areas. In fact, several studies have reported urban ecological differences related to socioeconomics, showing higher plant and native bird diversity values in wealthy neighborhoods (Hope et al., 2003; Kinzig et al., 2005; Melles, 2005). This phenomenon has been related to changes in the basic characteristics of urban habitats due to the 'luxury effect' (term used to describe the relationship between human wealth and elevated plant diversity in urban areas; Hope et al., 2003), deriving in an unfair distribution of urban green areas along socioeconomic urban gradients. Thus, it is imperative that city council plans are developed with the aim of generating even ecological conditions along cities, independent of the socioeconomic status of urban neighborhoods.   This follows the scheme of the 'environmental justice' social movement, which seeks to address the unequal distribution of environmental benefits, and questions whether environmental policies are fair to the people they affect (Bryant and Callewaert, 2003). One way of mitigating the existence of poor ecological conditions among low income neighborhoods is the establishment of 'green areas' by placing native plants in sidewalks, roofs, street ridges, abandoned lots, and other unexploited urban elements and areas.

6.3 Generating Complex Urban Green Networks

Connecting urban green areas can have several ecological and social benefits, such as providing environmental services that compensate the ecological problems created by urbanization and/or the agglomeration of people in small areas, as well as increasing the landscape quality of a city (Ribeiro and Barao, 2006; von Haaren and Reich, 2006 cita). Such networks need to be connected to natural areas surrounding the city, as well as interconnecting the major urban green areas within the city. Following the recommendations of research studies focused on the nature and function of urban greenways (e.g., Schiller and Horn, 1997; Ribeiro and Barao, 2006; Tan, 2006; Mason et al., 2007), we recommend future urban developments to establish major greenways running along rivers, streams, or boulevards that run through major sections of the city. These major greenways should not include large proportions of artificial structures and should have a minimum width of 100 m (following Mason et al., 2007). In order to generate functional urban green networks, other smaller green tracks should connect preexisting urban green areas, such as parks and open spaces, with at least one major greenway. These green tracks should be established by planting native trees and shrubs in gardens and sidewalks, generating 4-20 m paths, depending on the proportion of the green area they connect (following Tan, 2006).

Unfortunately, this last recommendation is only realistic for areas that will be urbanized in the future. Hence, we strongly suggest joining efforts towards generating the widest and longest possible corridors throughout already established cities. These corridors can be

created by connecting sidewalks, street ridges, gardens, open areas, and every other unexploited urban area deprived of trees. Achieving the interconnection of urban green areas along already established cities will not only benefit birds, but could also mitigate the island heat phenomenon caused by urban areas (Ferguson and Woodbury, 2007), which can have serious repercussions on human health (Patz et al., 2005).

6.4 Establishing Standard Protocols to Measure the Ecological Quality of Cities

Each city comprises a unique and complex dynamic system. Therefore, urban management and planning activities should be continuously evaluated in order to measure their effectiveness to improve the ecological quality of a city. We suggest that standard protocols ought to be established in order to evaluate the condition of bird communities, which can reflect a wide range of effects related to site-specific characteristics using both alpha- and beta-diversity approaches (Magurran, 2004). In order to standardize methods and allow further comparisons between cities, we recommend using a simple site-specific surveying method such as point-counts (following Ralph et al., 1993; Ralph et al., 1995), encompassed in a volunteer-based bird monitoring project, such as the Tucson Bird Count (Turner, 2003). Additionally, protocols should also be established to assess the quality of urban habitats using other bio-indicator taxa (e.g., insects, small mammals), and other environmental variables (e.g., water, air, and noise pollution).

6.5 Highlighting the Profits of Having High Ecological Quality Cities in Urban Environmental Education Plans

Although a large amount of scientific research concentrated on urban ecosystems has allowed the comprehension of urban systems, there is a gap between the scientists' perspective and the perspective of city residents (Hollweg et al., 2003). This lack of communication often generates apathy from citizens regarding urban ecosystem management and planning issues. Therefore, education on urban ecosystems can be employed to induce public awarness of urban environmental problems (UNESCO-UNEP, 1976). Establishing education activities that focus on teaching both children and adults to care about the ecosystems they depend on is imperative if we hope to develop new sustainable-thinking societies (Berkowitz et al., 2003; Chawala and Salvadori, 2003; Sprin, 2003). Since birds are highly charismatic, and are one of the few well represented wildlife groups within cities, they provide urban environmental educators with a unique opportunity to establishurban education programs.

Literature Cited

Baker, P. J., Bentley, A. J., Ansell, R. J. & Harris, S. (2005) Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Rev, 35*, 302-312.

Batty, M. (2008) The size, scale, and shape of cities. *Science, 319*, 769-771.

Berkowitz, A. R., Nilon, C. H. & Hollweg, K. S. (2003) The importance of understanding urban ecosystems: Themes. In A. R. Berkowitz, C. H. Nilon & K. S. Hollweg (Eds.), *Understanding urban ecosystems - A new frontier for science and education* (pp. 15-17). New York: Springer-Verlag.

Blair, R. B. (1996) Land use and avian species diversity along an urban gradient. *Ecol Appl, 6*, 506-519.

Blair, R. B. (2004) The effects of urban sprawl on birds at multiple levels of biological organization. *Ecol Soc, 9*, (5):2.

Bradshaw, A. D. (2003) Natural ecosystems in cities: A model for cities as ecosystems. In A. R. Berkowitz, C. H. Nilon & K. S. Hollweg (Eds.), *Understanding urban ecosystems - A new frontier for science and education* (pp. 77-94). New York: Springer-Verlag.

Bryant, B. & Callewaert, J. (2003) Why is understanding urban ecosystems important to people concerned about environmental justice? In A. R. Berkowitz, C. H. Nilon & K. S. Hollweg (Eds.), *Understanding urban ecosystems - A new frontier for science and education* (pp. 46-57). New York: Springer-Verlag.

Cappon, D. (1977) Urban stress. *Canadian Medical Association Journal, 116*, 9-10.

Chace, J. F. & Walsh, J. J. (2006) Urban effects on native avifauna: a review. *Landscape Urban Plann, 74*, 46-69.

Chawala, L. & Salvadori, I. (2003) Children for cities and cities for children: Learning to know and care about urban ecosystems. In A. R. Berkowitz, C. H. Nilon & K. S. Hollweg (Eds.), *Understanding urban ecosystems - A new frontier for science and education* (pp. 294-314). New York: Springer-Verlag.

Clergeau, P., Jokimäki, J. & Savard, J. P. L. (2001) Are urban bird communities influenced by the bird diversity of adjacent landscapes? *J Appl Ecol, 38*, 1122-1134.

Clergeau, P., Savard, J. P. L., Mennechez, G. & Falardeau, G. (1998) Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. *Condor, 100*, 413-425.

Collins, J. P., Kinzig, A., Grimm, N. B., Fagan, W. F., Hope, D., Wu, J. et al. (2000) A new urban ecology. *Am Sci, 88*, 416-425.

Crooks, K. R., Suarez, A. V. & Bolger, D. T. (2004) Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biol Conserv, 115*, 451-462.

Daniels, G. & Kirkpatrick, J. (2006) Does variation in garden characteristics influence the conservation of birds in suburbia? *Biol Conserv, 133*, 326-335.

de Anda-Tenorio, A. (2004) Las aves y la contaminación en la Ciudad de México. *La Jornada (Newspaper), March 1st*, La Jornada Ecológica.

DeGraff, R. M. & Wentworth, J. M. (1986) Avian guild structure and habitat associations in suburban bird communities. *Urban Ecol, 9*, 399-412.

Dhondt, A. A., Tessaglia, D. L. & Slothower, R. L. (1998) Epidemic mycoplasmal conjuntivitis in House Finches from Eastern North America. *J Wildl Dis, 43*, 265-280.

Eeva, T., Lehikoinen, E. & Rönkä, M. (1998) Air pollution fades the plumage of the Great Tit. *Funct Ecol, 12*, 607-612.

Emlen, J. T. (1974) An urban bird community in Tucson, Arizona: derivation, structure, regulation. *Condor, 76*, 184-197.

Ferguson, G. & Woodbury, A. D. (2007) Urban heat island in the subsurface. *Geophys Res Lett, 34*, L23713.

Fernández-Juricic, E., Jimenez, M. D. & Lucas, E. (2001) Bird tolerance to human disturbance in urban parks of Madrid (Spain): Management implications. In J. M. Marzluff, R. Bowman & R. Donnely (Eds.), *Avian conservation and ecology in an urbanizing world* (pp. 259-273). Boston, MA.: Kluwer Academic.

Fernández-Juricic, E. & Jokimäki, J. (2001) A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodivers Conserv, 10*, 2023-2043.

Fuller, R. A., Warren, P. H., Armstrong, P. R., Barbosa, O. & Gaston, K. J. (2008) Garden bird feeding predicts the structure of urban avian assemblages. *Divers Distrib, 14*, 131-137.

Furuseth, O. J. & Altman, R. E. (1991) Who's on the greenway: Socioeconomic, demographic, and locational characteristics of the greenway users. *Environm Manage, 15*, 329-336.

Gaston, K. J., Fuller, R. A., Loram, A., MacDonald, C., Power, S. & Dempsey, N. (2007) Urban domestic gardens (XI): variation in urban wildlife
 gardening in the United Kingdom
. *Biodivers Conserv, 16*, 3227-3238.

Gavareski, C. A. (1976) Relation of park size and vegetation to urban bird populations in Seattle, Washington. *Condor, 78*, 375-382.

Gidlöf-Gunnarsson, A. & Öhrström, E. (2007) Noise and well-being in urban residential environments: The potential role of perceived availability to nearby green areas. *Landscape Urban Plann, 83*, 115-126.

Grimm, N. B., Baker, L. J. & Hope, D. (2003) An ecosystem approach to understanding cities: Familiar foundations and uncharted frontiers. In A. R. Berkowitz, C. H. Nilon & K. S. Hollweg (Eds.), *Understanding urban ecosystems - A new frontier for science and education* (pp. 95-114). New York: Springer-Verlag.

Hahs, A. K. & McDonnell, M. J. (2006) Selecting independent measures to quantify Melbourne's urban–rural gradient. *Landscape Urban Plann, 78*, 435-448.

Hollweg, K. S., Berkowitz, A. R. & Nilon, C. H. (2003) Foundations and frontiers from education theory and practice: Themes. In A. R. Berkowitz, C. H. Nilon & K. S. Hollweg (Eds.), *Understanding urban ecosystems - A new frontier for science and education* (pp. 229-231). New York: Spriger-Verlag.

Hope, D., Gries, C., Zhu, W., Fagan, W. F., Redman, C. L., Grimm, N. B. et al. (2003) Socioeconomics drive urban plant diversity. *PNAS, 100*, 8788-8792.

Johnsen, A. M. & VanDruff, L. W. (1987) Spring and winter distribution of introduced bird species and native bird species richness within a complex urban environment. In L. W. Adams & D. L. Leedy (Eds.), *Integrating man and nature in the metropolitan environment* (pp. 123-127). Columbia, MD.: National Institute of Urban Wildlife.

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. & Suhonen, J. (1998) Distribution and habitat selection of wintering birds in urban environments. *Landscape Urban Plann, 39*, 253-263.

Kark, S., Iwaniuk, A., Schalimtzec, A. & Banker, E. (2007) Living in the city: Can anyone become an "urban exploiter"? *J Biogeogr, 34*, 638-651.

Kinzig, A. P., Warren, P. S., Martin, C., Hope, D. & Katti, M. (2005) The effects of human socioeconomic status and cultural characteristics on urban patterns of biodiversity. *Ecol Soc, 10*, 23.

Kristan, W. B., Lyman, A. J., Price, M. V. & Rotenberry, J. T. (2003) Alternative causes of edge-abundance relationships in birds and small mammals of California coastal sage scrub. *Ecography, 26*, 29-44.

Lim, H. C. & Sodhi, N. S. (2004) Responses of avian guilds to urbanisation in a tropical city. *Landscape Urban Plann, 66*, 199-215.

López-Flores, V., MacGregor-Fors, I. & Schondube, J (In press) Artificial nest predation along a Neotropical urbanization gradient. *Landscape Urban Plann.*

Magurran, A. E. (2004) *Measuring Biological Diversity.* Oxford, UK: Blackwell Publishing.

MacGregor-Fors, I. (2008) Relation between habitat attributes and bird richness in a western Mexico suburb. *Landscape Urban Plann, 84*, 92-98.

MacGregor-Fors, I., Morales-Pérez, L. & Schondube, J. E. (In press A) From forests to cities: Effects of urbanization on subtropical mountain bird communities. *Studies in Avian Biology.,*

MacGregor-Fors, I., Morales-Pérez, L., Quesada, J. & Schondube, J. E. (In press B) Relationship between the presence of House Sparrows (Passer domesticus) and Neotropical bird community structure and diversity. *Biol Invasions.*

Martinuzzi, S., Gould, W. A. & Ramos González, O. M. (2007) Land development, land use, and urban sprawl in Puerto Rico integrating remote sensing and population census data. *Landscape Urban Plann, 79*, 288-297.

Marzluff, J. M., Bowman, R. & Donnely, R. (2001a) *Avian conservation and ecology in an urbanizing world.* Boston, MA.: Kluwer Academic.

Marzluff, J. M., Bowman, R. & Donnely, R. (2001b) A historical perspective on urban bird research: Trends, terms, and approaches. In J. M. Marzluff, R. Bowman & R. Donnely (Eds.), *Avian conservation and ecology in an urbanizing world* (pp. 1-17). Boston, MA.: Kluwer Academic.

Marzluff, J. M. & Ewing, K. (2001) Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. *Restor Ecol, 9*, 280-292.

Mason, J., Moorman, C., Hess, G. & Sinclair, K. (2007) Designing suburban greenways to provide habitat for forest-breeding birds. *Landscape Urban Plann, 80*, 153-164.

Matthews, A., Dickman, C. R. & Major, R. E. (1999) The influence of fragment size and edge on nest predation in urban bushland. *Ecography, 22*, 349-356.

McKinney, M. L. (2002) Urbanization, biodiversity and conservation. *BioScience, 52*, 883-890.

McKinney, M. L. (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv, 127*, 247-260.

McKinney, M. L. (2008) Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst, 11*, 161-176.

Melles, S., Glenn, S. & Martin, K. (2003) Urban bird diversity and landscape complexity: Species–environment associations along a multiscale habitat gradient. *Conserv Ecol, 7*, (1):5.

Melles, S. J. (2005) Urban bird diversity as an indicator of human social diversity and economic inequality in Vancouver, British Columbia. *Urban Hab, 3*, 25-48.

17

Miller, J. R., Fraterrigo, J. M., Hobbs, N. T., Theobald, D. N. & Wiens, J. A. (2001) Urbanization, avian communities, and landscape ecology. In J. M. Marzluff, R. Bowman & R. Donnely (Eds.), *Avian conservation and ecology in an urbanizing world* (pp. 117-137). Boston, MA.: Kluwer Academic.

Mills, G. S., Dunning, J. B. & Bates, J. M. (1989) Effects of urbanization on breeding bird community structure in Southwestern desert habitats. *Condor, 91*, 416-428.

Moll, G. (1997) America's urban forests: Growing concerns. *Am Forests, 103*, 14-18.

Morneau, F., Decarie, R., Pelletier, R., Lambert, D., DesGranges, J. L. & Savard, J. P. L. (1999) Changes in breeding bird richness and abundance in Montreal parks over a period of 15 years. *Landscape Urban Plann, 44*, 111-121.

Mörtberg, U. M. (2001) Resident bird species in urban forest remnants; landscape and habitat perspectives. *Landscape Ecol, 16*, 193-203.

Munyenyembe, F., Harris, J. & Hone, J. (1989) Determinants of bird populations in an urban area. *Aust J Ecol, 14*, 549-557.

Nilon, C. H., Berkowitz, A. R. & Hollweg, K. S. (2003) Introduction: Ecosystem understanding is a key to understanding cities. In A. R. Berkowitz, C. H. Nilon & K. S. Hollweg (Eds.), *Understanding urban ecosystems - A new frontier for science and education* (pp. 1-14). New York: Springer-Verlag.

Ortega-Álvarez, M., & MacGregor-Fors, I. (In press) Living in the big city: Effects of urban land-use on bird community structure, diversity, and composition. *Landscape Urban Plann.*

Parsons, H., Major, R. & French, K. (2006) Species interactions and habitat associations of birds inhabiting urban areas of Sydney, Australia. *Austral Ecol, 31*, 217-227.

Partecke, J., Schwabl, I. & Gwinner, E. (2006) Stress and the city: Urbanization and its effects on the stress physiology in European Blackbirds. *Ecology, 87*, 1945-1952.

Patz, J. A., Campbell-Lendrum, D., Holloway, T. & Foley, J. A. (2005) Impact of regional climate change on human health. *Nature, 438*, 310-317.

Pickett, S. T. A., Burch, W. R., Dalton, S., Foresman, T., Morgan, J. & Rowntree, R. (1997) A conceptual framework for the study of human ecosystems in urban areas. *Urban Ecosyst, 1*, 185-199.

Ralph, C. J., Droege, S. & Sauer, J. R. (1995) *Managing and monitoring birds using point counts: Standards and applications*. Albany, CA: USDA.

Ralph, C. J., Geupel, G. R., Pyle, P., Martin, T. E. & DeSante, D. F. (1993) *Handbook of field methods for monitoring landbirds*. Albany, CA: USDA.

Ribeiro, L. & Barao, T. (2006) Greenways for recreation and maintenance of landscape quality: Five case studies in Portugal. *Landscape Urban Plann, 76*, 79-97.

Rosenberg, K. V., Terrill, S. B. & Rosenberg, G. H. (1987) Value of suburban habitats to desert riparian birds. *Wilson Bull, 99*, 642-654.

Sacchi, R., Gentilli, A., Razzetti, E. & Barbieri, F. (2002) Effects of building features on density and flock distribution of feral pigeons *Columba livia* var. *domestica* in an urban environment. *Can J Zool, 80*, 48-54.

Sandström, U. G., Angelstam, P. & Mikusinski, G. (2006) Ecological diversity of birds in relation to the structure of urban green space. *Landscape Urban Plann, 77*, 39-53.

Schiller, A. & Horn, S. P. (1997) Wildlife conservation in urban greenways of the mid-southern United States. *Urban Ecosyst, 1,* 103-116.

Shaw, L. M., Chamberlain, D. & Evans, M. (2008) The House Sparrow *Passer domesticus* in urban areas: reviewing a possible link between post-decline 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.

Shwartz, A., Shirley, S. & Kark, S. (2008) How do habitat variability and management regime shape the spatial heterogeneity of birds within a large Mediterranean urban park? *Landscape Urban Plann, 84*, 219-229.

Simon, U., Kübler, S. & Böhner, J. (2007) Analysis of breeding bird communities along an urban-rural gradient in Berlin, Germany, by Hasse Diagram Technique. *Urban Ecosyst, 10*, 17-28.

Slabbekoorn, H. & Peet, M. (2003) Birds sing at a higher pitch in urban noise. *Nature, 424*, 267.

Smith, R. M., Warren, P. H., Thompson, K. & Gaston, K. J. (2006) Urban domestic gardens (VI): environmental

 correlates of invertebrate species richness

. *Biodivers Conserv, 15*, 2415-2438.

Sprin, A. W. (2003) Urban ecosystems, city planning, and environmental education: Literature, precedents, key concepts, and prospects. In A. R. Berkowitz, C. H. Nilon & K. S. Hollweg (Eds.), *Understanding urban ecosystems - A new frontier for science and education* (pp. 201-212). New York: Springer-Verlag.

Tan, K. W. (2006) A greenway network for Singapore. *Landscape Urban Plann, 76*, 45-66.

Turner, W. R. (2003) Citywide biological monitoring as a tool for ecology and conservation in urban landscapes: The case of the Tucson Bird Count. *Landscape Urban Plann, 65*, 149-166.

Turner, W. R., Nakamura, T. & Dinetti, M. (2004) Global urbanization and the separation of human from nature. *BioScience, 54*, 585-590.

(ISGS) United States Geological Survey (2007) *Fact sheet: Coping with diseases at bird feeders*. Denver, CO.: U.S. Geological Survey - National Wildlife Health Center.

(UNESCO-UNEP) United Nations Educational, Scientific and Cultural Organization – United Nations Environment Programme (1976) The Belgrad Charter - A Global Framework for Environmental Education. *Environmental Education Newsletter, 1*, 1-2.

Valiela, I. & Martinetto, P. (2007) Changes in bird abundance in Eastern North America: Urban sprawl and global footprint? *BioScience, 57*, 360-370.

von Haaren, K. & Reich, M. (2006) The German way to greenways and habitat networks. *Landscape Urban Plann, 76*, 7-22.

Woods, M. E., McDonald, R. A. & Harris, S. (2003) Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Rev, 33*, 174-188.

(WHO) World Health Organization (2000) *Addressing the links between Indoor air pollution, household energy and human health*. Washington, D.C.: World Health Organization.

Wu, C., Maurer, C., Wang, Y., Xue, S. & Davis, D. L. (1999) Water pollution and human health in China. *Environ Health Persp, 107*, 251-256.

Bird community responses to the establishment of small and medium-sized human settlements

Introduction

Urbanization and its processes cause dramatic environmental changes at multiple scales, including shifts in land-cover, the alteration of biogeochemical cycles, climate change, and the introduction of exotic species (Acevedo et al. 1999, Andersson 2006, Chace & Walsh 2006, Gratani & Varone 2007). Because urban habitats are quite different from natural ones, the establishment of urban systems limits the number and type of wildlife species that can colonize them (Marzluff et al. 2001, McKinney 2008). While some bird species are able to invade and survive within urban environments, these areas tend to comprise poorer bird communities when compared to natural habitats. Also, these communities are commonly dominated by a few, very abundant, generalist and opportunistic species (McKinney 2002, Faeth et al. 2005, Chace & Walsh 2006).

Shifts in bird diversity values following urbanization have been associated with various factors, including the change and homogenization of habitat attributes, the intensity of urbanization, and the establishment of opportunistic urban exploiter bird species (Emlen 1974, Gavareski 1976, Grussing 1980, Beissinger & Osborne 1982, Blair 1996, Melles et al. 2003, Chace & Walsh 2006). The size and shape of urban settlements can also affect the connectivity of the surrounding natural habitats (Bierwagen 2007), having an impact on the dynamics of species gains and losses at the landscape level (Marzluff 2005).

Urban bird ecology studies have, in part, concentrated on the measurement of differences between types of urbanized areas (*e.g.,* urban and rural; Yaukey 1996, Danielson et al. 1997, Clergeau et al. 1998, Simon et al. 2007). However, the effects that small to medium-sized human settlements have on bird communities remain unclear. In this study we evaluated how birds respond to three small to medium-sized human settlements using bird communities from pristine tropical dry forest as a control for comparisons. The three urbanization conditions included in this study comprise: (1) a small-sized "miniature city" surrounded by pristine continuous forest; (2) a small-sized human settlement surrounded by forest and abandoned agriculture plots; and (3) a medium-sized human settlement embedded in an agricultural matrix. We expected that urbanization in the three studied urban areas would represent a limitation for bird species richness, bird densities to be lowest in the settlement surrounded by pristine forests, and bird composition to differ among settlements in relation to their surrounding habitats.

Methods

Study area

This study was conducted on the Pacific coast of Jalisco, western Mexico, in the region of the Chamela-Cuixmala Biosphere Reserve and surrounding human settlements (19°30'N, 105°03'W to 19°23'N 105°58'W; Fig. 1). This region is characterized by a well-defined seasonality with a marked dry season from October to June (García-Oliva et al. 2002). Natural habitats within the Chamela-Cuixmala Biosphere Reserve comprise tropical dry deciduous and semi-deciduous forests (Noguera et al. 2002). However, land outside of the reserve zone is rapidly being transformed into cropfields, cattle pastures, and urban settlements (Durán et al. 2002, Noguera et al. 2002).

Bird surveys were carried out in small and medium-sized human settlements within the biome of tropical dry forest along the coast. A small human settlement was represented by the Estación de Biología Chamela (referred to as Biology Station hereafter), which is located on a small hill (80-100 m elevation) within pristine continuous tropical deciduous of the Chamela-Cuixmala Biosphere Reserve. The forest located inside the Biology Station is considered pristine because it has not been modified by human productive activities, being one of the few protected old-growth tropical dry forests remaining in the world (Noguera et al. 2002, Vega-Rivera 2007). The area of the Biology Station buildings is a peculiar urbanized area that does not fit to any of the categories proposed by Marzluff et al. (2001). Although it could be considered as an ex-urban site (*sensu* Marzluff et al. 2001) because it is completely surrounded by forest, however it has higher building density, and often surpasses the human density value given to ex-urban areas. The Biology Station is a highly developed small urbanized site (0.8 ha) with an average population of 10 residents, comprised of a couple of two-story dormitories, administrative offices, two laboratories, a library/museum, a large dinning room, a laundry room, workshops, a water tower, a volleyball court, and a one lane access paved road that leads to a central parking lot. This site offers a unique opportunity to evaluate the effects of a small human settlement on bird communities within the context of a pristine natural habitat.

We also surveyed two other larger human settlements outside the reserve, Careyes and Zapata, which were classified as rural *sensu* Marzluff et al. (2001). Careyes is a small-sized rural settlement (7.5 ha – 50 inhabitants; INEGI 2005) comprised by medium to high-income homesteads with large gardens, cobblestone streets, a medical clinic, and a soccer field. The settlement occurs in a small valley at 10-20 m elevation, along the Careyes stream, and surrounded by few abandoned cropfields and tropical deciduous forest on the hills to the North and South, with tropical semi-deciduous forest of the Careyes stream on the eastern edge, and the Federal Highway 200 on the western edge. Zapata is a medium-sized rural settlement (40 ha – 2,025 inhabitants; INEGI 2005), comprised by low-income homesteads, family orchards (traditional backyards), family owned grocery stores, unpaved streets, and a school. The settlement is surrounded by agricultural fields in a low-lying valley (10-20 m elevation) which would originally have comprised tropical semi-deciduous forest. While the human density of Zapata is larger than that defined by Marzluff et al. (2001) for a rural settlement, its socio-economic level, infrastructure and building characteristics are the average of rural areas throughout Mexico (urban settlements partially devoid of sewers and water pipes, mainly comprised by houses made of wood or bricks, mostly unfinished). The three human settlements considered in this study were established between 1960s and 1970s (Castillo et al. 2005), and have similar urbanization intensities.
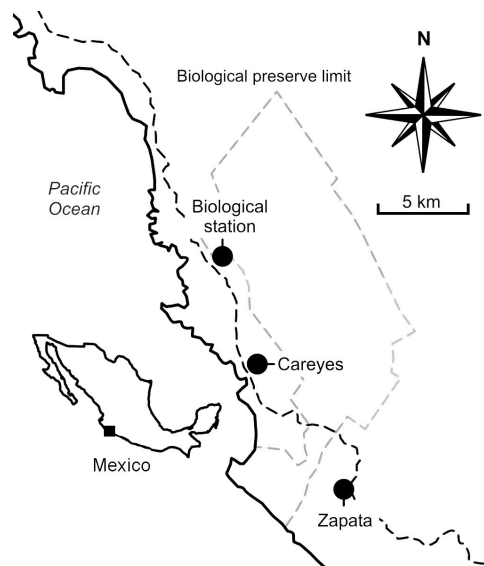
Figure 1. Map of study area.

Bird surveys

We surveyed resident and summer visitor bird communities during April and May 2008 from 07:00 to 10:00 hrs. We survey bird communities using limited 25 m-radius point-counts to maintain an identical sampled area per point count, and to ensure that all birds recorded were actively using the surveyed area and not in a different habitat attribute nearby. Point-counts were separated by a minimum distance of 200 m to maintain survey independence (Ralph et al. 1993, Bibby 2000). A 5-min count period was conducted at each point, recording all birds seen or heard (Ralph et al. 1993). We used a rangefinder (Bushnell Yardage Pro) to measure the distance from the observer to every bird detected within the limited-radius point-counts. We performed a total of 41 independent point-counts. Because of its size, only one 25 m radius point-count could be established within the area of the Biology Station buildings. Given that the settlement characteristics of the Biology Station are unique in the region, it was not possible to replicate this condition. Therefore, we sampled the area of the Biology Station buildings on 20 different days to determine the variation of its bird community. Because the data derived from these surveys are not independent, we consider them as a single data point that robustly describes the bird community of this area in the surveyed space and time.

To determine whether the effects of urbanization of the Biology Station were restricted to the buildings area, or had a gradual effect within the surrounding conserved tropical deciduous forest, we performed 10 independent point-counts at each distance of 200 m and 400 m radiating out from the building area in different directions. We carried out a further 10 independent point-counts at each of the two medium-sized urban settlements of Careyes and Zapata. At the both forest conditions and Careyes and Zapata, we located point-counts at a minimum distance of 200 m from each other to maintain survey independence (Ralph et al. 1993, Bibby 2000). We compared bird communities from the total point counts carried out in Careyes and Zapata with 10 randomly selected point counts performed at each forest condition (200m and 400m from the Biology Station). Also, we compared both the urbanized and forest sites with 10 of the 20 repetitions carried out in the Biology Station.

Data analysis

To determine whether our survey effort was sufficient to record a representative sample of the bird communities in the studied conditions, we computed an abundance-based coverage estimator (ACE; Chao & Lee 1992) using SPADE (Chao & Shen 2006). For this, we compared the mean predicted species from ACE with the total observed species at each condition. We also compared the upper bound confidence interval of the species prediction (ACE) for all surveyed conditions with the total non-aquatic summer migrant and resident species included in the bird-list of the Chamela region (Arizmendi et al. 1990).

To compare bird species richness values, we computed the mean number of predicted species and 95% confidence intervals using ACE for the forest and human settlement conditions surveyed in this study, using the suggested cut-off point of 10 individuals (Chao et al. 1993). In order to contrast bird species richness values among the surveyed conditions, we used the statistical expectation (mean ± 95% confidence intervals) of ACE, an abundance based coverage estimator. ACE uses the coefficient of variance of a sub-sample of rare species, determined by a cut-off point, to characterize the degree of heterogeneity among species discovery probabilities, and afterwards estimates the number of missing species in the sample (Chao & Shen 2006). Thus, the data provided by this expectation is independent of the sampling area size and/or sampling effort, and allows robust comparisons of the species richness values of different conditions/treatments as long as the sampling effort includes a proportional distribution of rare species within the sample (Chao & Lee 1992). While we sampled only one point-count in the Biology Station buildings, our continuous sampling provided us with a good estimation of the proportion of common and rare species in the area, allowing us to use this estimator.

To calculate bird densities, we computed individuals/ha (mean ± 95% confidence intervals) using Distance 5.0 (Thomas et al. 2005). This software calculates the probability of detection of individuals at increasing distances from the observer and estimates the number of bird individuals that exist within a surveyed area (Buckland et al. 2001). We computed bird densities for the entire bird community because Distance 5.0 estimates the number of bird individuals that exist within a surveyed area by calculating the probability of detection of individuals, and standardizing the number of detections along the concentric distances of observations (Buckland et al. 2004). This software can pool species to avoid biases resultant from differences in detection probabilities among species (Buckland et al. 2004), which could both over- or under-estimate due to the commonness/rarity of species and their differences in detection rates (Alldredge et al. 2007). We report the effective detection radius (EDR), Akaike's information criterion (AIC), and key function/series expansion (KF/SE) to describe the coverage of our surveys and the nature of the methods used by the program to calculate bird densities. To determine if species richness and bird density values were statistically different among the surveyed forest and human settlement conditions, we compared their 95% confidence intervals. If confidence intervals did not overlap, we considered the data to be statistically different with an $\alpha < 0.01$ (following Payton et al. 2003; M. Payton pers. comm.). Because we have only one point to represent the Biology Station building area, we compared this data point with the 95% confidence intervals to the rest of the studied conditions. Since we sampled one site in the Biology Station building area several times, we have a good description of that single point, but we cannot ensure that the characteristics of the bird community described for that site are the result of urbanization, or site-specific conditions. However, we do have a minimum of 10 independent points for the rest of the

studied conditions (i.e., TDF 400 m, TDF 200 m, Careyes, Zapata). Thus, in order to strengthen the analysis of our results, we first compared the urbanized conditions for which we have 10 independent replicates (i.e., Careyes, Zapata) and the forest conditions (i.e., TDF 400 m, TDF 200 m), and drew inferences from these comparisons. We contrasted the value for the one surveyed point at the Biology Station Buildings with our other findings. Finally, to evaluate if the size of the studied urban settlements affected their bird species richness, we conducted a Spearman rank correlation.

To evaluate shifts in bird community composition among the surveyed pristine continuous forest locations and human settlements, we computed an abundance based Bray-Curtis cluster analysis using BiodiversityPro (McAleece 1997), and calculated a species turnover index (β_{sim}; Lennon et al. 2001). This index calculates the relative magnitude of species gains and losses in relation to the sample with the lowest unique species, revealing whether the low number of species is due to a shift in its species composition or simply due to the loss of species in relation to the sample with the more unique species (Koleff et al. 2003, Gaston et al. 2007). To compare the structure (dominance/evenness) of bird communities recorded at the different studied conditions, we used species rank/abundance plots (Whittaker plots; Magurran 2004). We compared the slopes of the species rank/abundance plots using ANCOVA to contrast the dominance/evenness of the bird communities at different conditions, and to test whether the proportion of dominant and rare species were significantly different between conditions. As recommended by Magurran (2004), abundance data were log transformed ($\log_{10}$). Each rank/abundance regression summarizes the abundance distribution of each studied bird community, and represents a single independent value.

Finally, to describe the functional responses of local bird communities regarding their use of urban systems, we classified the recorded bird species based on their densities following Blair's (1996) categories: (1) urban exploiters – species found only in human settlements; (2) urban adapters – species found in both human settlements and forest conditions; and (3) urban avoiders – species found only in forest conditions.

Results

The proportion of recorded species in relation to the ACE mean predicted value was >73% in all cases, being highest in the Biology Station buildings (91%) and lowest in Careyes (73%). This indicates that our sampling effort was enough to record a representative sample of the local species that inhabited our study conditions at the surveyed space and time (Appendix 1). The estimations of the ACE, based on our entire data set, predicted a maximum of 121 non-aquatic summer migrant and resident bird species for the studied conditions. This represents 77% of the 157 non-aquatic summer migrant and resident bird species reported in the last three decades for the Chamela region (Arizmendi et al. 1990, J. H. Vega-Rivera pers. comm.).

Predictions from the ACE demonstrate that, independently of their size, all three human settlements of the Biology Station, Careyes and Zapata had significantly lower bird species richness than both the conserved tropical dry forest conditions of 200 m and 400 m (Fig. 2). The statistical expectation for species richness in the Biology Station buildings did not differ from those of Careyes and Zapata. Furthermore, bird species richness differed for pristine tropical dry forest at increasing distances from the Biology Station (Fig. 2). Values recorded in pristine continuous forests were two to three times

higher at a distance of 400 m (52.6 ± 5.4 predicted species) and 200 m (40.5 ± 4.7 predicted species), than those recorded at Careyes (19.1 ± 5.3 predicted species), Zapata (17.6 ± 2.8 species), and the Biology Station (17.5 ± 1.9 predicted species). Tropical dry forest 400 m away from the Biology Station buildings had the highest bird species richness, which was statistically different from tropical dry forest at 200 m. Mean predicted bird species richness was not related to the size of the studied urban conditions ($r = 0.5$, $P = 0.66$).
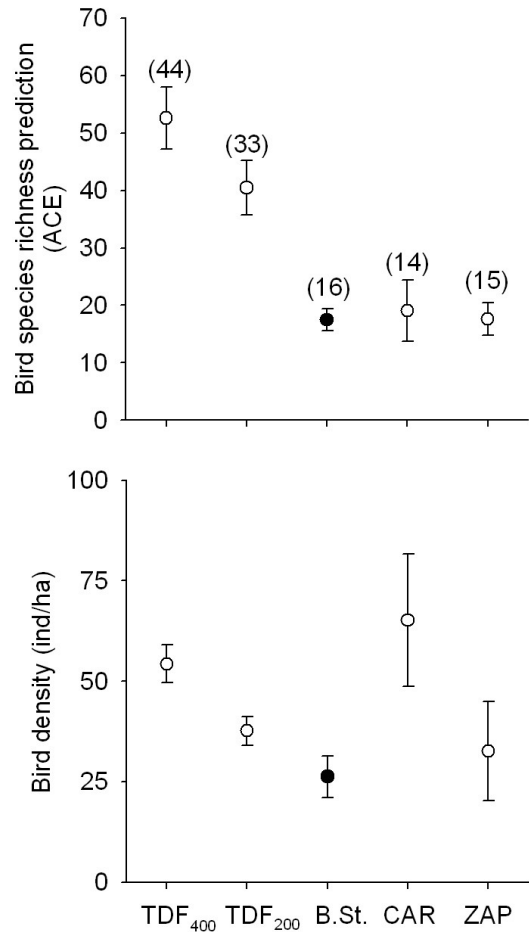

Figure 2. Bird community species richness values from the abundance-based coverage estimator (ACE) for the studied forest and human settlement conditions. Values in parenthesis represent the observed number of species per site. Our results show that, independently of their size, all three human settlements had bird communities with lower species richness than those from the forest conditions. Bird densities followed a different pattern, where a linear negative effect was recorded among both tropical dry forests conditions and the Biology Station buildings. However, bird densities showed to be statistically higher in Careyes when compared to the other two urbanized conditions. Data points represent computed means ± 95% confidence intervals.

Bird density values also differed among the surveyed conditions, and presented a linear negative effect among the two pristine tropical dry forests distances and the Biology Station buildings (Fig. 2). Bird density was significantly higher in tropical dry forest at 400 m from the Biology Station (54.3 ± 4.7 ind/ha; AIC = 1684.4, EDR = 26 m, KF/SE = Uniform/Polynomial) compared to tropical dry forest at 200 m (37.7 ± 3.7 ind/ha; AIC = 1231.4, EDR = 25.7 m, KF/SE = Hazard-rate/Coisine), and was

lowest at the Biology Station (26.3 ± 5.7 ind/ha; AIC = 449.9, EDR = 25 m, KF/SE = Uniform/Polynomial). Bird density was also significantly higher in Careyes (65.2 ± 16.5 ind/ha; AIC = 513.3, EDR = 25 m, KF/SE = Uniform/Hermite) compared to Zapata (32.6 ± 12.3 ind/ha; AIC = 315.1, EDR = 25 m, KF/SE = Uniform/Polynomial; Fig. 2). Bird density at the Biology Station was similar to that recorded for Zapata, but significantly lower than bird densities at Careyes (Fig. 2).
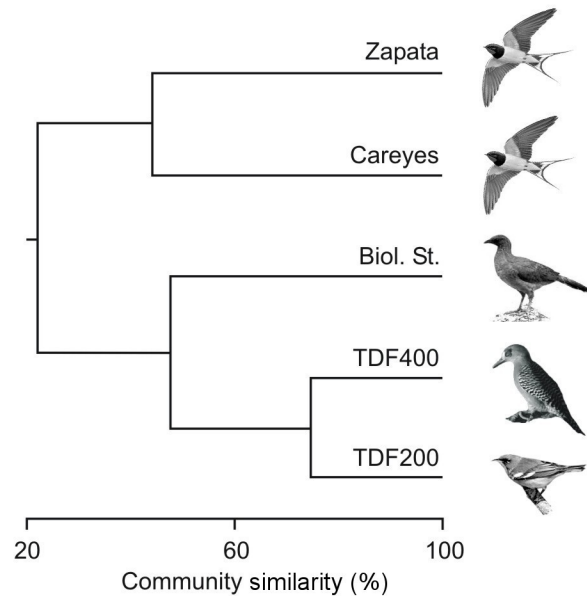

Figure 3. Bray-Curtis multivariate cluster analysis showing the % similarity among bird communities from the studied forest and human settlement conditions. This dendrogram shows that bird communities from the three conditions located within the biosphere reserve are more similar among them than in relation to those from Careyes and Zapata, located outside the biosphere reserve. Bird illustrations depict the most abundant species in each one of the studied conditions.

The abundance-based Bray-Curtis multivariate cluster analysis showed that the two distances of tropical dry forest shared the highest proportion of bird species (76% similarity; Fig. 3). Bird communities from the three studied conditions within the biosphere reserve (i.e., TDFs 400 m, TDFs 200 m, Biology Station buildings) were more alike, being clustered at 49% similarity, than those from human settlements located outside the biosphere reserve (Fig. 3). Bird communities from Careyes and Zapata formed another cluster, at 45% similarity. The difference between the two main clusters was high, showing only 22% similarity (Fig. 3). These results were consistent with β_{sim} species turnover rates. This index revealed that the proportion of shared species between Careyes and Zapata differed 35%, while the Biology Station building area was very different in relation to the other studied human settlements (Table 1). Bird community species turnover between the Biology Station and both distances of pristine forest was very low (< 0.06 dissimilarity), showing that most species recorded at the Biology Station are forest-dwelling species (Table 1).

26

Table 1. Species turnover values (β_{sim}) for the surveyed forest and
human settlement conditions.

	TDF 400m	TDF 200m	Biol. St.	Careyes
TDF 400m	-			
TDF 200m	0.14	-		
Biol. St.	0.0	0.06	-	
Careyes	0.25	0.64	0.71	-
Zapata	0.40	0.46	0.60	0.35

Slopes from the rank/abundance plots differed among forest and human settlements, revealing the existence of a gradient of bird communities with different levels of dominance. When the two distances of pristine continuous forests where compared, no differences where found between their slopes ($F_{1,74} = 0.69$, $P = 0.40$; Fig. 4). However, both forest conditions had bird communities that were less dominated compared to Careyes (TDFs 400 m: $F_{1,54} = 25.39$, $P < 0.001$; TDFs 200 m: $F_{1,44} = 23.91$, $P < 0.001$; Fig. 4). The dominance/evenness slope of the avian community recorded in Careyes differed from that of Zapata ($F_{1,25} = 12.92$, $P = 0.001$; Fig. 4). Although the dominance/evenness slope of the bird communities recorded at Zapata were not different from those of both forest conditions (TDFs 400 m: $F_{1,55} = 0.66$, $P = 0.41$; TDFs 200 m: $F_{1,45} = 0.30$, $P = 0.58$), their intercepts differed significantly (TDFs 400 m: $F_{1,55} = 70.31$, $P < 0.001$; TDFs 200 m: $F_{1,45} = 46.97$, $P < 0.001$). This indicates that although the evenness of the bird communities of Zapata is high, its bird community is comprised by few individuals pertaining to few species. The dominance/evenness slope of the bird community recorded at the Biology Station buildings did not differ with that of Zapata ($F_{1,27} = 3.41$, $P = 0.07$), but differed significantly from the other studied conditions (TDFs 400 m: $F_{1,56} = 6.94$, $P = 0.01$; TDFs 200 m: $F_{1,46} = 6.07$, $P = 0.01$; Careyes: $F_{1,26} = 6.58$, $P = 0.01$; Fig. 4).

Discussion

This study provides evidence of the effects that small and medium-sized human settlements can have on bird communities. Our results show that bird species richness decreases significantly when an area becomes urbanized, and suggests that for small and medium size human settlements (0.8- 40 ha) this effect could be independent of their size. The loss of bird species richness related to urbanization has been reported in previous urban ecology studies that have evaluated the effect of larger human settlements on bird communities (see Chace & Walsh 2006, Evans et al. 2009, MacGregor-Fors et al. 2009 and references therein). These studies have shown that the impoverishment of bird communities due to urbanization is related to: (1) shifts in habitat structure and composition (Jökimaki & Suhonen 1998, Green & Baker 2003, MacGregor-Fors 2008); (2) human activity (Blair 1996, Fernández-Juricic et al. 2001, Ortega-Álvarez & MacGregor-Fors 2009); (3) the invasion of urban habitats by urban exploiter species (Shochat 2004, MacGregor-Fors et al. 2010); (4) greater habitat fragmentation found in urban areas (Marzluff 2005); and (5) potential changes in predation risk (Evans 2004, López-Flores et al. 2009). However little is known on the relative role of these factors.

In our study, the human settlements of Careyes, Zapata and the Biology Station had significantly lower species richness than the two distances of conserved tropical dry forest. The Biology Station is totally surrounded by pristine continuous forest, lacks off-leash cats and dogs, and does not include urban exploiter bird species. Hence, our results suggest that habitat modification *per se* plays a crucial

role in the loss of bird species related to urbanization. Furthermore, the effect of habitat modification by urbanization seems to be exacerbated by low levels of human activity (e.g., walking between buildings, talking and shouting, driving vehicles, and working in gardens and buildings), as we found a linear rise in bird species richness values at increasing distances from the Biology Station buildings. Another factor that could affect our results was the size of the studied urban conditions. Area affects species diversity values (see Rosenzweig 1995 and references therein), and we found a positive non-significant relationship between the size of the studied urbanized areas and their bird species richness. Thus our results show that at the studied range of sizes (0.8- 40 ha), the area of the settlement only played a minor role in determining their bird species richness.
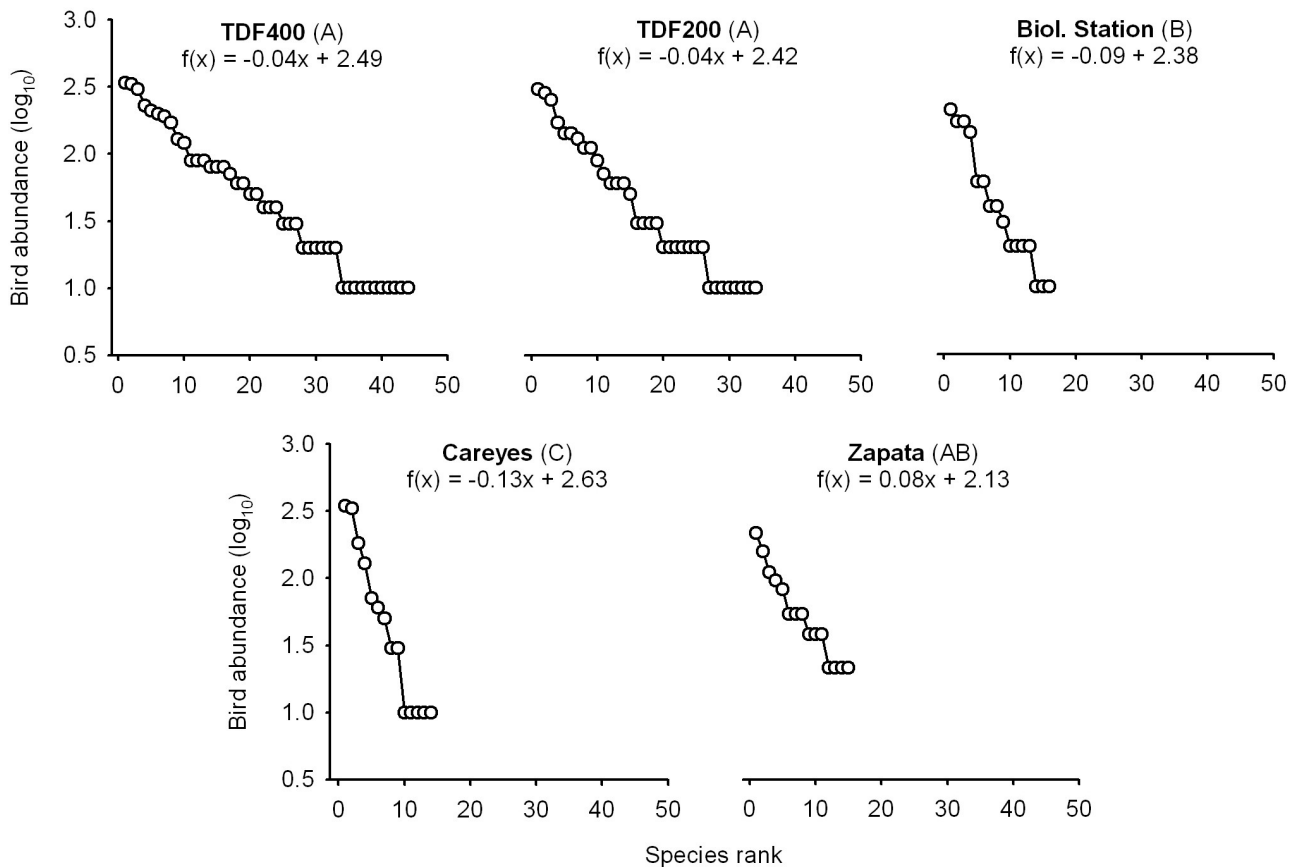
Figure 4. Bird community rank/abundance plots for the studied forest and human settlement conditions. Our results show that both forest conditions (TDFs 400 m and TDFs 200 m) had gentle slopes that did not differ statistically between them. However, they differed from those recorded at the Biology Station building area and Careyes, which showed steeper slopes. Although the regression slope of Zapata did not differ from those recorded at both forest conditions, its intercept was significantly lower. This indicates that although the slope of the bird community of Zapata is fairly even, it s bird community is comprised by few individuals pertaining to few species. Letters following the survey condition's name indicate statistical differences among slopes. The equation for each regression line is displayed.

Bird densities seem to respond to a gradient of human disturbance and habitat conditions among our studied conditions. When we compared bird densities considering the distance of 400 m into conserved tropical dry forest as a control, bird densities decreased significantly as we moved towards the Biology Station buildings. We believe that, similarly to the decrease recorded for bird species richness values, this is the result of human activities reducing habitat quality (Reijnen & Foppen 1994). Bird densities were lowest at the Biology Station building area, which could be caused by a combination of a habitat quality reduction for forest birds, and the absence of urban exploiter species at this site (see Chace & Walsh 2006, Evans et al. 2009, MacGregor-Fors et al. 2009, and references therein). Although we did not find significant differences in bird densities between Careyes and tropical dry forest at 400 m, Careyes had mean bird densities that were higher than the upper-bound 95% confidence intervals of the pristine control (TDFs 400 m). Such an increase in bird densities was caused by the large number of urban exploiter species recorded in Careyes (Appendix 1). This is consistent with the results from previous studies that show increases in bird density with urbanization (see Chace & Walsh 2006, Evans et al. 2009, MacGregor-Fors et al. 2009, and references therein). Bird densities in Zapata were significantly lower than in Careyes, despite the presence of a similar array of urban exploiter species. We believe that this is the result of site-specific conditions at Zapata. Even though Zapata is one of the largest human settlements in the region of Chamela, and 46% of its bird species are urban exploiters, its low socio-economic conditions reduce the availability of resources for birds as reported by Kinzig et al. (2005). As proposed by Shochat (2004), our results suggest that the quality and quantity of available resources can determine bird densities in urban areas.

Additionally, bird density values in Careyes and Zapata showed broad 95% confidence intervals, while forest conditions did not. We believe that this difference in the behaviour of bird densities between human settlements and forests was caused by the presence of urban exploiter species. Some of these species tend to present clumped distributions that increase the variation in density estimations. The wide 95% confidence intervals for bird densities at Careyes and Zapata were caused by two bird species: House Sparrows (*Passer domesticus*) and Barn Swallows (*Hirundo rustica*). These species comprised 53% and 42% of the total bird densities recorded at Careyes and Zapata, respectively. These species have been identified as urban exploiter species in other Mexican regions (Nocedal 1987, Cupul-Magaña 1996, MacGregor-Fors 2005, MacGregor-Fors et al. 2010), and different parts of the world (Blair 1996, McKinney 2002, Kark et al. 2007).

Bird community structure was shown to be fairly even in at both distances of conserved tropical dry forest. As expected for an urban site, Careyes showed a highly dominated bird community due to the abundance of urban exploiter species (Clergeau et al. 2006, McKinney 2006, Kark et al. 2007, MacGregor-Fors et al. 2010), while Zapata's bird community was fairly even, but presented a low number of individuals pertaining to few bird species. The lack of dominance at Zapata was due to the low density of urban exploiter species. Finally, the evenness of the bird community recorded at the Biology Station was more heavily dominated than the two distances of pristine tropical dry forest. Bird communities recorded at the Biology Station were comprised entirely of tropical forest-dwelling species. This community of native species was made up of forest-dwelling species that could be catalogued as urban adaptable, indicating the existence of a subset of native forest species that are able to withstand dramatic changes in habitat structure and human activity levels. This is similar to the

patterns reported by Staniforth (2002), where waterfowl and passerine birds associated with natural undisturbed habitats, in the absence of urban exploiter species, take advantage of the new conditions created by the development of human settlements. The existence of a subset of bird species that are able to tolerate the disturbance caused by human settlements as part of pristine tropical dry forest bird communities in our study could be the result of an adaptation to the regime of natural disturbance experienced by this habitat that is commonly affected by hurricanes (García-Oliva et al. 2002, Maass et al. 2002).

Our results show that habitat modifications caused by the establishment of small to medium-sized human settlements drastically affect bird species richness. While the three studied human settlements were established approximately 40 years ago, they comprise sizes that represent different early stages of urban growth: (1) early stage – Biology Station buildings; (2) intermediate stage – Careyes; and (3) latter stage – Zapata. These three human settlements represent the way in which Latin American urban areas tend to develop. In Latin America human settlements start as punctual developments that sprawl rapidly following a highly developed scheme that leaves few green areas (Sánchez Rodríguez & Bonilla 2007). This growth often occurs with poor, or no landscape planning and/or control. When human settlements are established immerse in a region dominated by wildlands, these are generally transformed to agricultural fields, including cropfields, cattle pastures, and sometimes orchards (López et al. 2001, Ávila Sánchez 2004, García de Alba 2009; unpubl. data). From this perspective, our results suggest that when an area becomes urbanized, regardless of it initial size, changes in habitat structure generate a significant loss in bird species richness by selecting those species that can inhabit the new urban condition from the local pool of species. Our results demonstrate that the initial dramatic loss of bird species is not generated by the arrival of urban exploiter species. Subsequent changes in human settlement size and the reduction of natural habitats surrounding the settlement allow the arrival of urban exploiter species, and therefore changes in bird community composition and structure. Thus, understanding the negative impacts that small-sized urbanized areas can have on bird communities, regardless of the degree of conservation of adjacent habitats, is crucial to generate urban habitats with characteristics that make them compatible to birds and many other wildlife species, following the conceptual framework of reconciliation ecology (Rosenzweig 2003).

Acknowledgements

Literature cited

Acevedo, W., L. R. Richards, and J. T. Buchanan. 1999. Analyzing land use change in urban environments. USGS Fact Sheet 188:99.

Alldredge, M. W., K. H. Pollok, T. R. Simons, and S. A. Shriner. 2007. Multiple-species analysis of point count data: A more parsimonious modeling framework. Journal of Applied Ecology 44:281–290.

Andersson, E. 2006. Urban landscapes and sustainable cities. Ecology and Society 11:34.

Arizmendi, M. C., H. Berlanga, L. Márquez-Valdemar, L. Navarijo, and F. Ornelas. 1990. Avifauna de la región de Chamela, Jalisco. Cuadernos del Instituto de Biología (4), México, D.F.

Ávila Sánchez, H. 2004. La agricultura en las ciudades y su periferia: Un enfoque desde la Geografía. Investigaciones Geográficas 53:98–121.

Beissinger, S. R., and D. R. Osborne. 1982. Effects of urbanization on avian community organization. The Condor 84:75–83.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. Mustoe. 2000. Bird census techniques. Academic Press, London.

Bierwagen, B. G. 2007. Connectivity in urbanizing landscapes: The importance of habitat configuration, urban area size, and dispersal. Urban Ecosystems 10:29–42.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, Oxford.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling. Oxford University Press, Oxford.

Castillo, A., A. Magaña, A. Pujadas, L. Martínez, and C. Godínez 2005. Understanding the interaction of rural people with ecosystems: A case study in a tropical dry forest of Mexico. Ecosystems 8:630–643.

Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: A review. Landscape and Urban Planning 74:46–69.

Chao, A., and S. M. Lee. 1992. Estimating the number of classes via sample coverage. Journal of the American Statistical Association 87:210–217.

Chao, A., and T. J. Shen [online]. 2006. Program SPADE (Species prediction and Diversity Estimation). Version 3.1 <http://chao.stat.nthu.edu.tw/softwareCE.html> (8 April 2010).

Chao, A., M. C. Ma, and M. C. K. Yang. 1993. Stopping rules and estimation for recapture debugging with unequal failure rates. Biometrika 80:193–201.

Clergeau, P., J. P. L. Savard, G. Mennechez, and G. Falardeau. 1998. Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. The Condor 100:413–425.

Clergeau, P., S. Croci, J. Jokimäki, M. L. Kaisanlahti-Jokimäki, and M. Dinetti. 2006. Avifauna homogenisation by urbanisation: Analysis at different European latitudes. Biological Conservation 127:336–344.

Cupul-Magaña, F. G. 1996. Incidencia de avifauna en un parque urbano de los Mochis, Sinaloa, Mexico. Ciencia ergo sum 3:193–200.

Danielson, W. R., R. M. DeGraff, and T. K. Fuller. 1997. Rural and suburban forest edges: Effect on egg predators and nest predation rates. Landscape and Urban Planning 38:25–36.

Durán, E., P. Balvanera, E. Lott, G. Segura, A. Pérez-Jiménez, A. Islas, and M. Franco. 2002. Estructura, composición y dinámica de la vegetación. In: Historia Natural de Chamela (F. A. Noguera, J. H. Vega-Rivera, A. N. García-Aldrete, and M. Quesada-Avendaño, eds.), pp. 443–472. Instituto de Biología, UNAM, México, D.F.

Emlen, J. T. 1974. An urban bird community in Tucson, Arizona: Derivation, structure, regulation. The Condor 76:184–197.

Evans, K. L. 2004. A review of the potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

Evans, K. L., S. E. Newson, and K. J. Gaston. 2009. Habitat influences on urban avian assemblages. Ibis 151:19–39.

Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. Bioscience 55:399–407.

Fernández-Juricic, E., M. D. Jimenez, and E. Lucas. 2001. Bird tolerance to human disturbance in urban parks of Madrid (Spain): Management implications. In: Avian conservation and ecology in an urbanizing world (J. M. Marzluff, R. Bowman, and R. Donnely, eds.), pp. 259–273. Kluwer Academic, Boston, MA.

García de Alba, L. G. 2009. El papel de las ciudades en el desarrollo regional. In: La situación demográfica de México (CONAPO , ed.), pp. 67–86. CONAPO, México, D.F.

García-Oliva, F., A. Camou, and J. M. Maass. 2002. El clima de la región central de la costa del Pacífico mexicano. In: Historia natural de Chamela (F. A. Noguera, J. H. Vega-Rivera, A. N. García-Aldrete, and M. Quesada-Avendaño, eds.), pp. 3–10. Instituto de Biología, UNAM, México D.F.

Gaston, K. J., R. G. Davies, C. D. L. Orme, V. A. Olson, G. H. Thomas, T. S. Ding, P. C. Rasmussen, J. J. Lennon, P. M. Bennett, I. P. F. Owens, and T. M. Blackburn. 2007. Spatial turnover in the global avifauna. Proceedings of the Royal Society B-Biological Sciences 274:1567–1574.

Gavareski, C. A. 1976. Relation of park size and vegetation to urban bird populations in Seattle, Washington. The Condor 78:375–382.

Gratani, L., and L. Varone. 2007. Plant crown traits and carbon sequestration capability by Platanus hybrida Brot. in Rome. Landscape and Urban Planning 81:282–286.

Green, D. M., and M. G. Baker. 2003. Urbanization impacts on habitat and bird communities in a Sonoran Desert ecosystem. Landscape and Urban Planning 63:225–239.

Grussing, D. 1980. How to control House Sparrows. Roseville Publ. House, California.

(INEGI) Instituto Nacional de Estadística Geografía e Informática 2005. II Conteo de población y vivienda 2005. INEGI, Aguascalientes.

Jokimäki, J., and J. Suhonen. 1998. Distribution and habitat selection of wintering birds in urban environments. Landscape and Urban Planning 39:253–263.

Kark, S., A. Iwaniuk, A. Schalimtzec, and E. Banker. 2007. Living in the city: Can anyone become an "urban exploiter"?. Journal of Biogeography 34:638-651.

Kinzig, A., P. Warren, C. Martin, D. Hope, and M. Katti. 2005. The effects of human socioeconomic status and cultural characteristics on urban patterns of biodiversity. Ecology and Society 10:23.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. Journal of Animal Ecology 72:367–382.

Lennon, J. J., P. Koleff, and J. J. D. Greenwood. 2001. The geographical structure of British bird distributions: Diversity, spatial turnover and scale. Journal of Animal Ecology 70:966–979.

López-Flores, V., I. MacGregor-Fors, and J. E. Schondube. 2009. Artificial nest predation along a neotropical urban gradient. Landscape and Urban Planning 92:90-95.

López, E., G. Bocco, M. Mendoza, and E. Duhau. 2001. Predicting land-cover and land-use change in the urban fringe: A case in Morelia city, Mexico. Landscape and Urban Planning 55:271–285.

Maass, J. M., V. Jaramillo, A. Martínez-Yrízar, F. García-Oliva, A. Pérez-Jiménez, and J. Sarukhán. 2002. Aspectos funcionales del ecosistema de selva baja caducifolia en Chamela, Jalisco. In: Historia natural de Chamela (F. A. Noguera, J. H. Vega-Rivera, A. N. García-Aldrete, and M. Quesada-Avendaño, eds.), pp. 525–542. Instituto de Biología, UNAM, México, D.F.

MacGregor-Fors, I. 2005. Listado ornitológico del Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Jalisco, México: Un espacio suburbano. Huitzil 6:1-6.

MacGregor-Fors, I. 2008. Relation between habitat attributes and bird richness in a western Mexico suburb. Landscape and Urban Planning 84:92-98.

MacGregor-Fors, I., L. Morales-Pérez, J. Quesada, and J. E. Schondube. 2010. Relationship between the

presence of House Sparrows (*Passer domesticus*) and Neotropical bird community structure and diversity. Biological Invasions 12:87-96.

MacGregor-Fors, I., R. Ortega-Álvarez, and J. E. Schondube. 2009. On the ecological quality of urban systems: An ornithological perspective. In: Urban planning in the 21st century (D. S. Graber, and K. A. Birmingham, eds.), pp. 51–66. Nova Science Publishing, New York, NY.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Publishing, Oxford.

Marzluff, J. M. 2005. Island biogeography for an urbanizing world: How extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosystems 8:157–177.

Marzluff, J. M., R. Bowman, and R. Donnely. 2001. A historical perspective on urban bird research: Trends, terms, and approaches. In: Avian conservation and ecology in an urbanizing world (J. M. Marzluff, R. Bowman, and R. Donnely, eds.), pp. 1–17. Kluwer Academic, Boston, MA.

McAleece, N. 1997. BioDiversity Professional. Version 2 <http://www.sams.ac.uk/research/software> (8 April 2010).

McKinney, M. L. 2002. Urbanization, biodiversity and conservation. Bioscience 52:883-890.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260.

McKinney, M. L. 2008. Do humans homogenize or differentiate biotas? It depends. Journal of Biogeography 35:1960-1961.

Melles, S., S. Glenn, and K. Martin. 2003. Urban bird diversity and landscape complexity: Species-environment associations along a multiscale habitat gradient. Conservation Ecology 7:5.

Nocedal, J. 1987. Las comunidades de pájaros y su relación con la urbanización en la ciudad de México. In: Aportes a la ecología urbana de la ciudad de México (E. Rapoport, and I. R. López-Moreno, eds.), pp. 73–109. Limusa, México, D.F.

Noguera, F. A., J. H. Vega-Rivera, and A. N. García-Aldrete. 2002. Introducción. In: Historia natural de Chamela (F. A. Noguera, J. H. Vega-Rivera, A. N. García-Aldrete, and M. Quesada-Avendaño, eds.), pp. xv-xxi. Instituto de Biología, UNAM, México, D.F.

Ortega-Álvarez, R., and I. MacGregor-Fors. 2009. Living in the big city: Effects of urban land-use on bird community structure, diversity, and composition. Landscape and Urban Planning 90:189-195.

Payton, M. E., M. H. Greenstone, and N. Schenker. 2003. Overlapping confidence intervals or standard error intervals: What do they mean in terms of statistical significance?. Journal of Insect Science 3:34.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Gen. Tech. Rep. PSW-GTR-144, Albany.

Reijnen, R., and R. Foppen. 1994. The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for Willow Warblers (*Phylloscopus trochilus*) Breeding Close to a Highway. Journal of Applied Ecology 31:85-94.

Rosenzweig, M. 2003. Win-win ecology: How the Earth's species can survive in the midst of human enterprise. Oxford University Press, Oxford, .

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Sanchez Rodriguez, R., and A. Bonilla. 2007. Urbanización, cambios globales en el ambiente y desarrollo sustentable en América Latina. IAI-INE-UNEP, São José dos Campos.

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

Simon, U., S. Kübler, and J. Böhner. 2007. Analysis of breeding bird communities along an urban-rural gradient in Berlin, Germany, by Hasse Diagram Technique. Urban Ecosystems 10:17–28.

Staniforth, R. J. 2002. Effects of urbanization on bird populations in the Canadian Central Actic. Arctic

55:87–93.

Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, J. R. B. Bishop, and T. A. Marques. 2005. Distance 5.0. Release 1. Research Unit for Wildlife Population Assessment, University of St. Andrews.

Vega-Rivera, J. H. 2007. The biological station of Chamela: A privileged site for research. Tropinet 18:5.

Yaukey, P. H. 1996. Patterns of avian population density, habitat use, and flocking behavior in urban and rural habitats during winter. Professional Geographer 48:70–81.

Appendix 1. Bird species recorded in this study.

Species	Urban use	Food guild	Main nesting sites	Ind. / point count				
				TDFs 400m	TDFs 200m	Biol. St.	Careyes	Zapata
Ortalis poliocephala	Urban adaptable	Frugivore	Trees	1.15	0.45	1.05		0.1
Buteo magnirostris	Urban avoider	Carnivore	Trees	0.05				
Columba livia	Urban exploiter	Granivore	Buildings				1.3	
Columbina inca	Urban adaptable	Granivore	Trees/shrubs	0.4	0.15	0.1	0.3	
Columbina passerina	Urban adaptable	Granivore	Shrubs/ground	0.45		0.05		
Columbina talpacoti	Urban adaptable	Granivore	Trees/shrubs	0.05			0.7	0.2
Leptotila verreauxi	Urban adaptable	Granivore	Trees/shrubs/ground	1.5	1.25	0.2		
Aratinga canicularis	Urban avoider	Granivore	Termitaria	0.2	0.1			
Amazona finschi	Urban avoider	Granivore	Tree cavities	0.15				
Glaucidium brasilianum	Urban avoider	Carnivore	Tree/cactus cavities	0.2	0.15			
Amazilia rutila	Urban adaptable	Nectarivore	Trees/shrubs	0.85	0.7	0.15	0.5	0.3
Heliomaster constantii	Urban avoider	Nectarivore	Trees	0.1				
Stellula calliope	Urban avoider	Nectarivore	Trees/shrubs	0.05				
Trogon citreolus	Urban avoider	Frugivore	Termitaria	0.35	0.3			
Melanerpes chrysogenys	Urban adaptable	Insectivore	Tree cavities	1.7	1.4	0.3		0.5
Picoides scalaris	Urban avoider	Insectivore	Tree cavities		0.1			
Dryocopus lineatus	Urban avoider	Insectivore	Tree cavities	0.25				
Xiphorhynchus flavigaster	Urban adaptable	Insectivore	Tree cavities	1	0.65	0.1		
Camptostoma imberbe	Urban avoider	Insectivore	Trees		0.05			
Empidonax sp.	Urban avoider	Insectivore	Trees	0.05	0.05			
Pyrocephalus rubinus	Urban exploiter	Insectivore	Trees				0.1	
Attila spadiceus	Urban adaptable	Insectivore	Trees	1.05	0.85	0.3		
Myiarchus tuberculifer	Urban adaptable	Insectivore	Tree/cactus cavities	0.3	0.3	0.1		
Myiarchus cinerascens	Urban avoider	Insectivore	Tree/cactus cavities	0.15	0.1			
Myiarchus tyrannulus	Urban adaptable	Insectivore	Tree/cactus cavities	0.25	0.1	0.05		
Myiozetetes similis	Urban avoider	Insectivore	Trees/shrubs	0.05				
Tyrannus melancholicus	Urban adaptable	Insectivore	Trees	0.05		0.3		
Pachyramphus aglaiae	Urban avoider	Insectivore	Shrubs	0.05				
Tityra semifasciata	Urban avoider	Frugivore	Tree cavities	0.1	0.1			
Vireo gilvus	Urban avoider	Insectivore	Trees	0.4	0.25			
Vireo flavoviridis	Urban avoider	Insectivore	Trees/shrubs	0.1	0.05			
Cyanocorax sanblasianus	Urban adaptable	Granivore	Trees	0.45	0.55	0.85		0.1
Stelgidopteryx serripennis	Urban exploiter	Insectivore	Cavities					0.1
Hirundo rustica	Urban exploiter	Insectivore	Buildings				3.5	1.6
Thryothorus sinaloa	Urban avoider	Insectivore	Trees/shrubs/rocks	0.45	0.15			
Thryothorus felix	Urban avoider	Insectivore	Trees/shrubs/rocks	0.2	0.05			

Species	Urban use	Food guild	Main nesting sites	Ind. / point count				
				TDFs 400m	*TDFs 200m*	*Biol. St.*	*Careyes*	*Zapata*
Uropsila leucogastra	Urban avoider	Insectivore	Shrubs	0.1	0.3			
Polioptila nigriceps	Urban avoider	Insectivore	Trees/shrubs	0.05				
Turdus rufopalliatus	Urban adaptable	Frugivore	Trees/shrubs		0.05			0.2
Parula pitiayumi	Urban adaptable	Insectivore	Trees	1.65	1.5	0.85		
Seiurus aurocapilla	Urban avoider	Insectivore	Ground	0.05				
Saltator coerulescens	Urban adaptable	Omnivore	Unknown	0.1	0.05			0.3
Volatinia jacarina	Urban adaptable	Granivore	Shrubs	0.1			0.1	0.1
Sporophila torqueola	Urban exploiter	Granivore	Trees/shrubs				0.6	0.6
Arremonops rufivirgatus	Urban avoider	Granivore	Shrubs/ground	0.05				
Aimophila ruficauda	Urban exploiter	Granivore	Shrubs/ground				0.1	
Pheucticus chrysopeplus	Urban avoider	Granivore	Trees/shrubs	0.6	0.55			
Granatellus venustus	Urban avoider	Omnivore	Shrubs	0.15	0.15			
Cyanocompsa parellina	Urban adaptable	Granivore	Trees/shrubs	0.4	0.1	0.1		
Passerina versicolor	Urban avoider	Granivore	Trees/shrubs	0.05				
Passerina leclancherii	Urban avoider	Granivore	Shrubs	0.3	0.1			
Quiscalus mexicanus	Urban exploiter	Omnivore	Trees				1.8	0.3
Icterus pustulatus	Urban adaptable	Omnivore	Trees	0.65	0.35	0.2	0.1	0.2
Cacicus melanicterus	Urban adaptable	Omnivore	Trees	0.95	0.7	0.7	0.1	0.7
Spinus psaltria	Urban adaptable	Granivore	Trees/shrubs		0.05		0.3	
Passer domesticus	Urban exploiter	Omnivore	Buildings/trees				3.3	1.1

Relationship between the presence of House Sparrows (*Passer domesticus*) and Neotropical bird community structure and diversity

**Ian MacGregor-Fors · Lorena Morales-Pérez ·
Javier Quesada · Jorge E. Schondube**

Abstract Invasive exotic species pose an important threat to biodiversity worldwide. However, there is little information on the effects that specific exotic bird species have on native biota. The House Sparrow is an excellent ecological model to evaluate the effect that an invasive exotic species has on native bird communities. Our study describes the relationship of the presence and abundance of House Sparrows with the structure, diversity, and composition of native bird communities in West Mexico. We used two approaches to compare House Sparrow invaded and non-invaded bird communities: (1) at a small geographic-scale that allowed us to evaluate shifts in avian communities with presence of the House Sparrow under similar environmental conditions; and (2) at the landscape-level to evaluate the effect of this species under a scenario of greater environmental heterogeneity. Results from both approaches show that areas invaded by House Sparrows have heavily-dominated avian communities with low species richness, while non-invaded areas exhibit highly-even and species-rich bird communities. Species turnover analysis indicates that the decrease in the number of bird species in House Sparrow invaded areas is caused by species loss, rather than a shift in species composition. Our results indicate that the invasion of an area by the House Sparrow, through synergistic interactions with human activities, determines the composition, structure, and diversity of native bird communities.

Keywords House Sparrow · Exotic species · Human-altered ecosystems · Urban ecology · Bird communities · Biodiversity

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Introduction

The anthropogenic introduction of exotic species represents a significant component of global change (Zaret and Paine 1973; Vitousek et al. 1997; Smith and Knapp 2001). Successful invasions of exotic species often cause major changes to native ecosystems (Wilson and Belcher 1989; Hawkes et al. 2005; Gritti et al. 2006). Exotic species can affect native biota at different ecological levels, modifying species population dynamics, community structure, or even ecosystems level processes (Kalinoski 1975; Gowaty 1984; Fritts and Rodda 1998). Humans have

frequently introduced bird species into new areas (e.g., House Sparrows, Rock Pigeons, European Starlings, Monk Parakeets), yet our knowledge of their effects on native bird communities is limited (Chace and Walsh 2006).

The House Sparrow (*Passer domesticus*) is a good biological model to study human-caused bird species invasions. This sparrow, native to Europe and North Africa, was introduced to North America in 1850 from England and Germany (Baker 1995; Bull and Farrand 1997). Originally introduced to Brooklyn, New York, the House Sparrow has broadened its distributional range within urban and suburban areas throughout North America (Sibley 2001).

The success of the House Sparrow as an invasive species has been attributed to four natural-history traits that make it an excellent urban exploiter species (sensu Blair 1996; Kark et al. 2007): (1) it is an aggressive species that attacks birds of similar, or smaller size at feeding sites, and actively destroys nests of other species (McGillivray 1980; Gowaty 1984; Kimball 1997); (2) it is a dietary generalist that feeds on grain, insects, fruit and even human litter (Gavett and Wakeley 1986; Kimball 1997); (3) it has colonial-communal nesting strategies that allows its abundance to increase at an accelerated rate once it has invaded a new area (Kalinoski 1975; McGillivray 1980; Gowaty 1984); and (4) it can effectively expand its limits through human-altered landscapes (Kark et al. 2007). The House Sparrow is reported to negatively affect some North American native species such as the House Finch (*Carpodacus mexicanus*) and Eastern Bluebird (*Sialia sialis*) (Kalinoski 1975; Gowaty 1984), though the effects that the House Sparrow may have on native bird communities has not been evaluated. The aim of this study is to describe the relationship between the presence of House Sparrows presence and the structure and diversity of Neotropical bird communities. For this, we used two approaches: (1) a small geographic-scale study that allowed us to compare House Sparrow-invaded and non-invaded bird communities under the same environmental conditions. And (2) a landscape-scale study that allowed us to evaluate: (a) if the community structure of invaded and non-invade sites is related to environmental variation, and (b) if the presence of House Sparrows, regardless of habitat structure and environmental attributes, is related to bird communities with similar structures.

Methods

Study area and field methods

We conducted our study in the Cuitzeo watershed, located in the state of Michoacán in West Mexico. This watershed is highly heterogeneous due to its topography, with an altitudinal range of 1,800–3,500 m asl, and associated habitats of fir forests, pine forests, oak forests, pine-oak forests, and subtropical shrublands. In addition, human activities have created several anthropogenic habitats: crop-fields, plantations, cattle-grazing grasslands, and urban sites. To understand the possible negative effects of House Sparrow invasions on Neotropical bird communities we used two approaches: (1) a small geographic-scale study in the peri-urban belt of the city of Morelia; and (2) a landscape-level analysis of bird communities within the watershed.

For the small geographic-scale study, we sampled 20 sites on the peri-urban belt of this rapidly growing city. Ten sites, located within the city perimeter, were invaded by the House Sparrow in the last 5 years. This invasion was the result of House Sparrows using peri-urban habitats affected by the most recent expansion of the city of Morelia (López et al. 2001). The other ten sites, which have not yet been invaded by the House Sparrow, were located 2–2.5 km away from invaded sites. Both invaded and non-invaded areas were similar in relation to their habitat characteristics. All of our sampling sites were located in plantations dominated by trees of the genus *Eucalyptus* with no difference in herbaceous plant ($t_{18} = 0.11$, $P = 0.92$), shrub ($t_{18} = 0.10$, $P = 0.91$), tree ($t_{18} = 0.91$, $P = 0.37$), and construction cover ($t_{18} = 0.24$, $P = 0.80$). This allowed us to control most habitat structure attributes, and thus, to evaluate the influence of House Sparrow presence on the structure, diversity, and composition of the native bird community.

At the landscape-level we surveyed a total of 574 sites distributed among eight habitat types in an area of $\sim 2,000$ km^2. Of these, 204 sites were located within the city of Morelia, 30 in small human settlements, 30 in pine-oak forests, 30 in conifer forests, 30 in oak forests, 90 in subtropical shrublands, 90 in cropfields, and 70 in cattle-grazing grasslands. Altitude, climate, and habitat varied greatly among sites. Our goal was to compare bird

community structure between sites were the House Sparrow was present and sites without this invasive species using a scenario of high environmental variation, to evaluate the relative roles that environmental variation and the invasion of House Sparrows may play on shaping native bird communities. We expected that if House Sparrow presence is a factor that molds native bird communities, all sites invaded by House Sparrows would have similar community structure, regardless of their environmental attributes. Furthermore, we expected that sites that were not invaded by this exotic species would show bird communities that differ in response to their environmental attributes. Finally, with this analysis we aimed to identify those habitat variables that where related to the House Sparrow's abundance.

To measure bird community structure, we carried out 10 min unlimited radius point-counts (following Ralph et al. 1996). We conducted all our sampling from 0700 to 1100 h visiting $\sim$20 sites per day. Point counts were located at a minimum distance of 250 m from each other to ensure survey independence (Ralph et al. 1996; Huff et al. 2000). To understand temporal variation in bird communities each site was surveyed in September 2006, and again in July 2007.

Data analysis

Small geographic-scale approach

Bird community structure (dominance/evenness) in invaded and non-invaded areas was analyzed using species rank/abundance plots (as suggested by Magurran 2004). In order to assess differences in dominance/evenness at invaded and non-invaded sites, and to test if the proportion of dominant and rare species varied among sites, we compared the slopes of the rank/abundance plots using analysis of covariance (ANCOVA). Because rank/abundance curves are not linear, abundance data was log transformed (Magurran 2004). We used a rarefaction analysis to compare bird species richness among sites (EstimateS platform; Colwell 2005). Rarefaction curves are computed species accumulation curves based on the repeated re-sampling of all pooled samples. These curves represent the statistical expectation for observed accumulation curves (Gotelli and Colwell 2001), enabling the comparison of the statistically expected species richness of each

community at the same sampling effort or abundance (Moreno 2001). To facilitate comparisons with other studies, we also report Fisher's α diversity index values ($\alpha \pm 95\%$ confidence intervals). We applied a nested design GLM-ANOVA to determine whether bird abundances differed in presence or absence of the House Sparrow. To compare diversity values (interaction of species richness and abundances) between invaded and non-invaded areas, we computed a Bray-Curtis multivariate cluster analysis (BioDiversity Pro platform; McAleece 1997). We calculated species turnover between areas using β_{sim} (Lennon et al. 2001). This index quantifies the relative magnitude of species gains and losses in relation to the sample with the least number of unique species. This approach allowed us to evaluate whether bird communities in invaded areas may have exchanged species, or have simply lost them.

Landscape-level approach

To compare sites with and without House Sparrows at the landscape-level, we used all sites where House Sparrows were present ($n = 241$), and used a pseudo-random number generator (Wichman and Hill 1982) to randomly select 241 of the total 325 surveys where House Sparrows were absent. To evaluate bird community structure (dominance/evenness), we generated rank/abundance plots, and applied ANCOVA to compare plots between sites with and without House Sparrows. We also used ANCOVA to compare the bird community structure (dominance/evenness) of 20 randomly selected landscape-level surveys with those of the small geographic-scale approach. Finally, we conducted a stepwise multiple regression analysis to model House Sparrow abundance in relation to habitat attributes (height and cover of trees, shrubs, herbaceous plants, and buildings).

Results

Small geographic-scale approach

Bird community structure differed between House Sparrow invaded and non-invaded areas (ANCOVA of rank/abundance plots: $F_{1,54} = 6.10$, $P = 0.016$). All invaded sites exhibited communities that were dominated by the House Sparrow (Fig. 1). There

were 175 more individuals of the most abundant species (House Sparrow), than the next ranked species (Barn Swallow—*Hirundo rustica*). House Sparrows represented almost one half of the total bird abundance at invaded sites (48.7 ± 3.9% SE of all individuals detected). Bird communities exhibited higher evenness at non-invaded sites (Fig. 1). The highest difference between the most abundant species

at these sites (Lesser Goldfinch—*Carduelis psaltria*), and the next ranked species (House Finch—*Carpodacus mexicanus*), was of 19 individuals.

Community diversity values differed between invaded and non-invaded sites (Fig. 2). Bird species richness was significantly higher at non-invaded sites (34.0 ± 5.34 computed species at 247 individuals;
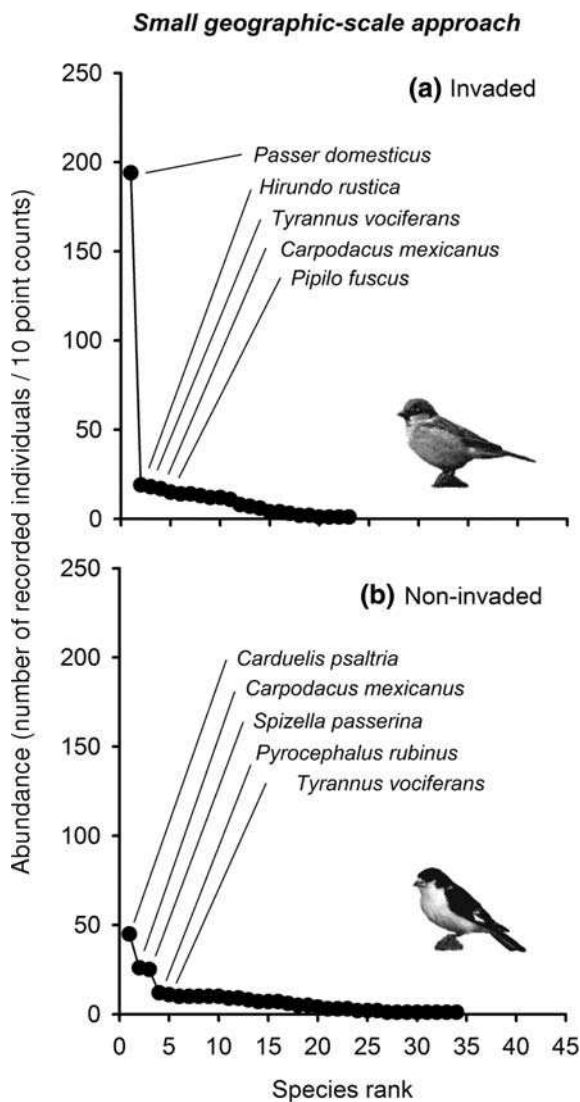

Fig. 1 Structure of bird communities at a small geographic-scale in the peri-urban belt of Morelia city. Rank/abundance plots for invaded and non-invaded bird communities show that invaded areas were highly dominated by the House Sparrow. The sparrow's presence was associated with lower species richness and changes in the species ranking order. Illustrations show the most abundant species for each community
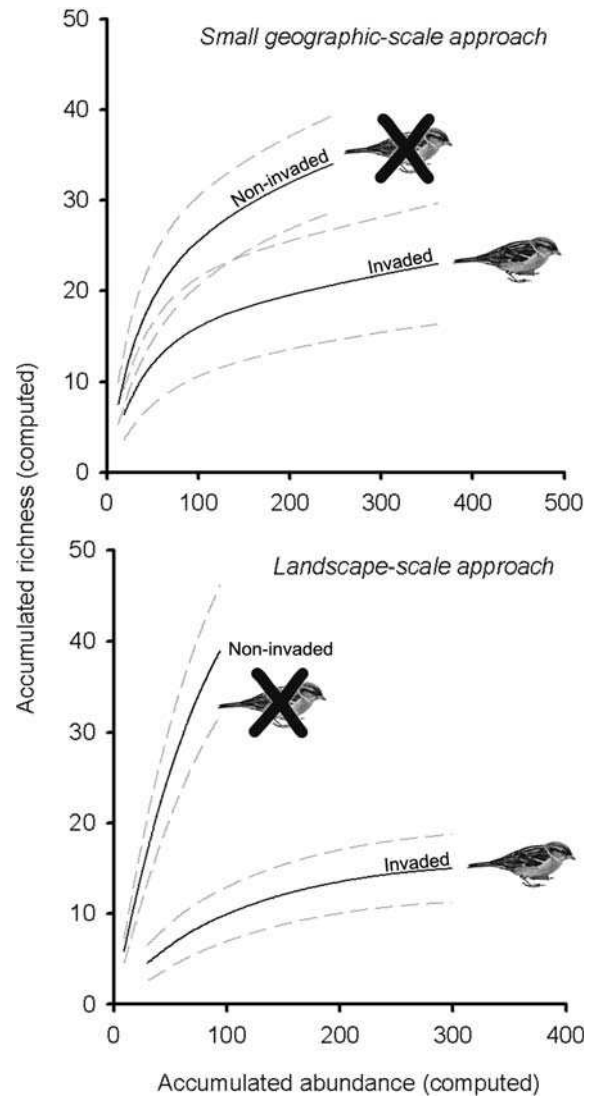

Fig. 2 Diversity differences in bird communities between House Sparrow invaded and non-invaded sites, at both the small geographic-scale and the landscape-level. Regardless of the spatial analysis used, invaded areas showed lower species richness than non-invaded ones, while total bird abundances were higher at invaded areas due to the large number of House Sparrows present in them. *Solid lines* represent mean accumulated species (computed) while *dashed lines* correspond to their 95% confidence intervals

Fisher's $\alpha = 10.68 \pm 0.52$), than at invaded sites (23 ± 6.67 computed species at 247 individuals; Fisher's $\alpha = 5.47 \pm 0.26$). However, bird abundances were higher at invaded sites (18.95 ± 2.76 individuals/point count), than at non-invaded sites (13.00 ± 1.55 individuals/point count). Differences in abundance values were significantly related to the presence of House Sparrows in both the 2006 and the 2007 surveys (GLM-ANOVA: $F_{1,36} = 14.8$, $P < 0.001$). The Bray-Curtis multivariate cluster analysis demonstrated high similarity between surveys in 2006 and 2007 at invaded sites (80.2%), followed by non-invaded sites (60.2%). However, there was low similarity in surveys between invaded and non-invaded sites ($36.4 \pm 3.12\%$). Of the 36 recorded bird species, 21 were shared by both areas, two were exclusive to invaded sites, and 13 were exclusive to non-invaded sites (Table 1). Thus, the β_{sim} value for the invaded and non-invaded areas was very low (0.08 dissimilarity), showing that invaded sites lost a great proportion of species rather than shifting their community composition.

Landscape-level approach

House Sparrows were recorded in two habitats: human settlements and cropfields. Urban sites with House Sparrows were highly heterogeneous in habitat attributes: 0–80% tree cover, 0–18 m tree height, 0–40% shrub cover, 0–7 m shrub height, 0–80% herbaceous plant cover, 0–3 m herbaceous plant height, and 0–100% built cover. Cropfields in which House Sparrows were recorded were located at a maximum distance of 609 m from any human settlement, and up to 14 km from Morelia city. Two bird species were only present in House Sparrow invaded areas: the Rock Pigeon—*Columba livia* and the Vaux's Swift—*Chaetura vauxi*. On the other hand, 32 native species were only recorded in non-invaded sites (Table 2).

Comparison of the 241 invaded and the 241 non-invaded sites showed significant differences in bird community dominance/evenness. Invaded sites had highly dominated communities, while non-invaded sites presented fairly even ones (Fig. 3). The slopes of the rank abundance plots for invaded and non-invaded sites were different (ANCOVA: $F_{1,53} = 4.46$, $P < 0.001$). To separate the potential impact of human activities (urbanization, agriculture), we compared

Table 1 Bird species recorded in invaded and non-invaded areas at the peri-urban belt of Morelia (small geographic-scale approach)

Species	Abundance (ind./10 point counts)	
	Invaded	Non-invaded
Columbina inca	12	5
Leptotila verreauxi	0	1
Cynanthus latirostris	8	9
Amazilia beryllina	7	7
Amazilia violiceps	0	1
Melanerpes formicivorus	0	3
Melanerpes aurifrons	6	7
Contopus pertinax	2	9
Contopus sordidulus	0	2
Empidonax sp.	0	1
Pyrocephalus rubinus	14	12
Tyrannus vociferans	18	11
Hirundo rustica	19	7
Psaltriparus minimus	3	0
Campylorhynchus gularis	11	7
Catherpes mexicanus	12	2
Thryomanes bewickii	4	6
Troglodytes aedon	1	5
Polioptila caerulea	1	10
Sialia sialis	2	9
Turdus rufopalliatus	1	1
Ptilogonys cinereus	0	2
Vermivora celata	0	3
Vermivora ruficapilla	0	1
Dendroica coronata	0	6
Dendroica nigrescens	0	3
Wilsonia pusilla	0	1
Piranga flava	0	1
Sporophila torqueola	14	9
Pipilo fuscus	15	10
Spizella passerina	1	25
Melospiza lincolnii	0	1
Passerina caerulea	4	4
Carpodacus mexicanus	17	23
Carduelis psaltria	13	43
Passer domesticus	194	0

bird community evenness at House Sparrow invaded and non-invaded sites for only urban and cropfield areas. We found that in both urban and agricultural sites, non-invaded communities were different from those invaded by House Sparrows (ANCOVA urban:

Table 2 List of native species ($n = 32$) recorded exclusively in non-invaded sites at the landscape level

Species
Accipiter cooperii
Zenaida macroura
Columbina passerina
Leptotila verreauxi
Lampornis amethystinus
Eugenes fulgens
Selasphorus platycercus
Trogon elegans
Melanerpes formicivorus
Colaptes auratus
Lepidocolaptes leucogaster
Attila spadiceus
Sayornis nigricans
Myiarchus tuberculifer
Myiarchus nuttingi
Vireo belli
Vireo atricapilla
Cyanocitta stelleri
Aphelocoma ultramarina
Poecile sclateri
Catharus occidentalis
Peucedramus taeniatus
Parula superciliosa
Dendroica occidentalis
Ergaticus ruber
Atlapetes pileatus
Melozone kieneri
Aimophila ruficeps
Oriturus superciliosus
Ammodramus savannarum
Euphonia elegantissima
Carduelis pinus

Fig. 3 Rank/abundance plots for House Sparrow invaded and non-invaded bird communities at the landscape-level. Rank/abundance plots for invaded and non-invaded bird communities show an almost identical pattern to the one found for the small geographic-scale approach (see Fig. 1). Bird communities of invaded areas at the landscape-scale approach were also highly dominated by the House Sparrow, regardless of the high environmental heterogeneity present in the sampled sites

$F_{1,28} = 5.44$, $P = 0.026$; ANCOVA agricultural: $F_{1,21} = 66.37$, $P < 0.001$).

Results at the landscape-level were similar to those observed at the small geographic-scale. When we compared the community structure of invaded sites of the landscape-scale approach (20 randomly selected sites) with the data from the small geographic-scale we found no differences in the slopes of their rank/abundance plots (ANCOVA: $F_{1,40} = 0.24$, $P = 0.62$). Non-invaded sites at the landscape-level had rank/abundance plots that differed in their slope with invaded sites at the small geographic-scale (ANCOVA: $F_{1,82} = 4.23$, $P = 0.04$). Non-invaded
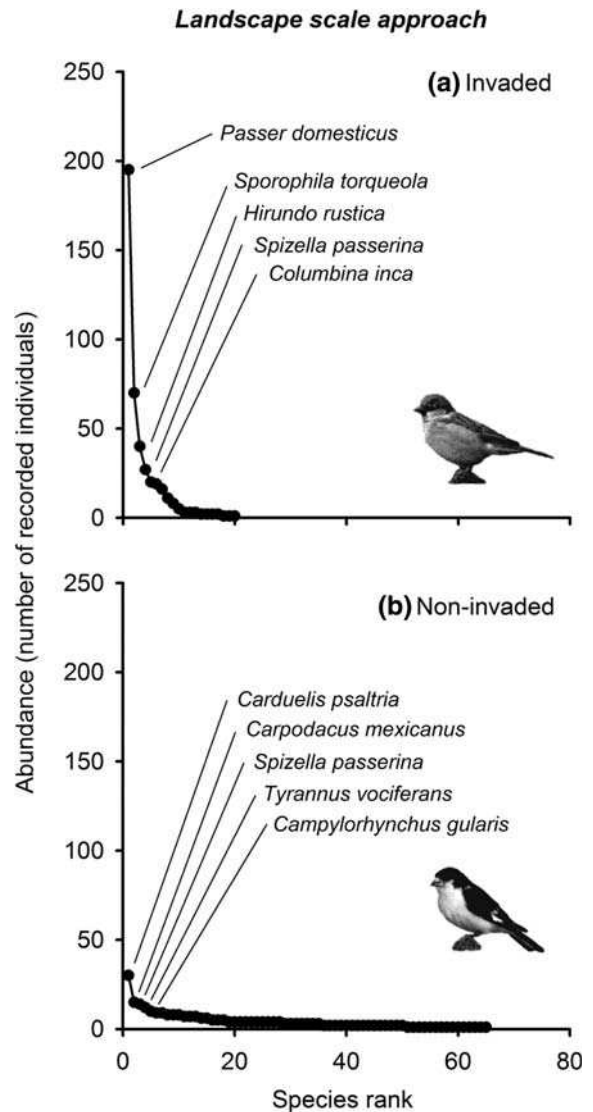
sites at both the landscape and small geographic scales differed significantly in community evenness (ANCOVA: $F_{1,96} = 8.45$, $P < 0.001$). The stepwise multiple regression analysis showed that House Sparrow abundance had a positive relation with built cover and building height, and a negative relation with shrub cover (Table 3).

Table 3 Relationship between House Sparrow abundance and habitat structure variables

General model	$R = 0.44$	$F_{3,548} = 46.08$		$P = 0.001$
	Beta	SE	$t(548)$	P
Intercept			5.18538	0.000000
Shrub cover	−0.116999	0.040161	−2.91327	0.003723
Construction cover	0.155195	0.068247	2.27403	0.023350
Building height	0.260973	0.067942	3.84109	0.000137

Discussion

Our results show that areas invaded by the House Sparrow differ greatly from non-invaded areas, regardless of their environmental conditions or level of human disturbance (i.e., urbanization, agriculture). At the small geographic-scale we established a negative relationship between the presence of House Sparrows and native bird species richness. We also found a positive relationship between House Sparrow presence and total bird abundance. At the landscape-level, bird community diversity and structure exhibited patterns that did not differ from those found at the small geographic-scale. In this section we discuss shifts in bird community diversity, structure, and composition at House Sparrow invaded and non-invaded sites, focusing on the importance of the House Sparrow as a molder of native bird communities.

There was a dramatic decrease in the evenness of bird communities where House Sparrows were present. This was caused by a reduction in bird species richness and an increase in bird abundances at invaded sites. Our results are consistent with patterns of diversity generated by other invasive species of different taxa, such as plants, invertebrates, and fishes (Vitousek et al. 1997; Gritti et al. 2006). The increase in total bird abundance at invaded sites was caused by a dramatic increase in the number of House Sparrow individuals. This is not surprising, since House Sparrows have been found to be a dominant species in the communities where they occur all over the world (Emlen 1974; Gavareski 1976; Cupul-Magaña 1996; Clergeau et al. 1998; White et al. 2005), and are an excellent example of an invasive urban exploiter species.

The species turnover analysis at both scales showed that the bird composition of invaded and non-invaded sites was similar; however, invaded sites had low species richness due to the loss of several native species. Because our sampling sites for the small geographic-scale approach were environmentally very similar, our results suggest that the presence of the House Sparrow is the cause of native species loss. This was supported by our results from the landscape-level approach, where regardless of environmental variation, invaded sites exhibited simpler, more dominated communities. One of the possible explanations for these patterns is the House Sparrow's aggressiveness towards native species (Kalinoski 1975; Gowaty 1984). At our study sites we observed House Sparrows violently attacking some native species at feeding sites (e.g., Lesser Goldfinch, White-collared Seedeater, Golden-fronted Woodpecker). Similar aggressive interactions between the House Sparrow and local species have also been reported for other sites in North America (Kalinoski 1975; Grussing 1980; Gowaty 1984).

Bird communities of House Sparrow invaded sites at both the small geographic-scale and the landscape-level had similar structure and composition. This similarity could be generated by two urban-related forces: (1) shifts in the structure and composition of natural habitats to artificial impoverished systems; and (2) the attraction of exotic, invasive, and aggressive species that successfully exploit the resources and conditions of urban systems. As a result of these processes, a number of species may avoid the urban habitat due to the lack of appropriate habitat or their incapability to deal with aggressive urban exploiters. Other urban adaptable species that could live in urban conditions may also be limited by negative competition with urban exploiters. Alternatively, there may be an increase in the number of individuals of those species capable of exploiting urban conditions and resources (Blair 2001; McKinney 2002). Thus, the avifaunas of different cities are highly similar in comparison to the avifaunas of the adjacent habitats. Such a scenario makes urbanization a major cause of biotic homogenization, where animal communities are dominated by only a few species that are able to maintain healthy populations within urban habitats (Blair 2001; McKinney 2006).

However, in the case of non-invaded sites, bird communities differed between the small geographic

and landscape levels, and this appears to result from the environmental variation that exists between the homogeneous small geographic-scale sites, and the heterogeneous landscape-level sites. Our peri-urban sites, used at the small geographic-scale analysis, are extremely similar among them, and as a result, had almost identical bird communities. Because these sites are located in the area of influence of the city of Morelia, their bird communities are affected by urbanization processes and therefore present lower species richness than non-invaded sites with native vegetation in other areas of the watershed (MacGregor-Fors et al., in press). Bird communities inhabiting non-invaded sites at the landscape-scale approach overestimate species richness because they comprise the bird communities that exist in all the habitats present in the Cuitzeo watershed. Therefore, their high species richness is an artifact of our analysis that conglomerates the high environmental variation present in our study area.

At the landscape-level we only recorded House Sparrows within human-altered urban and agricultural systems. This is a factor that could obscure our findings by confounding the effects of human activity and House Sparrow presence on the structure and diversity of bird communities. Nevertheless, when considering only urban and agricultural areas, bird communities still differed between invaded and non-invaded sites. Non-invaded human-altered areas have communities that are richer and more even than human-altered areas invaded by House Sparrows. Non-invaded human-altered sites have bird communities that are intermediate in the slope of their rank/abundance plots between non-invaded natural sites and invaded-sites (all Newman-Keuls post hoc tests P values < 0.001; Fig. 4). This suggests that even though human alteration has an effect on bird community structure and diversity, House Sparrow invasion plays a crucial role in determining species richness and abundance of avian communities.

Our results show that House Sparrow abundance is related to urbanized and open areas with a low density of shrubs. This is a very common scenario within Latin-American cities, where the House Sparrow has invaded and become highly abundant. Curiously, while the House Sparrow has expanded its numbers and distribution range across the American continent, European populations are declining (Shaw et al. 2008). Robinson et al. (2005) have
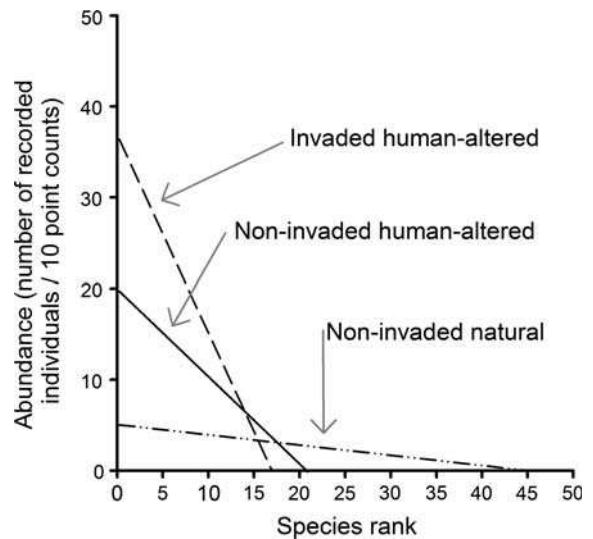
Fig. 4 Slopes from rank/abundance plots indicating the dominance/evenness of invaded and non-invaded bird communities: (1) House Sparrow invaded human-altered habitats (urban and agricultural sites; *segmented line*); (2) non-invaded human-altered habitats (urban and agricultural sites; *solid line*); and (3) non-invaded natural habitats (native forests and shrubland sites; *segmented-dotted line*). Our results indicate that although human activities modify the structure of bird communities, the presence of House Sparrows is crucial to determine the dominance/evenness values of the bird communities they invade

related these declines to the industrialization of agricultural activities that no longer allow the House Sparrow to exploit agricultural leftovers as food. Also, the fact that European cities have become cleaner in the last few years, reducing the availability of litter as a food resource, could have negative effects on this species' populations, although others factors such as the change in habitat structure in cities could also explain this negative trend (Shaw et al. 2008). These factors could be taken advantage of to limit House Sparrow populations in America, and reduce the negative effects of this species on native bird communities.

References

Baker M (1995) Environmental component of latitudinal clutch-size variation in house sparrows (*Passer domesticus*). Auk 112:249–252

Blair RB (1996) Land use and avian species diversity along an urban gradient. Ecol Appl 6:506–519. doi:10.2307/2269387

Blair RB (2001) Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous avifauna? In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology in an urbanizing world. Kluwer, Norwell

Bull J, Farrand J (1997) National audubon society field guide to North American birds—eastern region. Alfred A. Knopf, New York

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74:46–69. doi:10.1016/j.landurbplan.2004.08.007

Clergeau P, Savard JPL, Mennechez G, Falardeau G (1998) Bird abundance and diversity along an urban–rural gradient: a comparative study between two cities on different continents. Condor 100:413–425. doi:10.2307/1369707

Colwell RK (2005) EstimateS: statistical estimation of species richness and shared species from samples. Available online. http://purl.oclc.org/estimates

Cupul-Magaña FG (1996) Incidencia de avifauna en un parque urbano de los Mochis, Sinaloa, Mexico. Cienc ergo sum 3:193–200

Emlen JT (1974) An urban bird community in Tucson, Arizona: derivation, structure, regulation. Condor 76:184–197. doi:10.2307/1366729

Fritts TH, Rodda GH (1998) The role on introduced species in the degradation of island ecosystems: a case study of Guam. Annu Rev Ecol Syst 29:113–140. doi:10.1146/annurev.ecolsys.29.1.113

Gavareski CA (1976) Relation of park size and vegetation to urban bird populations in Seattle, Washington. Condor 78:375–382. doi:10.2307/1367699

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

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391. doi:10.1046/j.1461-0248.2001.00230.x

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

Gritti ES, Smith B, Sykes MT (2006) Vulnerability of Mediterranean Basin ecosystems to climate change and invasion by exotic plant species. J Biogeogr 33:145–157. doi:10.1111/j.1365-2699.2005.01377.x

Grussing D (1980) How to control House Sparrows. Roseville Publication House, California

Hawkes CV, Wren IF, Herman DJ, Firestone MK (2005) Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecol Lett 8:976–985. doi:10.1111/j.1461-0248.2005.00802.x

Huff MH, Bettinger KA, Ferguson ML, Brown MJ, Altman B (2000) A habitat-based point-count protocol for terrestrial birds, emphasizing Washington and Oregon. US Department of Agriculture, Portland

Kalinoski R (1975) Intra- and interspecific aggression in House Finches and House Sparrows. Condor 77:375–384. doi:10.2307/1366086

Kark S, Iwaniuk A, Schalaimtzek A, Banjer E (2007) Living in the city: can anyone become an 'urban exploiter'? J Biogeogr 34:638–651. doi:10.1111/j.1365-2699.2006.01638.x

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

Lennon JJ, Koleff P, Greenwood JJD (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. J Anim Ecol 70:966–979. doi:10.1046/j.0021-8790.2001.00563.x

López E, Bocco G, Mendoza M, Duhau E (2001) Predicting land-cover and land-use change in the urban fringe: a case in Morelia city, Mexico. Landsc Urban Plan 55:271–285. doi:10.1016/S0169-2046(01)00160-8

MacGregor-Fors I, Morales-Pérez L, Schondube JE (in press) From forests to cities: effects of urbanization on subtropical mountain bird communities. Stud Avian Biol

Magurran AE (2004) Measuring biological diversity. Blackwell, Oxford

McAleece N (1997) BioddDversity Professional. Available online. http://www.sams.ac.uk/activities/downloads/downloads.htm

McGillivray WB (1980) Communal nesting in the House Sparrow. J Field Ornithol 51:371–372

McKinney ML (2002) Urbanization, biodiversity, and conservation. Bioscience 52:883–890. doi:10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260. doi:10.1016/j.biocon.2005.09.005

Moreno CE (2001) Métodos para medir la biodiversidad. M&T-Manuales y Tesis SEA, Zaragoza

Ralph CJ, Geupel GR, Pyle P, Martin TE, DeSante DF, Milá B (1996) Manual de métodos de campo para el monitoreo de aves terrestres. US Department of Agriculture, Albany

Robinson RA, Siriwardena GM, Crick HQP (2005) Size and trends of the House Sparrow *Passer domesticus* population in Great Britain. Ibis 147:552–562. doi:10.1111/j.1474-919x.2005.00427.x

Shaw L, Chamberlain D, Evans M (2008) The House Sparrow *Passer domesticus* in urban areas: reviewing a possible link between post-decline distribution and human socioeconomic status. J Ornithol 149:293–299. doi:10.1007/s10336-008-0285-y

Sibley DA (2001) The Sibley guide to birds. Alfred A. Knopf, New York

Smith MD, Knapp AK (2001) Size of the local species pool determines invasibility of a C4-dominated grassland. Oikos 91:55–61. doi:10.1034/j.1600-0706.2001.920107.x

Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: a significant

component of human-caused global change. N Z J Ecol 21:1–16

White JG, Antos MJ, Fitzsimons JA, Palmer GC (2005) Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. Landsc Urban Plan 71:123–135. doi:10.1016/j.landurbplan.2004.02.006

Wichman BA, Hill ID (1982) Algorithm AS 183: an efficient and portable pseudo-random number generator. Appl Stat 31:188–190. doi:10.2307/2347988

Wilson SD, Belcher JW (1989) Plant and bird communities of native prairie and introduced Eurasian vegetation in Manitoba, Canada. Conserv Biol 3:39–44

Zaret TM, Paine RT (1973) Species introduction in a tropical lake. Science 182:449–455. doi:10.1126/science.182.4111.449

Capítulo V

Does size really matter?
Species-area relationships in human settlements

Introduction

Urbanized areas are one of the fastest growing human-created habitats, affecting biodiversity patterns at both local and regional scales (United Nations 2002; McKinney 2006). By replacing natural and agricultural habitats with human-made structures to satisfy human housing needs, urbanized areas exclude a large number of wildlife species (VanDruff and Rowse 1986; Chace and Walsh 2006; Evans et al. 2009 Ortega-Álvarez and MacGregor-Fors 2009). However, human settlements include a large array of resources that could be exploited by wildlife, and thus could act as reservoirs for those species able to reach them, use their resources, and survive their hazards (Emlen 1974). Among human-dominated landscapes, human settlements are well-defined systems, with borders that are ecologically isolated from adjacent habitats (Jokimäki 1999; Fernández-Juricic and Jokimäki 2001; Berkowitz et al. 2003; Batty 2008; Garaffa et al. 2009; MacGregor-Fors 2010). Thus, human settlements can be considered "ecological islands", with the extent of their wildlife communities determined in large part by their size (Davis and Glick 1978; Clergeau et al. 2004).

Previous studies have demonstrated that species richness increases at a decreasing rate in relation to the size of an area (Cain 1938; Connor and McCoy 1978; Rosenzweig 1995; Begon et al. 2006). Such increase in species richness has been closely related to habitat heterogeneity (Boeklen 1986; Báldi 2008, Shen et al. 2009). For birds in particular, species richness has been positively related to the size of habitat patches (Diamond and Mayr 1976; Boeklen 1986, McIntyre 1995; Winter et al. 2006). There are two main effects of the size of human settlements on wildlife species: (1) differences in habitat connectivity; and (2) changes in species richness. Bierwagen (2007) found that larger urban areas have low habitat connectivity values for wildlife, while small- and medium-sized human settlements can maintain or even increase landscape connectivity. Garaffa et al. (2009) explored the effect of human settlement size on bird community structure in Argentinian human settlements ranging from 0.9–10 km2. This study showed that changes in bird communities from rural areas to the urban core depended on the size of the urbanized area. Jokimäki and Kaisanlahti-Jokimäki (2003) found that the composition of wintering bird communities changed in relation to settlement size in Finland (1-8.5 km in diameter). Both studies indicate the existence of human settlement size thresholds affecting bird communities. Urbanized areas larger than such size thresholds have poorer bird communities , which differ from the ones of surrounding rural areas. However, little is known about the way in which the bird species-area relationship occurs across a wide spectrum of human settlement sizes, including large cities.

The aim of this study was to evaluate how species-area relationships occur in human settlements and compare them to those found in a non-urban habitat (i.e., shrubland). We predicted bird species

richness to increase asymptotically with human settlement size. We also expected the bird species-area relationship in human settlements to differ from that of the non-urban habitat in two ways: (1) its slope should be steeper, indicating a higher increase of species in relation to area size for human settlements, and (2) it would asymptote at a lower number of species than the non-urban habitat patches.

Methods

Study area

This study was carried out in northern Michoacán, west-central Mexico. In order to have a representative sample of human settlements with different sizes, we surveyed 13 human settlements (Fig. 1), including the state capital (Morelia: 106.4 km2), two medium-sized cities (Uruapan: 19.25 km2; Zamora: 10.2 km2), one small-sized city (Zinapécuaro: 3.46 km2), and nine other towns, located at least 1.5 km away from each other, with areas ranging from 0.16–1.86 km2 (Table 1). In general, the studied settlements are surrounded by croplands mixed with shrublands, and in some cases small forest patches. We also surveyed bird communities in five shrubland patches ranging from 0.03–28 km2 within the Cuitzeo watershed, where 10 of the 13 studied settlements are located. Shrubland patches were surrounded entirely by another habitat, mainly cropfields and forest, and were located 4–19 km away from the city of Morelia: (1) 0.03 km2 shrubland patch: 6 km SW; (2) 5.25 km2 shrubland patch: 19 km SW; (3) 7 km2 shrubland: 9 km N; (4) 12 km2 shrubland patch: 4 km NNW; and (5) 28 km2 shrubland patch: 17 km NNE. To avoid biogeographic-based biases of comparing bird species richness and composition from patches of different sizes, we concentrated our surveys inside a single geographic region of the Neovolcanic Transversal Axis (Fig. 1).
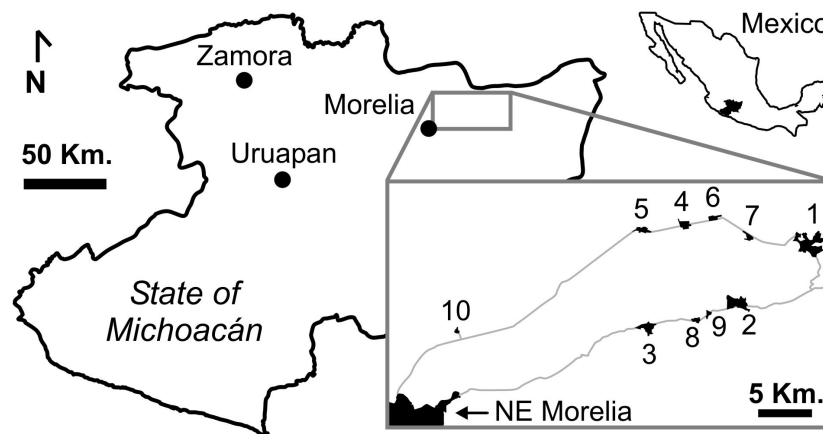

Figure 1. Location of the 13 studied human settlements. The gray line in the inset represents major roads. Numbers within the inset: (1) Zinapécuaro; (2) Queréndaro; (3) Indaparapeo; (4) Francisco Villa; (5) Tzintzimeo; (6) Sn. Bernardo; (7) J. Ma. Morelos; (8) Sn. Lucas Pío; (9) Col. Guadalupe; and (10) Sn. Pedro Sauces.

Bird surveys

We surveyed birds during the breeding season of three consecutive years (May-June 2006, March-April 2007, and March-April 2008) from 07:00 to 11:00. For bird samplings, we carried out point counts (unlimited radius) located at least 250 m away from each other to assure survey independence (Ralph et al. 1996; Huff et al. 2000). All birds seen or heard were recorded and included in our analyses. We selected the sites for our point counts by randomly placing a grid along the polygon of each urbanized area and locating one point count at each intersection. Because we surveyed cities and towns of many different sizes, we used a 250 x 250 m grid for settlements smaller than 10 km2, and a 500 x 500 m grid for settlements larger than 10 km2, with the number of total bird surveys carried out within each settlement being proportional to its size (Table1). To establish our shrubland surveys, we followed the same procedure, using a 250 x 250 m grid. During the three sampling years, all bird surveys were conducted simultaneously by two observers with the same level of training to avoid sampling bias. Each point count location was only visited once.

Analyses

Because our study compares human settlements and shrubland patches of different sizes, the number of independent surveys that could be carried out within each patch differed. In order to eliminate this bias, we estimated bird species richness for each surveyed human settlement and shrubland patch using an abundance-based coverage estimator (ACE; Chao and Lee 1992) employing a Poisson model and cut-off point of 10 individuals (SPADE; Chao and Shen 2006). ACE uses the coefficient of variance of a sub-sample of rare species, determined by a cut-off point, to characterize the degree of heterogeneity among species discovery probabilities, and afterwards estimates the number of missing species in the sample (Chao and Shen 2006). Thus, we calculated ACE for each habitat patch using six independent point count locations, which represent the lowest number of point counts performed in most small-sized human settlements. Because we could only perform four point counts in three small-sized human settlements (i.e., Sn. Pedro Sauces, Col. Guadalupe, J. Ma. Morelos), we combined their data to achieve the minimum sample size of six point-counts, and consider the resulting species richness value for an average of their patch sizes. Since using only six point counts to describe the bird species richness of larger habitat patches could be misleading, we randomly selected 10 samples of six point counts for patches >1 km2, and used the average value of the 10 predictions to represent patch species richness. This allowed us to generate a comparable set of bird species richness predictions for all surveyed settlements and shrublands, irrespective of total sampling effort. We considered the comparable estimated species richness value for each habitat patch as one data point in our analyses.

We assessed two species-area relationships: (1) among the 13 surveyed human settlements; and (2) among the five surveyed shrubland patches. For this we performed linear regressions between the size of the studied human settlement and shrubland patches and their estimated bird species richness. As species-area relationships are not linear (see Rosenzweig 1995 and references therein), we transformed our data (log10-log10). To evaluate if the rates at which bird species richness increases with patch size differed among human settlements and shrublands, we performed ANCOVA to compare their slopes and intercepts. As linear species-area relationships do not allow identifying if species richness values stop increasing as the size of the patches increase, we used non-transformed data to perform a logarithmic regression. Because non-linearized species-area relationships tend to "saturate", we

modelled the asymptotic relationship between species richness and area size using Michaelis-Menten kinetics to determine the maximum number of bird species that could exist in a human settlement or shrubland. We assumed the maximum number of species in a habitat (Smax) to be equivalent to Vmax, species number to be equivalent to reaction rate (V0), and patch size to be equivalent to substrate concentration ([S]). In order to obtain Smax and the patch size at which this value was reached in each habitat, we analysed our data using the Eadie-Hofstee representation of the Michaelis-Menten model (Atkins and Nimmo 1975; Lehninger 1988).

Variables other than patch size have been related to bird species richness in urban systems (i.e., built cover, plant species richness, tree cover, or human population density; DeGraff and Wentworth 1986; Munyenyembe et al. 1989; Blair 1996; Allen and O'Conner 2000; Pautasso 2007; Tratalos et al. 2007; MacGregor-Fors 2008; Aurora et al. 2009; Pautasso and Dinetti 2009; Strohbach et al. 2009; Trollope et al. 2009; among others). Based on the latter, we used linear regressions to test whether other variables were related to bird species richness. Because 80% of the tested variables were strongly correlated among each other, we did not perform a multivariate analysis as we could not avoid multicollinearity (StatSoft Inc 2010). Thus, in addition to linear regression analyses, we used a Bonferroni correction to reduce Type I errors (α/k, where k is the number of analyses; 0.05/5), using an $\alpha = 0.01$. As this method tends to increase Type II errors to unacceptable levels (Nakagawa 2004), we calculated the statistical power of our regressions, considering a minimum power value of 0.80 (following Park 2008).

Finally, to evaluate if the size of the studied human settlements was related to changes in bird community composition, we used the Jaccard coefficient of similarity (Jaccard 1912) in two analyses. First, we performed a multivariate cluster analysis (average linkage) using BioDiversity Professional (McAleece 1997) to determine how similar the bird communities were across the sampled human settlements. Second, we evaluated if the similarity of bird communities changed in relation to the size of human settlement. For this, we used the Jaccard similarity values output by BioDiversity Professional for each human settlement in relation to the largest studied city (i.e., Morelia) and correlated them to the size of the human settlements in our dataset.

Results

Both species-area relationships showed that species richness increased significantly in relation to patch size (Fig. 2). Estimated bird species richness was strongly and significantly related to the size of the studied human settlement ($r^2 = 0.67$, $P = 0.001$) and shrubland patches ($r^2 = 0.75$, $P = 0.04$). The slopes and intercepts of the log-log species-area relationships were statistically different between human settlement and shrublands. Shrubland species-area relationship had a shallower slope, and started at a higher species richness value than the species-area relationship recorded in human settlements (slopes: $F_{1,13} = 5.98$, $P = 0.02$; intercepts: $F_{1,13} = 27.14$, $P < 0.001$; Fig. 2).

When fitted to the logarithmic function, the species-area relationship only remained significant in human settlements (human settlements: $r^2 = 0.61$, $P = 0.002$; shrublands: $r^2 = 0.69$, $P = 0.08$). Using a comparable patch size of 30 km^2 to contrast bird species richness at both studied habitats, the regression line for shrublands had a value of 31.2 predicted bird species, while human settlements showed ~30% less species richness (22.5 predicted bird species). The maximum number of species per habitat (S_{max}) was 1.4 times higher in shrublands (28.7 species) when compared to human settlements

Table 1. Size, number of surveys, vegetation traits, human population values, and bird species richness values for the 13 surveyed human settlements.

City/town	Size (km²)	Number of surveys[1]	Built cover (%)[2]	Tree cover (%)[2]	Plant richness[2]	Human density (ind / km²)[3]	Total human population	Bird species richness (ACE)[4]
Sn. Pedro Sauces	0.16	4	75	5.5	2.3	9668.7	1547	7.3
Col. Guadalupe	0.22	4	35	15	3.8	3700	814	7.3
Sn. Lucas Pío	0.3	6	50	17	3.4	9483.4	2845	9.6
J. Ma. Morelos	0.37	4	40	1.5	3.8	5891.9	2180	8.9
Sn. Bernardo	0.41	6	45	11.7	2.8	529.3	217	10.1
Tzintzimeo	0.56	8	80	16.3	4.5	2112.5	1183	9.9
Francisco Villa	0.61	6	70	16.7	2.1	1767.2	1078	10.3
Indaparapeo	1.06	12	70	11.5	3.6	6170.8	6541	14.9
Queréndaro	1.86	20	60	11.6	2.8	4534.9	8435	15.1
Zinapécuaro	3.46	28	80	8.1	1.3	4239.9	14670	8.8
Zamora	10.2	43	90	10.1	1.8	12510.4	127606	19.7
Uruapan	19.25	80	90	16.5	3.9	12414.3	238975	32.9
Morelia	106.4	204	85	16.1	4.1	5714.5	608049	20.5

[1]Although the total number of surveys differs among human settlements due to their size, we used an equal number of surveys per settlement for the analysis (see note 4 for details).

[2]Average values for all surveys.

[3]Data obtained from the Count of Population and Housing from 2005 (INEGI 2005) and divided by the size of each settlement.

[4]As stated in the methods, we calculated ACE using six independent point counts, the lowest number of point counts performed in most small-sized human settlements, to avoid sampling effort bias. Due to the large number of surveys performed in settlements >1 km², we randomly selected 10 samples of six point counts for patches for Indaparapeo, Queréndaro, Zinapécuaro, Zamora, Uruapan, and Morelia, and used the average value of the 10 predictions to represent patch species richness.
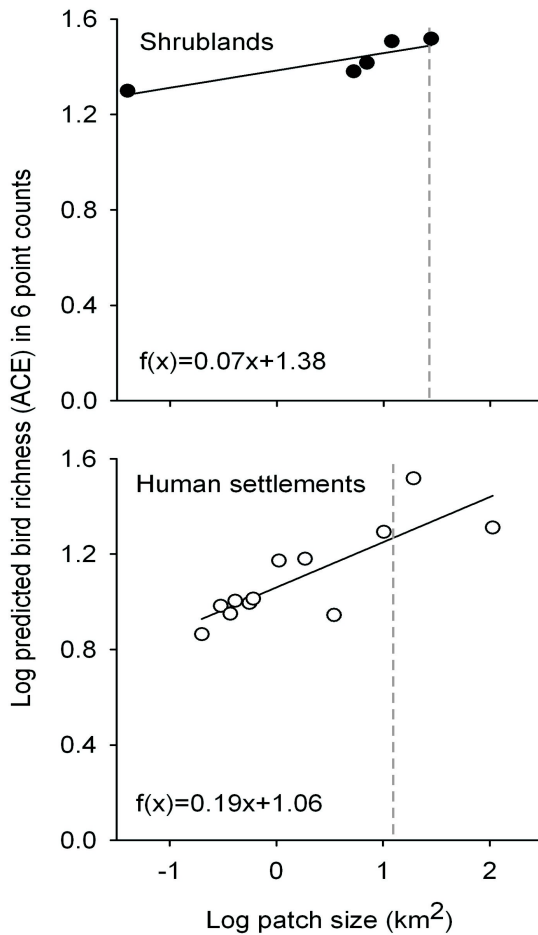
Figure 2. Log-log species-area relationship for birds in shrubland and human settlement patches. While the species-area relationship occurred for both habitats, the slope was steeper and the intercept starts in a significantly lower species richness value in human settlements, when compared to shrublands. The equation of the regression line for each species-area relationship is displayed. Segmented grey lines represents the patch size at which non-linear analyses suggest that species richness stops increasing.

(20.1 species). In human settlements, S_{max} was reached at a patch size of 12.59 km², while patch size required to reach S_{max} shrublands was 28.71 km². These values were only used for comparative purposes among habitats as they do not represent real S_{max} values due to their calculation from a sub-sample of medium- to large-sized settlements.

When we evaluated possible relationships regarding human settlement variables that could affect bird species richness, only patch size showed a strong and significant relationship ($r^2 = 0.67$, $P = 0.001$, statistical power $= 0.93$). The rest of the variables we examined showed non-significant relationships related to both α (<0.01 after Bonferroni correction) and statistical power: (1) built cover ($r^2 = 0.39$, $P = 0.03$, statistical power $= 0.60$); (2) human population density ($r^2 = 0.14$, $P = 0.19$, statistical power $= 0.25$); (3) plant species richness ($r^2 = 0.06$, $P = 0.38$, statistical power $= 0.12$); and (4) tree cover ($r^2 = 0.11$, $P = 0.28$, statistical power $= 0.17$).

The multivariate cluster analysis using the Jaccard coefficient of similarity showed that the recorded bird communities pertain to three main groups (Fig. 3). The first group consisted of 20 of the total recorded bird species that were shared by most human settlement sizes in our study (Table 2). This group is represented in the dendrogram as the basal line between clusters (up to 17.5% similarity), and indicates the existence of a "basic-urbanization package" of species that are able to exploit urban resources independently of human settlement size. The second group was comprised of a large cluster containing bird communities from all small- to medium-sized human settlements (0.16–3.46 km^2; Table 2). The remaining cluster included the bird communities associated with large-size human settlements (10.2–106.4 km^2; Table 2), which indicates the existence of an "urbanization-growth package" of species. We also found a positive significant correlation between the Jaccard similarity value for each human settlement in relation to the largest city in the study (Morelia) and human settlement size (r = 0.94, $P < 0.001$; Fig. 3).
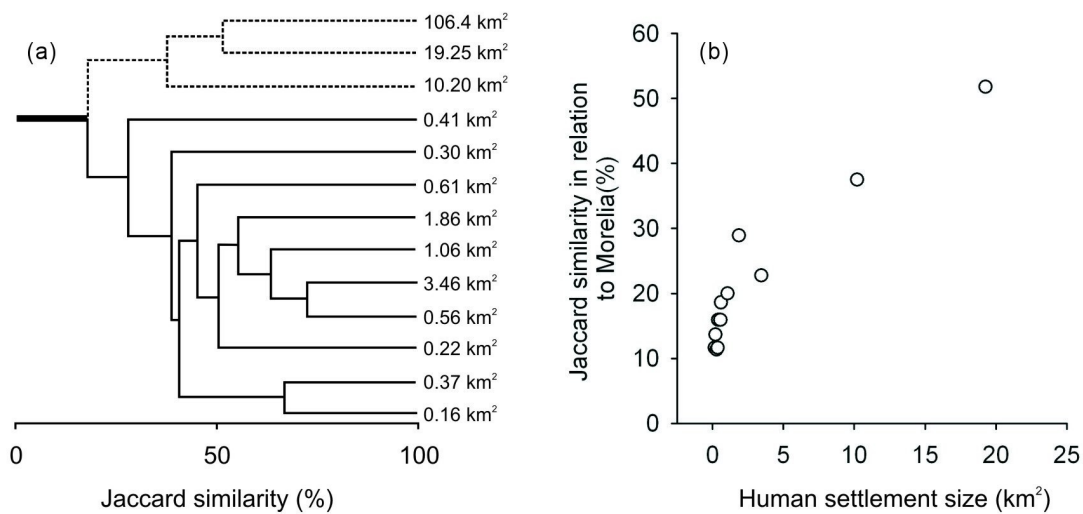

Figure 3. (a) The multivariate cluster analysis revealed the existence of two main groups of bird species associated with human settlement size: (1) a "basic-urbanization package" of bird species generated by a 17.5% similarity among all human settlements (basal bold solid line); and (2) a "urbanization-growth package" comprised of bird species recorded only in large-size human settlements (10.2–106.4 km^2; segmented lines). The large cluster comprised of small- and medium-sized settlements (0.16–3.46 km^2; solid lines) is generated by the absence of the "urbanization-growth package". (b) The relationship between the Jaccard similarity value for each settlement in relation to the largest human settlement and settlement size, shows a linear increase in similarity as settlement size increases. This result indicates that small- and large-sized human settlements have strikingly different bird community compositions.

Discussion

Although species-area relationships have been widely studied by ecologists using habitat patches of different sizes in the past (Cain 1938; MacArthur and Wilson 1963; MacArthur and Levins 1967; Connor and McCoy 1979; Boecklen 1986; Rosenzweig 1995, Martin and Goldenfeld 2006; Magura et al. 2008; Dengler 2009; among others), such relationship for birds in human settlements of different sizes had not been described. Our study shows that species-area relationships occur for bird

communities in human settlements of different sizes. However, the way in which bird species richness rises in relation to human settlement size differs greatly from the pattern found for a non-urban habitat (i.e., shrubland) located in the same region. In this section, we first discuss the ecological implications of the differences found in the species-area relationship across the habitat types in our study. Second, we consider the relative role that factors other than patch size could play in determining bird species richness in human settlements of different sizes. Third, we focus on bird community shifts related to the size of human settlements. Finally, we underline the existence of human settlement patch size thresholds and their role in determining species richness and composition of urban-dwelling bird communities.

Our results show that both studied species-area relationships differ greatly (Fig. 2). Both the intercept and the slope of the log-log species-area relationships differed significantly between the two studied habitat types. The difference between the intercepts was caused by small-sized human settlements having lower bird species richness than small shrubland patches. The difference between the slopes indicates that species richness rises faster in relation to patch size in human settlements than it does in shrubland patches. However, while human settlements exhibited a steeper species-area slope, bird species richness values were ~30% lower in human settlements than in shrublands when using a comparable patch size of 30 km^2. Similar patterns have been observed in previous studies assessing species-area relationships in human-disturbed landscapes. Carey et al. (2006) reported that species-area relationships for subalpine plants show different trends, with sites where human disturbance is recent exhibiting lower intercepts with steeper slopes than those that had a longer time to recover from previous human disturbance. The similarity between our results and those of Carey et al. (2006) suggests that human disturbance regimes affect the species area relationships similarly in both natural and human-altered ecosystems, lowering species richness in small size patches and modifying the rate at which species are added as patch size increases.

Our analyses relating different habitat traits in the studied human settlements (i.e., tree cover, built cover, human population density, plant species richness, human settlement size) indicates that only human settlement size is related to bird species richness. Our results are similar to those of Pautasso and Dinetti (2009), who reported that total human population size, a variable closely related to human settlement size, was positively correlated with total bird species richness. However, our results differed from previous findings for the other variables, which have found bird species richness in urban areas to be: (1) positively related to tree cover (e.g., Munyenyembe et al. 1989; MacGregor-Fors 2008; Trollope et al. 2009); (2) negatively related to built cover (Blair 1996; Tratalos et al. 2007); (3) negatively related to human population density (Strohbach et al. 2009); and (4) positively related to plant species richness (Pautasso 2007). One possible cause explaining the recorded differences between our results and those from other studies could be the scale of analysis. Most of the urban bird ecology studies that we reviewed focus their analysis at a local level, relating habitat attributes with the bird species found in the same plot. This allows a higher level of detail when measuring and correlating variables. At our level of analysis, we are considering entire human settlements as operative units. This scale does not allow us to measure site-specific responses, but permits understanding of human settlements as discrete units (Manel et al. 2000). For example, in a small-scale study, sampling points with trees have more bird species than sites without trees. However, when working at a city level, using average values eliminates the variance of the variables that are causing the relationship, pinpointing the relative importance of local analyses (Evans et al. 2009). In fact, a previous study performed in Morelia

(MacGregor-Fors et al. in press) shows that total bird species richness is related to habitat traits, such as tree cover. Thus, our results suggest that the remaining 33% of the variance explaining bird species richness in the human settlements not related to human settlement size should be caused by habitat-specific variables.

Our results also demonstrate important bird community composition shifts related to the size of the studied human settlements. The multivariate cluster analysis revealed the existence of two main groups of bird species associated with human settlement size. First, a "basic-urbanization package" of bird species generated by a 17.5% similarity among all human settlements. This set of species, shared by most of the studied settlements, was comprised of similar proportions of insectivore, omnivore, and granivore species that nest mainly in trees, shrubs, cavities, and buildings. This result is fairly similar to what has been found for other urban areas, with urbanization favouring insectivore, granivore, omnivore, and cavity nesting species (see Chace and Walsh 2006 and references therein; MacGregor-Fors 2008). Second, an "urbanization-growth package" including bird species recorded only in large-size human settlements (10.2–106.4 km^2). This set of species is comprised of birds pertaining to a diverse set of food guilds (i.e., insectivore, granivore, omnivore, frugivore, nectarivore, carnivore), mainly dominated by insectivore species. Species included in the "urbanization-growth package" mainly use vegetation components for nesting, while just a few nest in cavities or buildings. Interestingly, this package includes species that nest on the ground or in tall grasses (i.e., *Geothlypis poliocephala, G. speciosa, Myadestes occidentalis, Sturnella magna*).

Two recent studies have assessed bird species traits related to urbanization. Their results show that birds that can become established in urban areas tend to be omnivorous, gregarious, sedentary, enclosed-nesting, and widespread species with large breeding ranges, elevated dispersal ability, high adult survival rate, and high annual fecundity (Croci et al. 2008; Møller 2009). Our results support the findings from both cited studies, showing that the "basic-urbanization package" is comprised by generalist widespread bird species. On the other hand, the "urbanization-growth package" is concordant with the urban-intolerant group of species determined by Croci et al. (2008). Comparable to our "urbanization-growth package", this group is comprised of species that, among other traits, are solitary, and are ground- and/or open-nesters. Recording a high number of bird species with traits that could make them "intolerant" to urbanization could be explained by two non-exclusive hypotheses: (1) the existence of intra-specific source-sink dynamics within urban areas and along urban-wildland matrixes (Schoech and Bowman 2001; Anderies et al. 2007); and/or (2) birds using urban habitats due to the abundance and predictability of food resources (Shochat 2004; Robb et al. 2008) but reproducing in nearby non-urban habitats. Finally, our results from the Jaccard index analysis (Fig. 3b) reinforce the existence of an "urbanization-growth package", as the proportion of shared species increases in relation to the largest settlement as the size of the smaller settlements increases.

Our results demonstrate that bird species richness increases and species composition changes with human settlement size, suggesting that urban areas act as ecological islands. This is similar to what Pyšek (1998) and MacGregor-Fors (2010) have found for the flora and bird communities of urban areas. Based on our results, we identified two bird community thresholds related to the size of human settlements. Our data show that bird species richness reaches its asymptote in human settlements ranging from 10.2–19.25 km^2. We also found an important difference in bird community composition, generated by the existence of an "urbanization-growth package", that occurs in settlement sizes larger

than 10.2 km^2. Similarly, previous studies have reported thresholds in bird species richness and community composition related to the total human population of human settlements (Jokimäki and Kaisanlahti-Jokimäki 2003; Garaffa et al. 2009). When considering total human population of the human settlements in our study, our thresholds are reached at ~128,000 inhabitants. This value is 1.2 times larger than the higher threshold value reported by Jokimäki and Kaisanlahti-Jokimäki (2003) for Finnish cities (105,000 inhabitants), and 3.6 times than the higher threshold value reported by Garaffa et al. (2009) for Argentinean cities (35,000 inhabitants). These differences show that none of the reported thresholds are constant among bio-regions. Thus, the size of human settlements should be taken into account when performing urban ecology studies, and/or when managing urban-dwelling wildlife.

Table 2. Bird species recorded in the studied human settlements. Based on the multivariate cluster analysis (Jaccard), we classified the recorded bird species in two categories: (1) basic-urbanization package: species represented in all the range of studied human settlement sizes; (2) urbanization-growth: species unique to medium- to large-sized settlements (>10.2 km^2).

Package	Species	Food guild[1]	Nesting
Basic-urbanization	Carpodacus mexicanus	Granivore	Tree/shrub
	Catherpes mexicanus	Insectivore	Cavity
	Columba livia	Granivore	Building
	Columbina inca	Granivore	Tree/shrub
	Crotophaga sulcirostris	Insectivore	Tree/shrub
	Hirundo rustica	Insectivore	Building
	Icterus bullockii	Omnivore	Tree
	Melanerpes aurifrons	Omnivore	Cavity
	Passer domesticus	Omnivore	Building/tree
	Pipilo fuscus	Granivore	Tree/shrub
	Pyrocephalus rubinus	Insectivore	Tree
	Quiscalus mexicanus	Omnivore	Tree
	Spinus psaltria	Granivore	Tree/shrub
	Sporophila torqueola	Granivore	Tree/shrub
	Tyrannus vociferans	Insectivore	Tree
	Vireo gilvus	Insectivore	Tree
	Icterus abeillei*	Omnivore	Tree
	Icterus pustulatus*	Omnivore	Tree
	Stelgidopteryx serripennis*	Insectivore	Cavity
	Tachycineta thalassina*	Insectivore	Cavity
Urbanization-growth	Aeronautes saxatalis	Insectivore	Cavity
	Agelaius phoeniceus	Omnivore	Shrub
	Amazilia beryllina	Nectarivore	Tree/shrub
	Amazilia violiceps	Nectarivore	Tree/shrub
	Bubulcus ibis	Omnivore	Tree/shrub
	Buteo jamaicensis	Carnivore	Tree
	Campylorhynchus gularis	Insectivore	Tree/shrub
	Catharus aurantiirostris	Insectivore	Shrub
	Chaetura vauxi	Insectivore	Tree/Building
	Contopus pertinax	Insectivore	Tree
	Contopus sordidulus	Insectivore	Tree
	Corvus corax	Omnivore	Tree
	Cynanthus latirostris	Nectarivore	Tree/shrub

Table 2. (continued)

Package	Species	Food guild[1]	Nesting
Urbanization-growth	*Elanus leucurus*	Carnivore	Tree
	Geothlypis poliocephala	Insectivore	Grass
	Geothlypis speciosa	Insectivore	Grass
	Heliomaster constantii	Nectarivore	Tree
	Icterus wagleri	Omnivore	Tree
	Lanius ludovicianus	Carnivore	Tree/shrub
	Melanotis caerulescens	Insectivore	Tree/shrub
	Molothrus aeneus	Granivore	Parasite
	Myadestes occidentalis	Frugivore	Ground
	Myiarchus nuttingi	Insectivore	Tree/cavity
	Myioborus miniatus	Insectivore	Tree/cavity
	Nycticorax nycticorax	Omnivore	Tree
	Passerina caerulea	Granivore	Tree/shrub
	Passerina versicolor	Granivore	Tree/shrub
	Petrochelidon pyrrhonota	Insectivore	Cavity
	Pheucticus melanocephalus	Granivore	Tree/shrub
	Picoides scalaris	Insectivore	Cavity
	Piranga flava	Insectivore	Tree
	Ptilogonys cinereus	Frugivore	Tree
	Sialia sialis	Insectivore	Cavity
	Spizella passerina	Granivore	Shrub
	Sturnella magna	Insectivore	Ground
	Thryomanes bewickii	Insectivore	Cavity
	Toxostoma curvirostre	Insectivore	Tree/shrub
	Troglodytes aedon	Insectivore	Cavity
	Turdus assimilis	Frugivore	Tree
	Turdus migratorius	Frugivore	Tree/shrub
	Turdus rufopalliatus	Frugivore	Tree/shrub
	Volatinia jacarina	Granivore	Tree/shrub
	Zenaida asiatica	Granivore	Shrub

[1]Primary feeding preference. When three or more main feeding groups are implied, we grouped species under "omnivore".

*Species that were recorded only in small- to medium-sized settlements (0.16–3.46 km^2) using the point count method. However, they were recorded in large-sized settlements (10.2–106.4 km^2) between surveys. Thus, we consider them in the "basic-urbanization package".

Acknowledgments

Literature cited

Allen, A.P., O'Conner, R.J. (2000) Hierchical correlates of bird assemblage structure on Northeastern U.S.A. lakes. *Environmental Monitoring and Assessment*, **62**, 15–37.

Anderies, J.M., Katti, M., Shochat, E. (2007) Living in the city: Resource availability, predation, and bird population dynamics in urban areas. *Journal of Theoretical Biology*, **247**, 36–49.

Atkins, G.L. & Nimmo, I.A. (1975). A comparison of seven methods for fitting the Michaelis-Menten equation. *Biochemical Journal,* **149,** 775-777.

Aurora, A.L., Simpson, T.R., Small, M.F., Bender, K.C. (2009) Toward increasing avian diversity: Urban wildscapes programs. *Urban Ecosystems*, **12**, 347–358.

Báldi, A. (2008). Habitat heterogeneity overrides the species-area relationship. *Journal of Biogeography*, **35**, 675-681.

Batty, M. (2008). The size, scale, and shape of cities. *Science*, 319, 769-771.

Begon, M., Townsend, C.R. & Harper, J.L. (2006). *Ecology: From individuals to ecosystems*, London, Blackwell Publishing.

Berkowitz, A.R., Nolon, C.H. & Hollweg, K.S. (2003). *Understanding urban ecosystems - A new frontier for science and education*, New York, Springer-Verlag.

Bierwagen, B.G. (2007) Connectivity in urbanizing landscapes: The importance of habitat configuration, urban area size, and dispersal. *Urban Ecosystems*, **10**, 29–42.

Blair, R.B. (1996) Land use and avian species diversity along an urban gradient. *Ecological Applications*, **6**, 506–519.

Boecklen, W.J. (1986). Effects of habitat heterogeneity on the species-area relationships of forest birds. *Journal of Biogeography*, **13**, 59-68.

Cain, S.A. (1938). The species-area curve. *American Midland Naturalist*, **19**, 573-581.

Carey, S., Harte, J., del Moral, R. (2006) Effect of community assembly and primary succession on the species-area relationship in disturbed ecosystems. *Ecography*, **29**, 866–872.

Chace, J.F. & Walsh, J.J. (2006). Urban effects on native avifauna: a review. *Landscape and Urban Planning*, **74**, 46-69.

Chao, A. & Lee, S.M. (1992). Estimating the number of classes via sample coverage. *Journal of the American Statistical Association*, **87**, 210-217.

Chao, A. & Shen, T.J. (2006). *Program SPADE (Species prediction and Diversity Estimation)*. Version 3.1. <http://chao.stat.nthu.tw>.

Clergeau, P., Croci, S. & Jokimäki, J. (2004) How useful are urban island ecosystems for defining invader patterns? *Environmental Conservation,* **31,** 181–184.

Connor, E.F. & McCoy, E.D. (1979). The statistics and biology of the species-area relationship. *American Naturalist*, **113**, 791-833.

Croci, S., Butet, A. & Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits? *The Condor*, **110**, 223-240.

Davis, A.M. & Glick, T.F. (1978). Urban ecosystems and island biogeography. *Environmental Conservation,* **5,** 299–304.

DeGraff, R.M., Wentworth, J.M. (1986) Avian guild structure and habitat associations in suburban bird communities. *Urban Ecology*, **9**, 399–412.

Dengler, J. (2009) Which function describes the species-area relationship best? A review and empirical evaluation. *Journal of Biogeography*, **36**, 728–744.

Diamond, J.M., Mayr, E. (1976) Species-area relation for birds of the Solomon Archipelago. *Proceedings of the National Academy of Sciences of the United States of America*, **73**, 262–266.

Emlen, J.T. (1974) An urban bird community in Tucson, Arizona: Derivation, structure, regulation. *The Condor*, 76, 184-197.

Evans, K.L., Newson, S.E., Gaston, K.J. (2009) Habitat influences on urban avian assemblages. *Ibis*, **151**, 19–39.

Fernández-Juricic, E. & Jokimäki, J. (2001). A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity and Conservation*, **10**, 2023-2043.

Garaffa, P.I., Filloy, J. & Bellocq, M.I. (2009). Bird community responses along urban–rural gradients: Does the size of the urbanized area matter? *Landscape and Urban Planning*, **90**, 33-41.

Jaccard, P. (1912) The distribution of the flora in the alpine zone. *New Phytologist*, **11**, 37-50.

Huff, M.H., Bettinger, K.A., Ferguson, M.L., Brown, M.J. & Altman, B. (2000). *A habitat-based point-count protocol for terrestrial birds, emphasizing Washington and Oregon*, Portland, U.S. Department of Agriculture.

Jokimäki, J. (1999). Occurrence of breeding bird species in urban parks: Effects of park structure and broad-scale variables. *Urban Ecosystems*, **3**, 21-34.

Jokimäki, J. & Kaisanlahti-Jokimäki, M.L. (2003). Spatial similarity of urban bird communities: A multiscale approach. *Journal of Biogeography*, **30**, 1183-1193.

Lenhinger, A.L. (1988). *Bioquímica*, Barcelona, Ediciones Omega.

MacArthur, R.H. & Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *American Naturalist*, **101**, 377-385.

MacArthur, R.H. & Wilson, E.O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373-387.

MacGregor-Fors, I. (2008) Relation between habitat attributes and bird richness in a western Mexico suburb. *Landscape and Urban Planning*, **84**, 92-98.

MacGregor-Fors, I. (2010). How to measure the urban-wildland ecotone: Redefining 'peri-urban' areas. *Ecological Research*, **25**, 883-887.

MacGregor-Fors, I., Morales-Pérez, L. & Schondube, J.E. (In press). From forests to cities: Effects of urbanization on subtropical mountain bird communities. *Studies in Avian Biology*.

Magura, T., Báldi, A. & Horváth, R. (2008). Breakdown of the species-area relationship in exotic but not in native forest patches. *Acta Oecologica-International Journal of Ecology*, **33**, 272-279.

Manel, S, Buckton, S.T. & Ormerod, S.J. (2000). Testing large-scale hypothesis using surveys: The effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology* **37**, 765-770.

Martin, H.G. & Goldenfeld, N. (2006). On the origin and robustness of power-law species–area relationships in ecology. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 10310-10315.

McAleece, N. (1997) *BioDiversity Professional*. <http://www.sams.ac.uk/research/software>.

McIntyre, N.E. (1995). Effects of forest patch size on avian diversity. *Landscape Ecology*, **10**, 85-99.

McKinney, M.L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247-260.

Møller, A.P. (2009) Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, **159**, 849–858.

Munyenyembe, F., Harris, J., Hone, J. (1989) Determinants of bird populations in an urban area. *Australian Journal of Ecology*, **14**, 549-557.

Nakagawa, S. (2004) A farewell to Bonferroni: The problems of low statistical power and publication bias. *Behavioral Ecology*, **15**, 1044-1045.

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 and Urban Planning*, **90**, 189-195.

Park, H.M. (2008) *Hypothesis testing and statistical power of a test*. Indiana, The Trustees of Indiana University.

Pautasso, M. (2007) Scale dependence of the correlation between human population presence and vertebrate and plant species richness. *Ecology Letters*, **10**, 16–24.

Pautasso, M., Dinetti, M. (2009) Avian species richness human population and protected areas across Italy's regions . *Environmental Conservation*, **36**, 22-31.

Pyšek, P. (1998) Alien and native species in Central European urban floras: A quantitative comparison. *Journal of Biogeography*, **25**, 155-163.

Ralph, C.J., Geupel, G.R., Pyle, P., Martin, T.E., DeSante, D.F. & Milá, B. (1996). *Manual de métodos de campo para el monitoreo de aves terrestres*, Albany, CA., U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Gen. Tech. Rep. PSW-GTR-144.

Robb, G.N., McDonald, R.A., Chamberlain, D.E. & Bearhop, S. (2008). Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment*, **6**, 476-484.

Rosenzweig, M.L. (1995). *Species diversity in space and time*, Cambridge, Cambridge University Press.

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

Schoech, S.J., Bowman, R. (2001) Variation in the timing of breeding between suburban and wildland Florida Scrub-Jays: Do physiologic measures reflect different environments? *Avian conservation and ecology in an urbanizing world* (eds J.M. Marzluff, R. Bowman and R. Donnely), pp. 289-306. Kluwer Academic, Boston.

Shen, G., Yu, M., Hu, X.S., Mi, X., Ren, H., Sun, I.F., Ma, K. (2009) Species-area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. *Ecology*, **90**, 3033–3041.

Strohbach, M.W., Haase, D., Kabsich, N. (2009) Birds and the city: Urban biodiversity, land Use, and socioeconomics. *Ecology and Society*, **14(2)**, 31.

StatSoft Inc. (2010) *Electronic Statistics Textbook*, Tulsa, StatSoft. WEB.

Tratalos, J., Fuller, R.A., Evans, K.L., Davies, R.G., Newson, S.E., Greenwood, J.J.D., Gaston, K.J. (2007) Bird densities are associated with household densities. *Global Change Biology*, **13**, 1685-1695.

Trollope, S.T., White, J.G., Cooke, R. (2009) The response of ground and bark foraging insectivorous birds across an urban–forest gradient. *Landscape and Urban Planning*, **93**, 142–150.

United Nations (2002). *World urbanization prospects: the 2001 revision, data tables and highlights*, New York, Population Division of the Department of Economic and Social Affairs.

VanDruff, L.W. & Rowse, R.N. (1986). Habitat association of mammals in Syracuse, New York. *Urban Ecology*, **9**, 413-434.

Winter, M., Johnson, D.H., Shaffer, J.A., Donovan, T.M. & Svedarsky, W.D. (2006). Patch size and landscape effects on density and nesting success of grassland birds. *Journal of Wildlife Management*, **70**, 158-172.

Migrating to the city: Responses of neotropical migrant bird communities to urbanization

Introduction

Urbanization is one of the human activities that severely threatens biodiversity (Czech and Krausman 1997, Czech et al. 2000). By substituting natural habitats with urban structures and different plant species, the process of urbanization leads to habitat homogenization (Moll 1997, Blair 2001). These modifications are usually intense and long-term, leaving no opportunity for ecological succession to occur (McKinney 2006). Financial and commercial centralization in urban areas has lead human population from being mainly rural to becoming mostly urban in the last decade, deriving in the expansion of urban areas worldwide (United Nations 2004, Grimm et al. 2008).

In general, urban ecology studies have shown negative effects of urbanization on bird communities, with bird species richness decreasing and abundances of only a few human-related species increasing with urbanization (Chace and Walsh 2006, Ortega-Álvarez and MacGregor-Fors 2009, Chiari et al. 2010, MacGregor-Fors et al. in press). Elevated bird abundances in urban areas tend to be related to a few exotic species (e.g., House Sparrow–*Passer domesticus*, Rock Pigeon–*Columba livia*, European Starling–*Sturnus vulgaris*; Emlen 1974, Gavareski 1976, Jokimäki and Kaisanlahti-Jokimäki 2003, MacGregor-Fors et al. 2010), which often alter urban bird community evenness (Ortega-Álvarez and MacGregor-Fors 2009, MacGregor-Fors et al. 2010, in press). Nevertheless, there is a dearth of knowledge on the effects that habitat transformation due to urbanization have on neotropical migrant bird communities (e.g., Rodewald and Shustack 2008, Kohut et al. 2009). As far as we know, only one study has described the migrant bird community of a neotropical city (Mexico City; Nocedal 1987), but does not offer information on the factors affecting neotropical migrant bird diversity.

In this study, we evaluated how neotropical migrant birds respond to urbanization. Our main objectives were: (1) to evaluate shifts in neotropical migrant bird community density and species richness related to the replacement of natural habitats by urban ones; and (2) to identify which habitat variables determine neotropical migrant density and species richness. Drawn from what has been reported for urban resident bird communities, we predicted that neotropical migrant bird species richness would decrease, while the abundance of a few migratory species able to exploit human settlements would increase within urban areas.

Methods

Study area

This study was carried out within the Cuitzeo watershed, located in north-east Michoacán, West

Mexico. The watershed is located within one of the most important areas for migratory landbird conservation in the Americas, and comprises one of the regions that sustain highest species richness and densities of neotropical migrant birds in the world (Rich et al. 2004). Our surveys were conducted in the city of Morelia and native forests similar to those that formerly covered the area now occupied by the city (pine-oak, and oak forests; Madrigal 1997). Morelia is a colonial city established during the sixteenth century (19°42'07"N, 101°11'33'W; ~ 1925 m asl), which has undergone rapid and unplanned development in the last decades (López et al. 2001, Vargas Uribe 2008). At present, Morelia covers an area ~ 100 km^2 and has a population that exceeds one million inhabitants (Vargas Uribe 2008). The surveyed native forests patches are the most well-preserved we could find within the Cuitzeo watershed and were located ~28 km away from the center of the city (i.e., ~8 km South, ~14 km South, ~18 km East, ~24 km Southwest, ~49 km Northeast, ~53 km Northeast). We assume that bird communities within the surveyed forest sites are representative of those that formerly occurred in the area now occupied by the city (MacGregor-Fors et al. in press).

Bird surveys

We surveyed neotropical migrant bird communities from December 2006 to February 2007. We conducted our surveys from 07:00 to 10:00, which consisted of 10 min point counts (unlimited radius; Ralph et al. 1996), located at least 250 m from each other in order to ensure survey independence (Ralph et al. 1996, Huff et al. 2000). We measured the distance from the observer to each bird registered, using a rangefinder (Bushnell Yardage Pro). All birds recorded using the habitat surveyed were included in our analysis.

We surveyed a total of 70 independent point counts within native forests. Within the city of Morelia, we carried out a citywide survey comprised of 204 independent points. Point counts for the citywide survey were established in each intersection of a 500 x 500 m grid randomly placed over the polygon of the city, allowing us to gather a random sample of the widespread residential and commercial areas within the city. Due to the non-homogeneous distribution of parks, cemeteries, and industrial areas within the city, we added 15 sampling points to obtain a representative sample of these urban land-uses. Of the 204 urban sampling points, 104 were located in residential-commercial areas, 60 in residential areas, 15 in parks, 12 in commercial areas, seven in cemeteries, and six in industrial areas. The number of sampling points per land-use categories is proportional to the total area covered by each land-use category within the city. For comparisons between forest and urban neotropical bird communities we randomly selected 70 points from the citywide survey.

Habitat characterization

We measured 17 variables within a 25 m radius area for all the points surveyed in both native forests and the city. This set of variables describes the four major components related to bird communities within each sampling point: (1) vegetation traits; (2) socio-economy; (3) urban infrastructure; and (4) human activities (Blair 1996, Melles et al. 2003, Chace and Walsh 2006, Evans et al. 2009). Of these, 12 variables describe vegetation (tree cover, species richness, abundance, height, and DBH; shrub cover, species richness, and height; herbaceous plant cover, species richness, and height; and ground cover); two represent urban infrastructure (cement cover and maximum building height); two describe human activity (cars passing / min, pedestrians passing / min); and one represents predation hazards (number

of dogs and cats). All variables were measured with the exception of cover variables which were estimated in the field using a percentage scale. Habitat trait data were collected by the same person. Additionally, we calculated the distance from each point count and the nearest city-edge and gathered information on human population density (inhabitants / km^2) and income (mean monthly income per neighborhood; INEGI 2003) for the different areas of the city. Because income data are presented as the number of inhabitants that receive < 1, 1 - 2, 2 - 5, and > 5 official minimum wages (1 official minimum wage ~ 4 US DLS / day), average income per neighborhood was calculated by adjusting these data to the distribution of richness, in relation to income, in Mexican medium-sized cities (López 2006). To calculate human population density, we measured the area of the neighborhood, and divided the number of inhabitants per neighborhood by its area.

To calculate bird densities, we computed individuals/ha (mean ± 95% confidence intervals) using Distance 5.0 (Thomas et al. 2005). This software calculates the probability of detection of individuals at increasing distances from the observer and estimates the number of bird individuals that exist within a surveyed area (Buckland et al. 2001). We computed bird densities for entire bird communities because Distance 5.0 estimates the number of bird individuals by calculating the probability of detection of individuals and standardizing the number of detections along the concentric distances of observations (Buckland et al. 2004). Distance 5.0 pools species to avoid biases resultant from differences in detection probabilities among species (Buckland et al. 2004), which could both over- or under-estimate due to the commonness/rarity of species and their differences in detection rates (Alldredge et al. 2007). We report the effective detection radius (EDR), Akaike's information criterion (AIC), and key function/series expansion (KF/SE) to describe the coverage of our surveys and the nature of the methods used by the program to calculate bird densities. EDR is the distance at which the probability of detecting an object at large distances equals the probability of not recording an object at distances larger than the EDR (Buckland et al. 1993). AIC is a measure of the goodness of fit to a model, which is computed by Distance 5.0 and is recommended for model selection (Buckland et al. 2004, Thomas et al. 2005). KFs are parametric functions to model the detection function (i.e., uniform, half-normal, hazard rate, negative exponential), and SEs are mathematical representations of the functions (i.e., coisine, simple polynomial, hermite polynomial) (Thomas et al. 2002, 2005).

To contrast bird species richness values among native forests and urban habitats, we used a rarefaction analysis. We computed the statistical expectation of bird species richness for each habitat type using EstimateS (Sobs [Mao Tao] ± 95% confidence intervals; Colwell 2005). Such expectation is calculated based on the repeated re-sampling of all pooled samples (Gotelli and Colwell 2001), allowing comparisons of the statistically expected species richness of the bird community recorded at each treatment using a similar computed accumulated abundance (Moreno 2001, Magurran 2004). To determine if species richness and bird density values were statistically different among treatments, we compared their 95% confidence intervals. If confidence intervals did not overlap, we considered the data to be statistically different with an α < 0.01 (following Payton et al. 2003; M. Payton pers. comm.).

We performed multiple regression analyses (full-model following Whittingham et al. 2006) between neotropical migrant species richness (number of species recorded at each point count) and abundance (number of individuals detected per species at each point count) and the 20 variables that describe each urban survey point to determine the relative importance of habitat attributes on neotropical

migrant bird communities. In order to avoid multicollinearity and to fit our data to the linearity and normality assumptions, prior to the performance of the multiple regression analysis, we transformed our data ($\log_{10}$) and searched for the existence of moderate-to-strong relationships between variables in order to determine their statistical independence. Although two variables remained non-normal, they were unimodal making the method robust enough with regard the violation of this assumption (StatSoft, Inc. 2010). When two or more variables showed moderate-to-strong significant relationships ($r > 0.5$, $P < 0.05$; Peck et al. 2008), we only considered the variable with the highest variance for the analysis.

Owing to the fact that the urban core of a city can represent a barrier that shapes bird communities (Fernández-Juricic and Jokimäki 2001, MacGregor-Fors in press), we evaluated if the distance from the city-edge affected neotropical migrants. For this, we analyzed the number of neotropical migrant individuals recorded at different distances from the city-edge (*sensu* MacGregor-Fors in press). We also analyzed the distances at which each neotropical migrant species was recorded in relation to the city-edge.

Results

We recorded a total of 19 neotropical migrant bird species. Of them, all were recorded in forest sites, but only 11 species were recorded in the city. Of the total 19 species, 88% were mainly insectivores, and 12% frugivore-insectivores (Table 1). Five of the recorded neotropical migrant bird species are considered in the North American Landbird Conservation Plan ("Watch List Species - Restricted distribution or low population size": Hermit Warbler –*Dendroica occidentalis*, Red-faced Warbler–*Cardellina rubrifrons*; "Additional Stewardship Species - High percent of Global Population in single biome": Yellow bellied Sapsucker–*Sphyrapicus varius*, Dusky Flycatcher–*Empidonax oberholseri*, Nashville Warbler–*Vermivora ruficapilla*; Rich et al. 2004).

Table 1. *Neotropical migrant bird species recorded in native forests and the city of Morelia. Numbers represent the total number of point counts in which each species was recorded in native forest sites (n = 70) and the citywide survey (n = 204).*

Species	Native forests	City of Morelia
Sphyrapicus varius	3	
Empidonax oberholseri-hammondii*	2	
Empidonax occidentalis**	2	
Vireo bellii	4	
Regulus calendula	21	3
Polioptila caerulea	8	23
Turdus migratorius	4	
Vermivora celata	8	3
Vermivora ruficapilla	18	8
Dendroica coronata	19	64
Dendroica nigrescens	13	4
Dendroica townsendi	13	3
Dendroica occidentalis	4	
Mniotilta varia	5	1
Setophaga ruticilla	1	1
Wilsonia pusilla	9	15

Table 1. (continued)

Species	Native forests	City of Morelia
Cardellina rubrifrons	2	
Piranga ludoviciana	2	6
Icterus cucullatus	1	

*We used a species complex due to these species' sympatric wintering distribution and morphological similarity.

**Although silent individuals of this species cannot be distinguished in the field from the Pacific-slope Flycatcher (*Empidonax difficilis*), the range of the latter does not include the Volcanic Belt.

Neotropical migrant bird densities were significantly higher in forest sites (38.2 ind / ha; 95% confidence intervals: 30.1–48.6; AIC = 949.3, EDR = 16.5 m, KF/SE = Uniform/Coisine) compared to the citywide survey (14.1 ind / ha; 95% confidence intervals: 9.8–20.1; AIC = 429.8, EDR = 21.7 m, KF/SE = Uniform/Hermite polynomial; Fig. 1).   Similar to the pattern found for bird densities, when we contrasted neotropical migrant bird species richness values in forest and urban habitats using a comparable accumulated abundance of 159 individuals (total abundance from the citywide sub-sample; n = 70), forests showed significantly higher neotropical migrant bird species richness (17.3 ± 1.2 species) compared to urban sites (9.1 ± 2.9 species; Fig. 1).
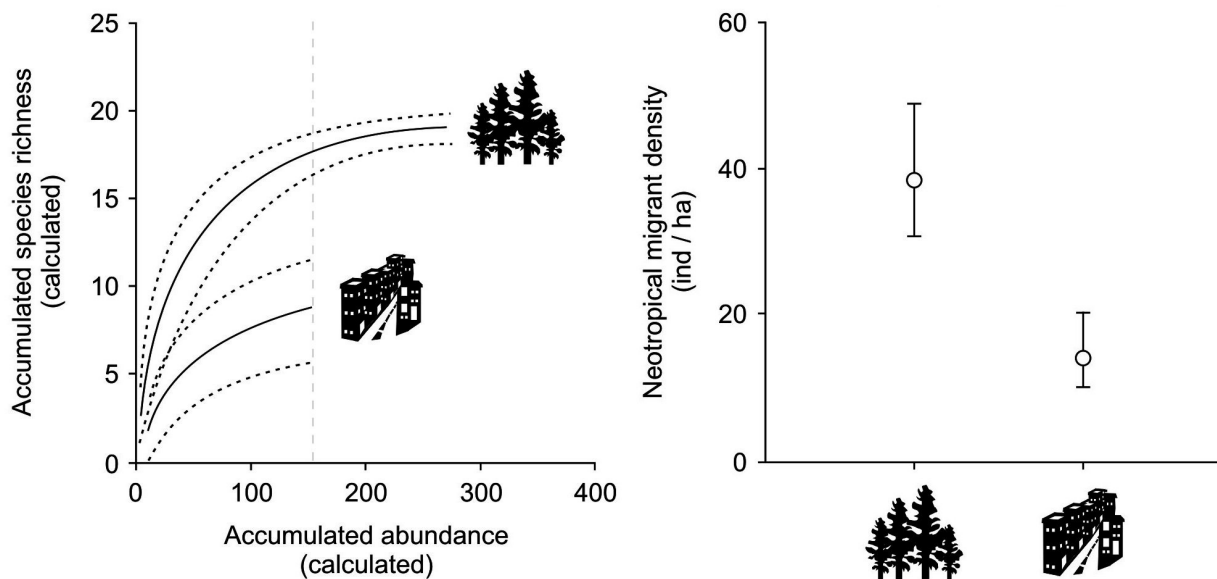
Figure 1. Diversity values for neotropical migrant bird communities in native forests and the city of Morelia. (Upper panel) Rarefaction analysis of bird species richness in native forests and the city shows that neotropical migrant bird species richness is significantly higher in native forests than in the city at a comparable abundance of 159 individuals (segmented vertical line). Solid black lines represent average species richness (Sobs [Mao Tao]) and segmented black lines 95% confidence intervals. (Lower panel) Bird densities (ind / ha) were almost three times higher in native forests than in the city (mean ± 95% confidence intervals).

Multiple regression analyses revealed that urban habitat traits affect neotropical migrant birds abundances and richness in a similar fashion. Tree cover was the only variable strongly and positively related to neotropical migrant bird species richness and abundance. While not significant, we found a negative relationship between human population density and neotropical migrant abundance (Table 2).

Table 2. Relationships between the measured urban habitat variables and neotropical migrant bird species richness and abundance. Significantly related variables are marked with an asterisk (*).

	Beta	SE	t_{47}	P
(a) Abundance (General model: $R^2 = 0.34$, $F_{9,47} = 2.80$, $P < 0.01$)				
Intercept			0.58973	0.558196
Tree cover*	0.486101	0.158101	3.07462	0.003505
Tree species richness	-0.171195	0.130604	-1.31079	0.196297
Shrub species richness	-0.153045	0.129360	-1.18309	0.242723
Cement cover	-0.084532	0.152053	-0.55594	0.580891
Maximum building height	0.028380	0.137321	0.20667	0.837162
Income	0.022469	0.141314	0.15900	0.874349
Human population density	-0.253723	0.145021	-1.74957	0.086721
Number of dogs and cats	0.048659	0.133106	0.36557	0.716328
Cars passing / min	0.081183	0.141730	0.57280	0.569512
(b) Species richness (General model: $R^2 = 0.32$, $F_{9,47} = 2.53$, $P < 0.01$)				
Intercept			-0.10809	0.914388
Tree cover*	0.495722	0.160821	3.08245	0.003430
Tree species richness	-0.007359	0.132851	-0.05539	0.956061
Shrub species richness	-0.099814	0.131585	-0.75855	0.451909
Cement cover	-0.084845	0.154669	-0.54856	0.585906
Maximum building height	0.067012	0.139683	0.47974	0.633636
Income	0.099919	0.143745	0.69512	0.490405
Human population density	-0.189023	0.147515	-1.28138	0.206347
Number of dogs and cats	-0.004563	0.135395	-0.03370	0.973260
Cars passing / min	-0.147005	0.144168	-1.01967	0.313104

When we analyzed the relationship between the distance of the city-edge and migratory species abundances, we recorded a significant decrease in the total number of neotropical migrant individuals towards the center of the city (Fig. 2a). In fact, the relationship for all the neotropical migrant individuals fitted significantly to an exponential decay model ($r^2 = 0.89$, $P = 0.001$). However, when we assessed possible effects of the distance from the city-edge by species, we found no differences (Kruskal-Wallis: $H_{8,118} = 7.61$, $P = 0.42$; Fig. 2b). While the mean distance from the geographic center of the city to its edge is of 5.5 km (SD = 1.64), neotropical migrant birds were present on average ~ 1 km from the city-edge, with maximum distances recorded for the Wilson's Warbler–*Wilsonia pusilla* (3.4 km), the Blue-gray Gnatcatcher–*Polioptila caerulea* (2.7 km), and the Yellow-rumped Warbler–*Dendroica coronata* (2.7 km; Fig. 2b).

Discussion

Our results show that neotropical migrant bird communities recorded within the city differ from those recorded in native forests. Neotropical migrant density (ind / ha) decreased with urbanization, being almost three-times higher in native forests when compared to the city (Fig. 1). This is the opposite to what has been found in previous studies focused on resident birds, which report higher bird densities

within cities (Walcott 1974, Gavareski 1976, Beissinger and Osborne 1982, Clergeau et al. 1998, Ortega-Álvarez and MacGregor-Fors 2009, MacGregor-Fors et al. in press). Our multiple regression results show that neotropical migrant bird abundance is positively related to tree cover and showed a negative tendency in relation to human population density (Table 2). Most neotropical migratory birds capable of living in urban areas are insectivorous that feed on the foliage of trees and large shrubs, and their numbers could be negatively affected by lower densities of optimal foraging sites, and/or lower densities of their preferred food resources in urban areas (Kohut et al. 2009). In native forests, the density of trees was highly homogeneous, allowing us to record at least one neotropical migrant bird in 92% of the 70 forest sites we surveyed. Trees in the studies urban area were patchily located, reducing the probability of recording neotropical migrants throughout the city (with at least one neotropical migrant in 58% of the urban sites surveyed). On the other hand, human population density is often related to highly developed areas that have low or null tree cover and are characterized by heavy human activity (McKinney 2002). In turn, human activities, such as passing pedestrians and cars have been identified to negatively affect native resident bird species richness and abundance, and to benefit the abundance of a few urban-exploiter species (Blair1996, Jokimäki and Suhonen 1998, Miller et al. 2001, Ortega-Álverez and MacGregor-Fors 2009).
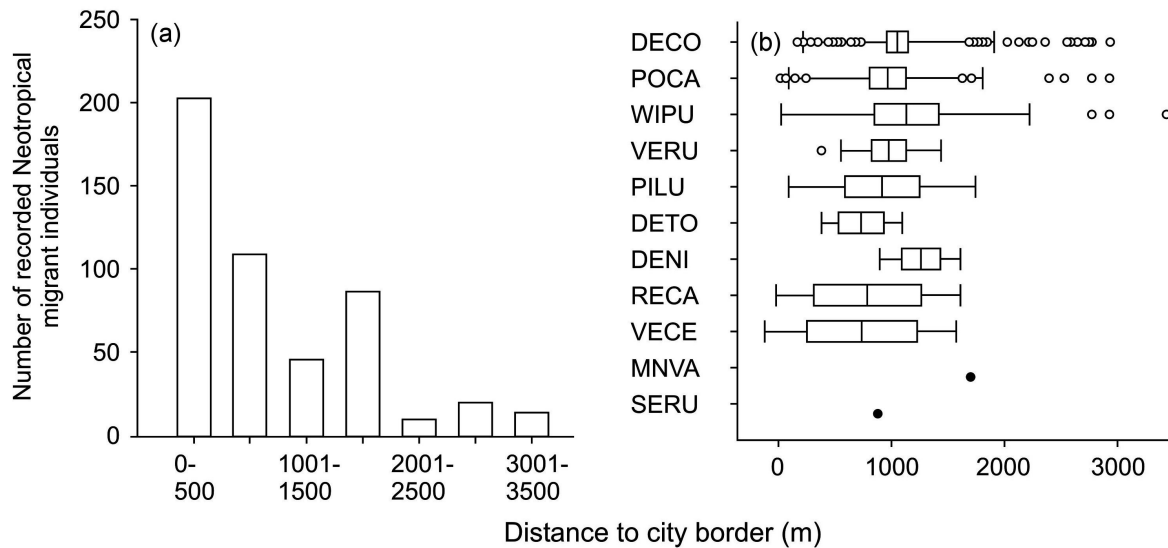

Figure 2. Number of total neotropical migrant individuals recorded in point counts at distance intervals from the edge of the city of Morelia (a), and distances at which each neotropical migrant bird species was recorded from the city-edge (b). Mean: mid-line; SE: box; SD: whisker; outliers: white circles; single observations: black circles. DECO = *Dendroica coronata*, POCA = *Polioptila caerulea*, WIPU = *Wilsonia pusilla*, VERU = *Vermivora ruficapilla*, PILU = *Piranga ludoviciana*, DETO = *Dendroica townsendi*, DENI = *Dendroica nigrescens*, RECA = *Regulus calendula*, VECE = *Vermivora celata*, MNVA = *Mniotilta varia*, SERU = *Setophaga ruticilla*.

Neotropical migrant species richness also decreased significantly with urbanization (Fig. 1), similarly to what has been reported for resident bird communities in cities all around the world (Gavareski 1976, Beissinger and Osborne 1982, Blair 2001, Evans et al. 2009, Ortega-Álvarez and MacGregor-Fors 2009, MacGregor-Fors et al. 2009, in press). This loss of resident species associated to

urbanization has been related to: (1) a decrease in vegetation volume, cover, and structure (Emlen 1974, Mills et al. 1989, MacGregor-Fors 2008, MacGregor-Fors et al. in press); (2) increased human activity in urban areas (Blair 1996, Fernández-Juricic 2000, Ortega-Álvarez and MacGregor-Fors 2009; MacGregor-Fors et al. in press); (3) changes in food resource availability (Shochat 2004, Robb et al. 2008); and (4) competition with exotic invasive species (MacGregor-Fors et al. 2010). In this study, only tree cover was positively related to neotropical migrant bird species richness (Table 2). Thus, our density and species richness results demonstrate that urbanization has a greater negative effect on neotropical migrant bird communities than it does on resident bird communities.

Although we found a decrease in the total number of individuals of neotropical migrant birds in relation to distance from the city-edge, this geographic variable was not significant when we analyzed our data by species. The relationship between neotropical migrant bird abundance and the distance to the city-edge in our study seems to be the result of the spatial distribution of urban green areas within the city of Morelia, with the city center being practically devoid of them (López et al. 2001, Vargas Uribe 2008).

Previous studies have shown that urbanization affects resident bird communities (e.g., Gavareski 1976, Blair 1996, Clergeau et al. 1998, Jokimäki and Suhonen 1998, Lim and Sodhi 2004, Melles 2005, Ortega-Álvarez and MacGregor-Fors 2009, MacGregor-Fors et al. in press). Our results show that urbanization has an even greater negative effect on neotropical migrant bird communities. However, some migrant species recorded using urban habitats within the city of Morelia are included in the North American Landbird Conservation Plan (Rich et al. 2004). While this could seem contradictory, it indicates that urbanization can act as a two-edged sword, affecting several migratory species while offering wintering habitats for some others. Our results indicate that neotropical migrant birds that can benefit from urban areas are clearly related to presence of green areas within urban environments. Although our results show that Morelia can shelter some neotropical migrant birds of conservation concern, further studies are needed to establish the role of cities as neotropical migrant bird conservation reservoirs, and their quality as wintering habitat.

Acknowledgments

Literature cited

Alldredge, M. W., K. H. Pollok, T. R. Simons and S. A. Shriner. 2007. Multiple-species analysis of point count data: A more parsimonious modeling framework. Journal of Applied Ecology 44:281–290.
Beissinger, S. R. and D. R. Osborne. 1982. Effects of urbanization on avian community organization. The Condor 84:75–83.

Blair, R. B. 2001. Creating a homogeneous avifauna, p. 459–486. *In* J, M. Marzluff, R. Bowman and R. Donnely [eds.], Avian conservation and ecology in an urbanizing world. Kluwer Academic, Boston, MA.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2004. Advanced distance sampling. Oxford University Press, Oxford.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, Oxford.

Buckland, S. T., D. R. Anderson, K. P. Burnham and J. L. Laake. 1993. Distance sampling: Estimating abundance of biological populations. Chapman and Hall, London.

Chace, J. F. and J. J. Walsh. 2006. Urban effects on native avifauna: A review. Landscape and Urban Planning 74:46–69.

Chiari, C., M. Dinetti, C. Licciardello, G. Licitra and M. Pautasso. 2010. Urbanization and the more-individuals hypothesis. Journal of Animal Ecology 79:366–371.

Clergeau, P, J. P. L. Savard, G. Mennechez and G. Falardeau. 1998. Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. The Condor 100:413–425.

Colwell, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. http://purl.oclc.org/estimates.

Czech, B. and P. R. Krausman. 1997. Distribution and causation of species endangerment in the United States. Science 22:1116.

Czech, B., P. R. Krausman and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. Bioscience 50:593–601.

Emlen, J. T. 1974. An urban bird community in Tucson, Arizona: Derivation, structure, regulation. The Condor 76:184–197.

Evans, K. L., S. E. Newson and K. J. Gaston. 2009. Habitat influences on urban avian assemblages. Ibis 151:19–39.

Fernández-Juricic, E. 2000. Local and regional effects of human disturbance on forest birds in a fragmented landscape. The Condor 102:247–255.

Fernández-Juricic, E. and J. Jokimäki. 2001. A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. Biodiversity and Conservation 10:2023–2043.

Gavareski, C. A. 1976. Relation of park size and vegetation to urban bird populations in Seattle, Washington. The Condor 78:375–382.

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu, X. Bai and J. M. Briggs. 2008. Global change and the ecology of cities. Science 319:756–760.

Huff, M. H., K. A. Bettinger, M. L. Ferguson, M. J. Brown and B. Altman. 2000. A habitat-based point-count protocol for terrestrial birds, emphasizing Washington and Oregon. U.S. Department of Agriculture, Portland.

(INEGI) Instituto Nacional de Estadística Geografía e Informática 2003. SCINCE por Colonias - Michoacán de Ocampo - XII Censo General de Población y Vivienda 2000. INEGI, Aguascalientes.

Jokimäki, J. and J. Suhonen. 1998. Distribution and habitat selection of wintering birds in urban environments. Landscape and Urban Planning 39:253–263.

Jokimäki, J. and M. L. Kaisanlahti-Jokimäki. 2003. Spatial similarity of urban bird communities: A multiscale approach. Journal of Biogeography 30:1183–1193.

Kohut, S. M., G. R. Hess and C. E. Moorman. 2009. Avian use of suburban greenways as stopover

habitat. Urban Ecosystems 12:487–502.

Lim, H. C. and N. S. Sodhi. 2004. Responses of avian guilds to urbanisation in a tropical city. Landscape and Urban Planning 66:199–215.

López, E., G. Bocco, M. Mendoza and E. Duhau. 2001. Predicting land-cover and land-use change in the urban fringe: A case in Morelia city, Mexico. Landscape and Urban Planning 55:271–285.

López, H. 2006. Avances AMAI: Distribución de niveles socioeconómicos en el México urbano. Datos, diagnósticos, tendencias 6:5–11.

MacGregor-Fors, I. 2008. Relation between habitat attributes and bird richness in a western Mexico suburb. Landscape and Urban Planning 84:92–98.

MacGregor-Fors, I. In press. How to measure the urban-wildland ecotone: Redefining 'peri-urban' areas. Ecological Research (DOI: 10.1007/s11284-010-0717-z).

MacGregor-Fors, I., L. Morales-Pérez and J. E. Schondube. In press. From forests to cities: Effects of urbanization on subtropical mountain bird communities. Studies in Avian Biology.

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

MacGregor-Fors, I., R. Ortega-Álvarez and J. E. Schondube. 2009. On the ecological quality of urban systems: An ornithological perspective, p. 51–66. *In* D, S. Graber and K. A. Birmingham [eds.], Urban Planning in the 21st Century. Nova Science Publishing, New York, NY.

Madrigal, X. 1997. Ubicacion fisiografica de la vegetacion en Michoacan, Mexico. Ciencia Nicolaita 15:65–75.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Publishing, Oxford.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260.

McKinney, M. L. 2002. Urbanization, biodiversity and conservation. Bioscience 52:883–890.

Melles, S. J. 2005. Urban bird diversity as an indicator of human social diversity and economic inequality in Vancouver, British Columbia. Urban Habitats 3:25–48.

Melles, S., S. Glenn and K. Martin. 2003. Urban bird diversity and landscape complexity: Species-environment associations along a multiscale habitat gradient. Conservation Ecology 7:5 [online].

Miller, J. R., J. M. Fraterrigo, N. T. Hobbs, D. N. Theobald and J. A. Wiens. 2001. Urbanization, avian communities, and landscape ecology, p. 117–137. *In* J, M. Marzluff, R. Bowman and R. Donnely [eds.], Avian conservation and ecology in an urbanizing world. Kluwer Academic, Boston.

Mills, G. S., J. B. Dunning and J. M. Bates. 1989. Effects of urbanization on breeding bird community structure in Southwestern desert habitats. The Condor 91:416–428.

Moll, G. 1997. America's urban forests: Growing concerns. American Forests 103:14–18.

Moreno, C. E. 2001. Métodos para medir la biodiversidad. M&T-Manuales y Tesis SEA, Zaragoza.

Nocedal, J. 1987. Las comunidades de pájaros y su relación con la urbanización en la ciudad de México, p. 73–109. *In* E. Rapoport and I. R. López-Moreno [eds.], Aportes a la ecología urbana de la ciudad de México. Limusa, México, D.F.

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

Payton, M. E., M. H. Greenstone and N. Schenker. 2003. Overlapping confidence intervals or standard error intervals: What do they mean in terms of statistical significance? Journal of Insect Science 3:34.

Peck, R., C. Olsen and J. Devore. 2008. Introduction to statistics & data analysis. Brooks/Cole, Belmont.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, D. F. DeSante and B. Milá. 1996. Manual de métodos de campo para el monitoreo de aves terrestres. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Gen. Tech. Rep. PSW-GTR-144, Albany, CA.

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W.

Demarest, E. H. Dunn, W. C. Hunter, E. E. Iñigo-Elias, J. A. Kennedy, A. M. Martell, A. O. Panjabi, D. N. Pashley, K. V. Rosenberg, C. M. Rustay, J. S. Wendt and T. C. Will. 2004. Partners in flight North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca, NY.

Rodewald, A. D. and D. P. Shustack. 2008. Urban flight: Understanding individual and population-level responses of Neartic-Neotropical migratory birds to urbanization. Journal of Animal Ecology 77:83–91.

Robb, G. N., R. A. McDonald, D. E. Chamberlain and S. Bearhop. 2008. Food for thought: Supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6:476–484.

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

StatSoft Inc. 2010. Electronic Statistics Textbook. StatSoft. WEB, Tulsa.

Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, J. R. B. Bishop and T. A. Marques. 2005. Distance 5.0. Release 1. Research Unit for Wildlife Population Assessment, University of St. Andrews.

Thomas, L., S. T. Buckland, K. P. Burnham, D. R. Anderson, J. L. Laake, D. L. Borchers and S. Strindberg. 2002. Distance sampling, p. 544–552. *In* A, H. El-Shaarawi and W. W. Piegorsch [EDS.], Encyclopedia of Environmetrics. John Wiley & Sons, Chichester.

United Nations 2004. World urbanization prospects: The 2004 revision. Population Division of the Department of Economic and Social Affairs, New York.

Vargas Uribe, G. 2008. Urbanización y Configuración Territorial en la región Valladolid-Morelia 1541-1991. Morevallado Editores, Morelia.

Walcott, C. F. 1974. Changes in bird life in Cambridge, Massachusetts from 1860 to 1964. The Auk 91:151–160.

Whittingham, M. J., Stephens, P. A., Bradbury, R. B., Freckleton, R. P. 2006. Why do we still use stepwise modelling in ecology and behaviour? Jornal of Animal Ecology 75:1182–1189.

Gray vs. green urbanization: Relative importance of urban features on urban bird communities

Introduction

Habitat structure and complexity are two of the main components determining bird community diversity (Swift, Larson, & DeGraff, 1984; Díaz, Armesto, Reid, Sieving, & Willson, 2005). The loss of specific habitat attributes directly affects those species that depend on the extirpated components (Berg, Ehnström, Gustafsson, Hallingbäck, Jonsell et al., 1994). In general, bird community diversity values under natural conditions are determined by vegetation attributes, mainly by tree features (Collins, 1980; DeGraff, Hestbeck, & Yamasaki, 1998; Díaz et al., 2005).

Although a wide array of components contribute to the type, physiognomy, and diversity of urban habitats (Emlen, 1974; McDonnell & Pickett,1990) our knowledge of the habitat features that affect bird communities within urban areas is biased towards vegetation (see Chace & Walsh, 2006; Evans, Newson, & Gaston, 2009; MacGregor-Fors, Schondube, & Ortega-Álvarez, 2009; and references therein). In general, vegetation traits have been positively related to native urban-dwelling bird species richness and abundances (e.g., native vegetation patch size, structure and floristic attributes of planted vegetation, shrub and tree richness, height and cover; DeGraff & Wentworth, 1986; Munyenyembe, Harris & Hone, 1989; Melles, Glenn & Martin, 2003; Crooks, Suarez & Bolger, 2004; Chace & Walsh, 2006; Donnely & Marzluff, 2006; MacGregor-Fors, 2008, among others). However, some vegetation features, under certain circumstances, have also shown negative relationships with the ecology of urban-dwelling birds (e.g., tree diversity, tree and shrub density, average tree DBH, understory cover, presence of some exotic plants; Jokimäki, 1999; MacGregor-Fors, 2008; Suárez-Rubio & Thomlinson, 2009; Evans et al., 2009; Rodewald, Shustack & Hitchcock, 2009).

In relation to non-vegetation variables, several previous studies have focused on the implications that human activities, socioeconomic status, anthropogenic feeding, urban infrastructure, and other urban-related hazards have on urban-dwelling birds. Human activities, generally measured as the number of passing cars and pedestrians in a given time, have shown both positive and negative relationships with urban bird community species richness and abundances (Blair, 1996; Leveau, 2008; Ortega-Álvarez & MacGregor-Fors, 2009; Villegas & Garritano-Zavala, 2010). Although, socioeconomic status has been generally related to more diverse native urban bird communities (Melles, 200; Fuller, Warren, Armsworth, Barbosa & Gaston, 2008; Strobach, Haase & Kabisch, 2009), a study carried out in the city of Morelia (Mexico) found no significant relationship between the socioeconomic level of urban areas and their bird communities (MacGregor-Fors, Morales-Pérez, & Schondube, in press).

Although the constant anthropogenic supply of feeding resources in urban areas has been related to population increases of certain bird groups (e.g., hummingbirds, sparrows; Kubetzki & Garthe, 2007;

Arizmendi, Lopez-Saut, Monterrubio-Solís, Flores-Moreno & Rodríguez-Flores, 2008; Robb, McDonald, Chamberlain & Bearhop, 2008) and has been adjudged as a crucial component explaining the global pattern of high urban bird population densities (Shochat, 2004), it has also been identified as a hazard, specially in feeders, as: (1) they are opportune sites for disease transmission (Dhondt, Tessaglia & Slowthower, 1998; USGS, 2007); (2) promote intra-specific competition, generally affecting small species (Parsons, Major & French, 2006; Robb et al., 2008); and (3) represent sites with high prey densities and predictability for bird predators (Robb et al., 2008).

Among other urban-related hazards, nest predation and window collisions head the list. Although nest predation was proposed to be "relaxed" in urban areas (Gering & Blair, 1999), recent studies have demonstrated that nest predation rates are higher in urban areas than in non-urban sites (Jokimäki, Kaisanlahti-Jokimäki, Sorace, Fernández-Juricic, Rodríguez-Prieto & Dolores, 2005; López-Flores, MacGregor-Fors, & Schondube, 2009). On the other hand, window collisions have been identified as an important source of avian mortality, representing the death of billions of birds worldwide (Cupul-Magaña, 2003; Klem, 2009).

Regarding the role that urban infrastructure has on urban bird communities, little has been investigated since Emlen's (1974) stated in his pioneer urban ecology study that "House tops and particularly their superstructures such as air-conditioner units and television aerials provide attractive song and resting perches. Edges of tile roofs, ledges under roofs, and dense vines growing on walls provide important nesting cover for several species. Telephone poles and wires provide abundant and well-distributed perches at elevations from 10 to 40 ft, while fence tops provide similar perches at lower levels." (p. 188). Of the few studies that have addressed such features, only two variables have been related to urban bird community diversity: (1) built cover; and (2) building height (Seather, Ringsby, Bakke, & Soleberg, 1999; Marzluff, Bowman, & Donnely, 2001; Boren & Hurd, 2005; MacGregor-Fors, in press a). On the one hand, built cover has been used as a surrogate of urbanization intensity, which often has negative effects on bird community diversity values (Marzluff et al., 2001), although intermediate levels of urbanization have been related to peaks in avian diversity (Blair, 1996; Tratalos, Fuller, Evans, Davies, Newson et al., 2007; Lepczyk, Flather, Radeloff, Pidgeon, Hammer et al., 2008). On the other hand, building height is related to the abundance of urban-exploiter species (i.e., House Sparrow–*Passer domesticus*, Rock Pigeon–*Columba livia*; MacGregor-Fors et al., in press a), which use building facades and roofs as roosting, nesting, and/or foraging areas (Seather et al., 1999; Boren & Hurd, 2005).

As described above, the effect that habitat features have on urban-dwelling birds depends on the life history of species, with great differences found among urban-exploiter and adaptable species (sensu Blair, 1996). Thus, in this study, we categorized birds based on their abundances as common, fairly common, and rare (see Data analysis section for further details) to determine the relative role that vegetation and non-vegetation habitat features have on urban-dwelling birds. For this, we measured 33 habitat features that describe the spatial distribution of urban components, habitat structure, biological heterogeneity, potential hazards for birds, housing density, and socioeconomic level in three neotropical cities. We expected: (1) common bird species richness and abundances to be positively related to built cover, housing density, and the density of urban infrastructure components (e.g., electric and telephone poles, cables, niches), independent of biological heterogeneity and socioeconomic level, and negatively related to urban hazards (e.g., number of windows, human activity); (2) fairly common

bird species richness and abundances to be positively related to intermediate built cover, vegetation components, biological heterogeneity, and socioeconomic level, and negatively related to urban hazards and housing density; and (3) rare species richness and abundances to be negatively related to built cover, urban infrastructure components, urban hazards, and housing density, and positively related to vegetation structural features and biological heterogeneity (Table 1).

Materials and methods

Study area

Our study was carried out in three cities located in northern Michoacán, west-central Mexico (Fig. 1). In order to have a representative sample of the urban bird communities in this region, we surveyed its three largest cities (i.e., Morelia, Uruapan, Zamora). Morelia (19°42'07" N, 101°11'33"W; ~1925 m asl) covers an area of 106.4 km² and has a human population that exceeds one million inhabitants (Vargas Uribe, 2008). Uruapan (19°24'33" N, 102°02'43"W; ~1630 m asl) covers an area of 19.2 km² and has a human population of ~240,000 inhabitants. Finally, Zamora (19°59'17" N, 102°17'30"W; ~1570 m asl) covers an area of 10.2 km² and has a human population of ~128,000 inhabitants. In general, all studied human settlements are surrounded by a landscape matrix of croplands mixed with shrublands, and some small forest patches.

Figure 1. Study area map.

Bird surveys

We surveyed diurnal breeding birds during March-April 2008 from 07:00 to 11:00 using 5 min point counts (25 m radius) located at least 250 m away from each other to assure survey independence (Ralph, Geupel, Pyle, Martin, DeSante, et al., 1996; Huff, Bettinger, Ferguson, Brown, & Altman, 2000). We used limited-radius point counts for assuring that all birds recorded were actively using the surveyed area and not nearby conditions with different habitat attributes, and to maintain an identical sampled area per point count. All birds seen or heard using the sampled area (e.g., perching, foraging, nesting) were recorded and included in our analyses. We established our sampling points by randomly placing a 500 x 500 m grid over the city of Morelia and a 250 x 250 m grid over the cities of Uruapan and Zamora, locating one point at each intersection. Thus, the number of surveys carried out within each city is proportional to its size (Morelia = 204; Uruapan = 80; Zamora = 43). Each point count location was visited once by the same observer.

Table 1. Specific hypothesis relating bird species richness and abundances for the three bird categories (i.e., common, fairly common, rare) and all variables measured to describe each survey site based on previously generated knowledge on how birds respond to urbanization. While we grouped all of the measured habitat variables into categories to generate specific hypothesis related to the richness and abundance of birds, we did not pool the values of them because me aimed to identify the relative role of each variable.

Habitat trait category	Bird category	Expected response
Spatial distribution	Common	Higher species richness and abundances in sites with higher built cover.
	Fairly common	Higher species richness and abundances in sites with intermediate built cover and presence of vegetation components.
	Rare	Higher species richness and abundances in sites with lowest built cover.
Biological heterogeneity	Common	Species richness and abundances independent of biological heterogeneity.
	Fairly common	Higher species richness and abundances in sites with high tree and shrub species richness.
	Rare	Higher species richness and abundances in sites with high tree and shrub species richness.
Habitat structure	Common	Higher species richness and abundances in sites with high density of urban infrastructure components.
	Fairly common	Higher species richness and abundances in sites with high density of urban vegetation components, but tolerant to the presence of urban infrastructure components.
	Rare	Higher species richness and abundances in sites with high density of vegetation components, basically devoid of urban infrastructure ones.
Hazards	Common	Low negative impact on species richness and abundances.
	Fairly common	Medium negative impact species richness and abundances.
	Rare	High negative impact species richness and abundances.
Housing density	Common	Higher species richness and abundances in sites with higher housing densities.
	Fairly common	Higher species richness and abundances in sites with low housing densities.
	Rare	Higher species richness and abundances in sites with low housing densities.
Socioeconomic level	Common	Species richness and abundances independent of socioeconomic level.
	Fairly common	Higher species richness and abundances in sites with high socioeconomic level.
	Rare	Higher species richness and abundances in sites with high socioeconomic level.

Habitat characterization

We measured 33 habitat variables within a 25 m radius area at each point count location in all the studied cities. All habitat measurements were conducted immediately after the bird censuses. The set of variables describe the spatial distribution of urban components, habitat structure, biological heterogeneity, potential hazards for birds, housing density, and socioeconomic level. Of them, six variables describe the spatial distribution of urban components (i.e., tree, shrub, herbaceous plant, ground, and built cover), 18 describe the habitat structure (i.e., tree abundance, maximum and minimum height, and diameter at breast height [DBH]; shrub maximum and minimum height, herbaceous plant maximum and minimum height, number of electric and telephone poles, cables, light poles, niches, balconies, lightning rods, antennas, and exposed construction rods; maximum and minimum building height); two describe biological heterogeneity (i.e., tree and shrub species richness); five the potential hazards for birds (i.e., number of windows, passing cars and pedestrians / min, number of cats and dogs recorded during the point count); one represents housing density (i.e., number of street doors), and one the socioeconomic level (i.e., categorical wealthiness). We measured socioeconomic level using a categorical scale ranging from 1 to 6, with 1 being the poorest sites and 6 the wealthiest, based on several characteristics: (1) construction materials used for house construction (e.g., cardboard, aluminum and asbestos ceilings, tiles, adobe, bricks, cement); (2) state of the facade; (3) number of cars and their model; (4) state of the surrounding urban infrastructure; (5) house size; and (6) number of family-owned stores located within housing units.

Data analysis

We performed multiple regression analyses (backward, stepwise) to assess which of the measured variables were related to bird species richness and abundances in the studied cities, using a statistical significance of $P < 0.05$. Because analyses including total bird species richness and/or abundances could be biased by the presence of a few very abundant species, in our case some urban-exploiter species, we separated the recorded bird species and abundances into three groups: (1) common species; (2) fairly common species; and (3) rare species (Table 2). We considered species to be common when the average number of individuals recorded per point count in each of the three studied cities was >1 (>327 individuals for all surveys). We considered species to be rare when the average number of individuals recorded per point count in each of the three studied cities was <0.03, representing <10 individuals recorded in all surveys (following the standard cut-off point of 10 individuals to determine rarity when predicting abundance-based species richness; Chao & Lee, 1992; Shen, Chao, & Lin, 2003). Finally, we considered species to be fairly common when the average number of individuals recorded per point count in each of the three studied cities was located between the set point values for abundant and rare species (>10 and <327 individuals in all surveys).

To avoid multicollinearity and comply with the linearity and normality assumptions of the analysis, we transformed our data ($\log_{10}$) prior to the performance of the multiple regression analyses, and sought for the existence of moderate-to-strong relationships between variables in order to determine their statistical independence. Although some variables remained non-normal, this method is quite robust with regard to violations of this assumption (StatSoft, Inc., 2010). When two or more variables showed moderate-to-strong significant relationships ($r > 0.5$, $P < 0.05$; Peck, Olsen, & Devore, 2008), we only considered the variable with the highest variance for the analysis. Based on the correlation

Table 2. Bird species recorded in Morelia, Uruapan, and Zamora. We considered species to be: (1) common - when the average number of individuals recorded per point count in the three cities was >1 (>327 individuals; (2) rare - when the average number of individuals recorded per point count in the three cities was <0.03 (<10 individuals); and (3) fairly common when the average number of individuals recorded per point count in the three cities was <1 and > 0.03. Species are displayed from most abundant to least abundant and alphabetically among groups.

Group	Species	Average abundance[1]
Common	*Passer domesticus*	8.15
	Hirundo rustica	3.11
	Columba livia	1.44
	Columbina inca	1.28
	Quiscalus mexicanus	1.11
Fairly common	*Pipilo fuscus*	0.91
	Sporophila torqueola	0.72
	Spinus psaltria	0.47
	Molothrus aeneus	0.40
	Catherpes mexicanus	0.32
	Carpodacus mexicanus	0.23
	Cynanthus latirostris	0.22
	Turdus rufopalliatus	0.22
	Melanerpes aurifrons	0.17
	Pyrocephalus rubinus	0.13
	Troglodytes aedon	0.10
	Tyrannus vociferans	0.09
	Thryomanes bewickii	0.09
	Stelgidopteryx serripennis	0.08
	Crotophaga sulcirostris	0.07
	Chaetura vauxi	0.06
	Toxostoma curvirostre	0.05
	Melanotis caerulescens	0.04
	Ptilogonys cinereus	0.04
Rare	*Aeronautes saxatalis*	0.03
	Passerina caerulea	0.03
	Turdus migratorius	0.03
	Corvus corax	0.02
	Amazilia beryllina	0.02
	Loxia curvirostra	0.01
	Bubulcus ibis	0.01
	Vireo gilvus	0.01
	Volatinia jacarina	0.01
	Agelaius phoeniceus	0.01
	Spizella passerina	0.01
	Amazilia violiceps	0.009
	Pheucticus melanocephalus	0.009
	Sturnella magna	0.009
	Accipiter striatus	0.006
	Catharus aurantiirostris	0.006
	Contopus pertinax	0.006
	Geothlypis poliocephala	0.006
	Geothlypis speciosa	0.006

Table 2. (continued)

Group	Species	Average abundance[1]
	Lanius ludovicianus	0.006
	Picoides scalaris	0.006
	Buteo jamaicensis	0.003
	Campylorhynchus gularis	0.003
	Contopus sordidulus	0.003
	Elanus leucurus	0.003
	Heliomaster constantii	0.003
	Icterus wagleri	0.003
	Myadestes occidentalis	0.003
	Myiarchus nuttingi	0.003
	Myioborus miniatus	0.003
	Nycticorax nycticorax	0.003
	Passerina versicolor	0.003
	Petrochelidon pyrrhonota	0.003
	Piranga flava	0.003
	Sialia sialis	0.003
	Turdus assimilis	0.003
	Zenaida asiatica	0.003

[1]Average number of individuals recorded per point count in each of the three studied cities.

matrix of the 33 measured variables, we removed 17 of them. The variables that were included in our analyses are: tree cover, shrub cover, herbaceous plant minimum height, built cover, maximum building height, number of electric and telephone poles, electric and telephone cables, doors, light poles, lightning rods, exposed construction rods, dogs, and cats; passing pedestrians / min, and socioeconomic status. As multiple regression analyses consider the interaction between variables, some models include significantly related variables only in the presence of other non-significantly related variables. Thus, although we used a statistical significance of $P < 0.05$, some non-significantly related variables are reported as part of the model that best explained variations in the dependent variable. While we grouped all of the measured habitat variables into categories to generate specific hypothesis related to the richness and abundances of birds, we did not pool the values of them because me aimed to identify the relative role of each variable.

With the aim of graphically presenting the relationships between common, fairly common, and rare bird species richness and abundances and the different habitat variables, we performed a principal components and classification analysis. This analysis merges independent variables with highest variance, expressing two or more variables in a factor (StatSoft, Inc., 2010). For this study, we used two principal factors to graphically represent how the 33 independent habitat variables were related to common, fairly common, and rare species richness and abundances.

Results

We recorded a total of 61 bird species in the three studied cities. Of them, five were common (>327 individuals: *Passer domesticus, Hirundo rustica, Columba livia, Columbina inca,* and *Quiscalus mexicanus*), 19 were fairly common (>10 and <327 individuals), and 37 were rare (<10 individuals) (Fig. 2; Table 2). Multiple regression analyses revealed that common species were only related to urban infrastructure features (i.e., cables, lightning rods, building height), while fairly common and rare species were related to habitat structure and urban-related hazards (Table 3).
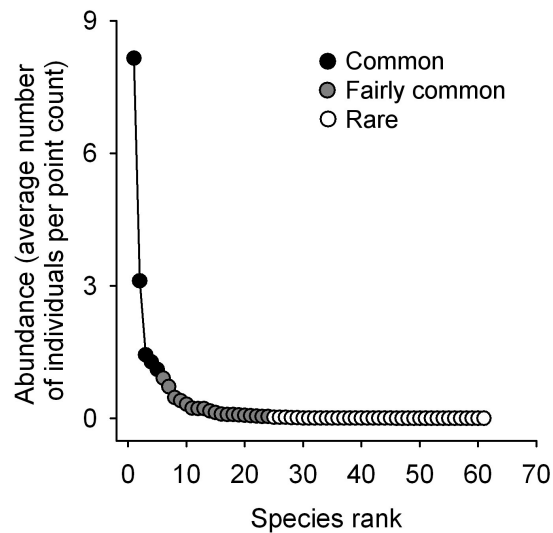

Figure 2. Rank/abundance plot for the bird communities recorded in the three studied cities.

Common species richness was positively related to the number of cables and the number of lightning rods, while their abundances were positively related to maximum building height (Table 3a,b). Fairly common species richness was positively related to tree and shrub cover, and negatively related to the number of passing pedestrians, with an important non-significant positive relationship with wealthiness (Table 3c). Fairly common species abundances were positively related to tree cover and negatively related to built cover, number of electric and telephone poles, and number of dogs, with an important non-significant positive relationship with wealthiness (Table 3d). Rare species richness was positively related to tree cover, herbaceous plant minimum height, and the number of electric and telephone poles, and negatively related to the number of dogs and passing pedestrians (Table 3e). Finally, rare species abundances were positively related to tree cover and to the number of electric and telephone poles, and negatively related to the number of light poles (Table 3f).

Table 3. Multiple regression analyses between common, fairly common, and rare species richness and abundance, and the 17 habitat variables measured within a 25 m radius area at each point count location in all the studied cities.

	Beta*	SE	t	P
(a) Common species richness (General model: R = 0.19, $F_{2,271}$ = 4.94, P = 0.007)				
Intercept			17.376	0.000
Number of cables	0.114	0.060	1.877	0.049
Number of lightning rods	0.173	0.060	-2.848	0.004
(b) Common abundances (General model: R = 0.25, $F_{1,272}$ = 18.52, P < 0.001)				
Intercept			-1.775	0.077
Max. building height	0.252	0.058	4.304	0.000
(c) Fairly common species richness (General model: R = 0.62, F^4_{269} = 43.63, P < 0.001)				
Intercept			3.003	0.002
Tree cover	0.483	0.050	9.584	0.000
Shrub cover	0.137	0.050	2.727	0.006
Passing pedestrians	-0.246	0.047	-5.148	0.000
Wealthiness**	0.078	0.047	1.638	0.102
(d) Fairly common abundance (General model: R = 0.49, $F_{6,267}$ = 14.70, P < 0.001)				
Intercept			3.369	0.000
Tree cover	0.280	0.061	4.541	0.000
Built cover	-0.154	0.065	-2.375	0.018
No. elect./telephone poles	-0.283	0.056	-5.039	0.000
Number of dogs	-0.120	0.059	-2.018	0.044
Wealthiness**	0.092	0.058	1.586	0.113
(e) Rare species richness (General model: R = 0.48, $F_{5,268}$ = 16.35, P < 0.001)				
Intercept			0.715	0.475
Tree cover	0.302	0.058	5.161	0.000
Herbaceous min. height	0.168	0.054	3.120	0.002
No. elect./telephone poles	0.167	0.057	2.923	0.003
Number of dogs	-0.184	0.060	-3.046	0.002
Passing pedestrians	-0.150	0.054	-2.762	0.006
(f) Rare abundance (General model: R = 0.38, $F_{3,269}$ = 11.11, P < 0.001)				
Intercept			-3.264	0.001
Tree cover	0.324	0.057	5.645	0.000
No. elect./telephone poles	0.143	0.060	2.370	0.018
Number of light poles	-0.187	0.061	-3.030	0.002

* In multiple regression analyses, Beta is the regression coefficient, representing the contribution of each independent variable to the prediction of the dependent variable (StatSoft, Inc., 2010).

** As multiple regression analyses consider the interaction between variables, some models include significantly related variables only in the presence of other non-significantly related variables. Thus, although we used a statistical significance of P < 0.05, some non-significantly related variables are reported as part of the model that best explained variations in the dependent variable.

The two main factors of the principal components and classification analysis explained 60% of the variance. Both factors were related to a gradient of urbanization intensity, with Factor 1 explaining 35.5% of the variance and Factor 2 explaining 25.4% of the variance. Common species richness and abundances were related to highly developed areas, while fairly common and rare species richness and abundances were related to well vegetated areas (Fig. 3).
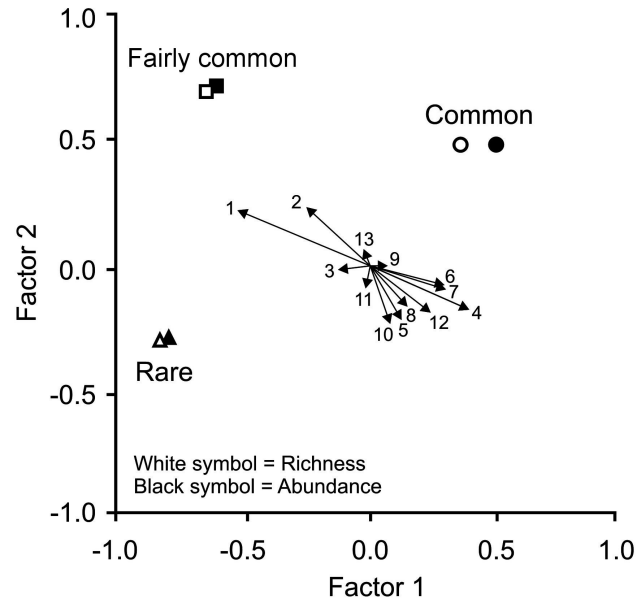

Figure 3. Principal component and correspondence analysis relating habitat traits and abundant, common, and rare species richness and abundance. Arrows in the center of the plot represent the intensity of relationship (length) and direction in relation to common, fairly common, and rare urban-dwelling bird species richness and abundances. 1 = tree cover; 2 = shrub cover; 3 = herbaceous plant minimum height; 4 = built cover; 5 = number of electric/telephone poles; 6 = number of electric/telephone cables; 7 = number of doors; 8 = number of light poles; 9 = maximum building height; 10 = number of lightning rods; 11 = number of dogs; 12 = passing pedestrians / min.

Discussion

Urban habitat features affect both positively and negatively urban-dwelling birds (see Chace & Walsh, 2006; Evans et al., 2009; MacGregor-Fors et al., 2009; and references therein). In general, our results agree with previous studies, showing that urban-dwelling bird species richness and abundances are positively related to vegetation features and wealthiness (Lim & Sohdi, 2004; Melles, 2005; MacGregor-Fors, 2008), and negatively related to intense human activities and high abundance of potential predators (Blair, 1996; Miller, Fraterrigo, Hobbs, Theobald, & Wiens, 2001; Sims, Evans, Tratalos & Gaston, 2008; López-Flores et al., 2009; Ortega-Álvarez & MacGregor-Fors 2009). Also, our results support the idea that urban intensity

has a negative effect on urban-dwelling bird communities, differing from previous studies reporting peaks in avian diversity in areas with intermediate levels of urbanization (Blair, 1996; Tratalos et al., 2007; Lepczyk et al., 2008).

As expected, common bird species richness and abundances showed positive significant relationships with built cover and urban infrastructure features (i.e., number of cables, number of lightning rods, maximum building height; Table 3a,b), and were independent of biological heterogeneity and socioeconomic level. These results are similar to what has been found for urban-exploiter species (Kark, Iwaniuk, Schalimtzec & Banker, 2007), defined as those species "adept at exploiting these [urbanization] changes and, consequently, should reach their highest densities in developed sites" (Blair, 1996). Our results were not surprising, as urban exploiter species are highly successful using human-related resources in highly developed areas, including crowded sites (Shochat, 2004; Ortega-Alvarez & MacGregor-Fors, 2009). Also, a major proportion of abundant bird species nest successfully on buildings and/or urban structures (Johnsen & VanDruff, 1987; Sacchi, Gentilli, Razzetti, & Barbieri, 2002), making them ecologically successful in highly developed urban areas. However, we found no relationship between urban hazards and housing densities with common bird species richness and abundances. This result suggests that measured urban related hazards (i.e., number of windows, passing cars and pedestrians / min, number of cats and dogs recorded during the point count) do not represent a limitation for urban-dwelling common bird species, such as *Passer domesticus, Hirundo rustica, Columba livia, Columbina inca,* and *Quiscalus mexicanus* (Table 2).

As expected, fairly common species richness and abundances were positively related to vegetation cover (i.e., tree and shrub) and were negatively related to two urban related hazard variables (i.e., passing pedestrians, number of dogs), with an important contribution of wealthiness. Unexpectedly, fairly common species did not show any relationship with housing density and biological heterogeneity, were negatively related to built cover and to one urban infrastructure variable (i.e., number of electric and telephone poles), and did not show significant relationships with passing cars and the number of cats. Our results indicate that fairly common species are attracted by the vegetation components of urban areas, such as tree and shrub cover (Jokimäki, 1999; Melles et al., 2003; Daniels & Kirkpatrick, 2003; MacGregor-Fors, 2008; Ortega-Álvarez & MacGregor-Fors, 2009; MacGregor-Fors et al., in press a). As noted by other authors, tree cover is a key element to maintain bird species within urban areas (Gavareski, 1976; Munyenyembe et al., 1989; MacGregor-Fors, 2008). In fact, trees are one of the most important vegetation components for urban-dwelling birds for roosting, nesting, hiding, and foraging (Mills, Dunning, & Bates, 1989; Munyenyembe et al., 1989). Shrubs within urban areas have been also identified as crucial for birds, acting as important nesting sites (Jokimäki, 1999; Leston & Rodewald, 2006), shelters from predators and human disturbance (Fernández-Juricic, Jimenez, & Lucas, 2001), and additional feeding resources (Melles et al., 2003). Finding negative relationships between fairly common bird abundances and built cover, and the number of electric telephone poles suggests that, although these species are adaptable to urban habitats, they are not exempt of the effects that artificial structures represent, often reducing and competing for the space available to establish vegetation components (Marzluff et al., 2001).

As previous studies have found, passing pedestrians tend to be negatively related to urban bird species richness (Blair, 1996; Fernández-Juricic, 2000; Miller et al., 2001), specially native urban-dwelling ones (Ortega-Álvarez & MacGregor-Fors, 2009; MacGregor-Fors et al., in press a). In fact, pedestrians have been identified as a component that interrupts bird foraging and often force them to fly away, decreasing their probabilities of using crowded sites for foraging (Fernández-Juricic & Tellería, 2000). Added to pedestrian activity, we found dogs to be negatively related to fairly common bird diversity. Important numbers of off-leash dogs chase birds within Mexican cities, often killing them, acting as major stressor agents that negatively affects some urban-dwelling bird species (Chávez-Zichinelli pers. comm.). Although cats have been identified as a major urban bird predation force (Mitchell & Beck, 1992), we did not record a significant negative relationship between them and fairly common bird abundances. The latter could be due to two non-exclusive explanations: (1) the fact that cats are more secretive than dogs, and we recorded very low cat numbers during our bird surveys (which could result in an underestimation of their densities); and (2) cat densities could be low because of the high numbers of free-ranging dogs present in the streets, an element that is not common in developed countries (pers. obs.). Thus, this result should be interpreted carefully.

Although our results only suggest that socioeconomic level represent an important, yet not significantly related variable to fairly common bird species richness and abundances. In general, wealthiness is related to urban habitat features that are crucial for these birds, such as tree and shrub cover and low human activity pressures (Melles, 200; Fuller, Warren, Armsworth, Barbosa & Gaston, 2008; Strobach, Haase & Kabisch, 2009). In the three cities we studied, this result seems to be caused by the presence of gardens in areas with higher socioeconomic level.

Rare bird species richness and abundances showed, as expected, positive relationships with tree cover, herbaceous plant height, and negative relationships with the number of light poles, dogs, and passing pedestrians. Unexpectedly, rare birds showed to be positively related with the number of electric and telephone poles, and showed no significant relationship with biological heterogeneity, housing density, and socioeconomic level. As stated before, trees are one of the most important vegetation components for urban adaptable birds (Mills, Dunning, & Bates, 1989; Munyenyembe et al., 1989), plus herbaceous plant height in our study area is closely related to unmanaged lots where native species find feeding and hiding resources, even within developed areas (MacGregor-Fors et al., in press a). Although the density of light poles does not seem as a variable that should affect rare birds, these urban structures are related to the presence and abundance of House Sparrows in the studied cities, where they use them to nest and roost (pers. obs.). Because House Sparrows can exclude up to 30% of the bird species from neotropical urban bird communities (MacGregor-Fors, Morales-Pérez, Quesada, & Schondube, 2010), urban structures that promote their numbers should have negative effects on other birds. Also, as stated above, dogs can act as important predators and stressor agents for urban-dwelling birds (Chávez-Zichinelli pers. comm.) and the number of passing pedestrians could be related to changes in foraging-escape dynamics that decrease the capability of birds to use highly human-frequented areas (Fernández-Juricic & Tellería, 2000).

Our results suggest that the positive relationship found between rare species and the number of electric and telephone poles is associated to the negative effect that this habitat feature had on fairly common bird abundances, allowing some rare species to be present where the competition with fairly common birds is less severe or null. However, this idea remains to be tested. Also, we believe that we did not find any relationship between socioeconomic level and rare birds because they mainly concentrate in urban green areas and wide well-vegetated median strips, which are generally present in different areas of a city, despite their wealthiness.

Because birds can act as ecological thermostats, providing information of the quality of the urban sites they occupy, we can use this information to promote urban biodiversity and improve the environmental quality that urban-citizens face daily (Turner, Nakamura, & Dinetti, 2004; MacGregor-Fors et al., 2009). Our study shows that highly developed urban areas only benefit the few species capable to face the hazards present in them, excluding most other bird species. Fairly common and rare bird species benefit from some specific vegetation features and human wealthiness, and are negatively affected by highly urbanized areas, human activities, the abundance of dogs, and the density of urban structures that attract aggressive urban-exploiter species. Thus, based on our results, we suggest that urban management and planning policies should take into account the following recommendations in order to increase habitat quality for birds within urban areas: (1) increasing tree and shrub cover within cities, not only within urban green areas, but in other land-uses (e.g., residential, industrial); (2) giving differential vegetation management to urban green areas in order to allow shrub and herbaceous plant growth; (3) controlling homeless dogs and restricting unleash dogs to specific areas; (4) concentrating heavy pedestrian traffic in highly developed areas; (5) restricting pedestrian activities within well-vegetated sites of urban green areas; and (6) considering the need of homogenizing the ecological quality throughout cities, regardless of socioeconomic boundaries.

Acknowledgments

References

Arizmendi, M. C., Lopez-Saut, E., Monterrubio-Solís, C., Juarez, L., Flores-Moreno, I., & Rodriguez-Flores, C. (2008). Efecto de la presencia de bebederos artificiales sobre la diversidad y abundancia de los colibries y el ámbito reproductivo de dos especies de plantas en un parque suburbano de la ciudad de México. *Ornitología Neotropical, 19, 491–500*.

Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., & Weslien, J. (1994). Threatened plant, animal, and fungus species in Swedish forests: Distributions and habitat associations.

Conservation Biology, *8, 718–731*.

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. *Ecological Applications*, *6, 506–519*.

Boren, J., & Hurd, B. J. (2005). *Controlling nuisance birds in New Mexico*. New Mexico State University: Cooperative Extension Service, College of Agriculture and Home Economics.

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape and Urban Planning*, *74, 46–69*.

Chao, A., & Lee, S. M. (1992). Estimating the number of classes via sample coverage. *Journal of the American Statistical Association*, *87, 210–217*.

Collins, S. L. (1980). A comparison of nest-site and perch-site vegetation structure for seven species of warblers. *Wilson Bulletin*, *93, 542–547*.

Crooks, K. R., Suarez, A. V., & Bolger, D. T. (2004). Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biological Conservation*, *115, 451–462*.

Cupul-Magaña, F. G. (2003). Nota sobre colisiones de aves en las ventanas de edificios universitarios en Puerto Vallarta, México. *Huitzil*, *4, 17–21*.

DeGraff, R. M., & Wentworth, J. M. (1986). Avian guild structure and habitat associations in suburban bird communities. *Urban Ecology*, *9, 399–412*.

Daniels, G., & Kirkpatrick, J. (2006). Does variation in garden characteristics influence the conservation of birds in suburbia? *Biological Conservation*, *133, 326–335*.

DeGraff, R. M., Hestbeck, J. B., & Yamasaki, M. (1998). Associations between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine, USA. *Forest Ecology and Management*, *103, 217–233*.

Dhondt, A. A., Tessaglia, D. L., & Slothower, R. L. (1998). Epidemic mycoplasmal conjunctivitis in House Finches from Eastern North America. *Journal of Wildlife Diseases*, *43, 265–280*.

Díaz, I. A., Armesto, J. J., Reid, S., Sieving, K. E., & Willson, M. F. (2005). Linking forest structure and composition: avian diversity in successional forests of Chiloé Island, Chile. *Biological Conservation*, *123, 91–101*.

Donnely, R., & Marzluff, J. M. (2006). Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. *Urban Ecosystems*, *9, 99–117*.

Emlen, J. T. (1974). An urban bird community in Tucson, Arizona: Derivation, structure, regulation. *The Condor*, *76, 184–197*.

Evans, K. L., Newson, S. E., & Gaston, K. J. (2009). Habitat influences on urban avian assemblages. *Ibis*, *151, 19–39*.

Fernández-Juricic, E., & Tellería, J. L. (2000). Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. *Bird Study*, *47, 13–21*.

Fernández-Juricic, E., Jimenez, M. D., & Lucas, E. (2001). Bird tolerance to human disturbance in urban parks of Madrid (Spain): Management implications. In: J.M. Marzluff, R. Bowman, & R. Donnely (Eds). *Avian conservation and ecology in an urbanizing world* (pp. 259–273). Boston: Kluwer Academic.

Fuller, R. A., Warren, P. H., Armstrong, P. R., Barbosa, O., & Gaston, K. J. (2008). Garden bird feeding predicts the structure of urban avian assemblages. *Diversity and Distributions*, *14, 131–137*.

Gavareski, C. A. (1976). Relation of park size and vegetation to urban bird populations in Seattle, Washington. *The Condor*, *78, 375–382*.

Gering, J. C., & Blair, R. B. (1999). Predation on artificial bird nests along an urban gradient: Predatory risk or relaxation in urban environments?. *Ecography*, *22, 532–541*.

Huff, M. H., Bettinger, K. A., Ferguson, M. L., Brown, M. J., & Altman, B. (2000). *A habitat-based point-count protocol for terrestrial birds, emphasizing Washington and Oregon*. Portland: U.S.

Department of Agriculture.

Johnsen, A. M., & VanDruff, L. W. (1987). Spring and winter distribution of introduced bird species and native bird species richness within a complex urban environment. In: L.W. Adams, & D. L. Leedy (Eds). *Integrating man and nature in the metropolitan environment* (pp. 123–127). Columbia: National Institute of Urban Wildlife.

Jokimäki, J. (1999). Occurrence of breeding bird species in urban parks: Effects of park structure and broad-scale variables. *Urban Ecosystems*, *3, 21-34*.

Kark, S., Iwaniuk, A., Schalimtzec, A., & Banker, E. (2007). Living in the city: Can anyone become an "urban exploiter"? *Journal of Biogeography*, *34, 638-651*.

Klem, D. (2009). Preventing bird-window collisions. *Wilson Journal of Ornithology*, *121, 314-321*.

Kubetzki, U., & Garthe, S. (2007). Nests With a View: Distribution, Nest Habitats and Diets of Roof-Breeding Common Gulls (Larus canus) in Northern Germany. *Waterbirds*, *30, 602-608*.

Lepczyk, C., Flather, C., Radeloff, V., Pidgeon, A., Hammer, R., & Liu, A. (2008). Human impacts on regional avian diversity and abundance. *Conservation Biology*, *22, 405-416*.

Leston, L. F. V., & Rodewald, A. D. (2006). Are urban forests ecological traps for understory birds? An examination using Northern Cardinals. *Biological Conservation*, *3, 566–574*.

Leveau, L. M. (2008). Dynamics of nectarivory in the House Sparrow in an urban environment. *Ornitología Neotropical* , *19, 275–281*.

Lim, H. C., & Sodhi, N. S. (2004). Responses of avian guilds to urbanisation in a tropical city. *Landscape and Urban Planning*, *66, 199–215*.

López-Flores, V., MacGregor-Fors, I., & Schondube, J. E. (2009). Artificial nest predation along a neotropical urban gradient. *Landscape and Urban Planning*, *92, 90-95*.

MacGregor-Fors, I. (2008). Relation between habitat attributes and bird richness in a western Mexico suburb. *Landscape and Urban Planning*, *84, 92-98*.

MacGregor-Fors, I., Morales-Pérez, L., & Schondube, J. E. (In press a). From forests to cities: Effects of urbanization on subtropical mountain bird communities. *Studies in Avian Biology*.

MacGregor-Fors, I., Morales-Pérez, L., & Schondube, J. E. (In press b). Migrating to the city: Responses of neotropical migrant bird communities to urbanization. *The Condor*.

MacGregor-Fors, I., Ortega-Álvarez, R., & Schondube, J. E. (2009). On the ecological quality of urban systems: An ornithological perspective. In: D.S. Graber, & K. A. Birmingham (Eds). *Urban Planning in the 21st Century* (pp. 51–66). New York: Nova Science Publishing.

Marzluff, J. M., Bowman, R., & Donnely, R. (2001). A historical perspective on urban bird research: Trends, terms, and approaches. In: J.M. Marzluff, R. Bowman, & R. Donnely (Eds). *Avian conservation and ecology in an urbanizing world* (pp. 1–17). Boston: Kluwer Academic.

McDonnell, M. J., & Pickett, S. T. A. (1990). Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology*, *71, 1232–1237*.

Melles, S. J. (2005). Urban bird diversity as an indicator of human social diversity and economic inequality in Vancouver, British Columbia. *Urban Habitats*, *3, 25–48*.

Melles, S., Glenn, S., & Martin, K. (2003). Urban bird diversity and landscape complexity: Species-environment associations along a multiscale habitat gradient. *Conservation Ecology*, *7, 5*.

Miller, J. R., Fraterrigo, J. M., Hobbs, N. T., Theobald, D. N., & Wiens, J. A. (2001). Urbanization, avian communities, and landscape ecology. In: J.M. Marzluff, R. Bowman, & R. Donnely (Eds). *Avian conservation and ecology in an urbanizing world* (pp. 117-137). Boston: Kluwer Academic.

Mills, G. S., Dunning, J. B., & Bates, J. M. (1989). Effects of urbanization on breeding bird community structure in Southwestern desert habitats. *The Condor*, *91, 416–428*.

Mitchell, J. C., & Beck, R. A. (1992). Free-ranging domestic cat predation on native vertebrates in rural and urban Virginia. *Virginia Journal of Science*, *43, 197–206*.

Munyenyembe, F., Harris, J., & Hone, J. (1989). Determinants of bird populations in an urban area.

Australian Journal of Ecology, *14, 549-557*.

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 and Urban Planning*, *90, 189-195*.

Parsons, H., Major, R., & French, K. (2006). Species interactions and habitat associations of birds inhabiting urban areas of Sydney, Australia. *Austral Ecology*, *31, 217-227*.

Peck, R., Olsen, C., & Devore, J. (2008). *Introduction to statistics & data analysis*. Belmont: Brooks/Cole.

Ralph, C. J., Geupel, G. R., Pyle, P, Martin, T. E., DeSante, D. F., & Milá, B. (1996). *Manual de métodos de campo para el monitoreo de aves terrestres*. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Gen. Tech. Rep. PSW-GTR-144.

Robb, G. N., McDonald, R. A., Chamberlain, D. E., & Bearhop, S. (2008). Food for thought: Supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment*, *6, 476–484*.

Rodewald, A. D., Shustack, D. P., & Hitchcock, L. E. (2009). Exotic shrubs as ephemeral ecological traps for nesting birds. *Biological Invasions*, *12, 33–39*.

Sacchi, R., Gentilli, A., Razzetti, E., & Barbieri, F. (2002). Effects of building features on density and flock distribution of feral pigeons Columba livia var. domestica in an urban environment. *Canadian Journal of Zoology*, *80, 48-54*.

Seather, B. E., Ringsby, T. H., Bakke, A., & Solberg, E. J. (1999). Spatial and temporal variation in demography of a house sparrow population. *Journal of Animal Ecology*, *68, 628–637*.

Sims, V, Evans, K., Newson, S., Tratalos, J., & Gaston, K. (2008). Avian assemblage structure and domestic cat densities in urban environments. *Diversity and Distributions*, *14, 387-399*.

Shen, T. J., Chao, A., & Lin, C. F. (2003). Predicting the number of new species in further taxonimic sampling. *Ecology*, *84, 798-804*.

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

StatSoft Inc. (2010). *Electronic Statistics Textbook*. Tulsa: StatSoft WEB.

Strohbach, M. W., Haase, D., & Kabsich, N. (2009). Birds and the city: Urban biodiversity, land Use, and socioeconomics. *Ecology and Society*, *14(2), 31*.

Swift, B. L., Larson, J. S., & DeGraff, R. M. (1984). Relationship of breeding bird density and diversity to habitat variables in forested wetlands. *Wilson Bulletin*, *96, 48–59*.

Tratalos, J., Fuller, R. A., Evans, K. L., Davies, R. G., Newson, S. E., Greenwood, J. J. D., & Gaston, K. J. (2007). Bird densities are associated with household densities. *Global Change Biology*, *13, 1685-1695*.

Turner, W., Nakamura, T., & Dinetti, M. (2004). Global urbanization and the separation of human from nature. *Bioscience*, *54, 585-590*.

USGS (2007). *Fact sheet: Coping with diseases at bird feeders.* U.S. Geological Survey - National Wildlife Health Center, Denver, CO.

Vargas Uribe, G. (2008). *Urbanización y Configuración Territorial en la región Valladolid-Morelia 1541-1991*. Morelia: Morevallado Editores.

Villegas, M., & Garitano-Zavala, Á. (2010). Bird community responses to different urban conditions in La Paz, Bolivia. *Urban Ecosystems*, *13, 375-391*.

Capítulo VIII

Discusión y conclusiones

En general, los resultados de este trabajo de tesis muestran que la urbanización es un agente de cambio que afecta drásticamente a las comunidades de aves sin importar su estatus migratorio. Sin embargo, dicho efecto no es igual en diferentes asentamientos humanos y depende de tipo de especies que componen a las comunidades de aves urbanas, del tamaño de los asentamientos y de las características específicas de cada sitio.

Al evaluar las diferencias entre las comunidades de aves migratorias presentes en la ciudad de Morelia y bosques conservados cercanos a la ciudad, fue evidente que la urbanización representa una limitación importante para el establecimiento de un gran número de especies de aves migratorias neotropicales. Sin embargo, a diferencia de lo que se ha encontrado para las comunidades de aves residentes, la densidad de aves migratorias fue mayor en los bosques conservados que en la ciudad de Morelia, lo que sugiere que no existen especies de aves migratorias explotadoras de ambientes urbanos. En cuanto a la distribución espacial de las especies de aves migratorias a lo largo de la ciudad de Morelia, encontramos que, en promedio, los registros fueron llevados a cabo en sitios ubicados a 1 km del borde de la ciudad, con valores máximos de 2.7 - 3.4 km en el caso de tres especies: *Wilsonia pusilla, Polioptila caerulea, Dendroica coronata*. Lo anterior parece estar relacionado con la escasez de cobertura arbórea en la zona centro de la ciudad, variable que explicó en mayor medida la presencia y abundancia de especies de aves migratorias en la ciudad. Aunque algunos de los resultados de esta sección muestran efectos negativos importantes de la urbanización sobre las especies de aves migratorias neotropicales, algunas de las especies registradas en la ciudad de Morelia son de interés para la conservación. Así, la urbanización puede ser considerada, desde el punto de vista de las comunidades de aves migratorias, como una espada de doble filo, limitando el establecimiento de territorios de invierno para muchas especies y ofreciendo hábitat de invierno a otras (Capítulo VI).

Como parte de los mecanismos que podrían explicar los patrones de diversidad de aves registrados en las últimas décadas en zonas urbanas, la respuesta de las comunidades de aves ante estadios tempranos de urbanización (Capítulo III) muestran que la riqueza de especies decae significativamente con la urbanización. Sin embargo, la equitatividad de las comunidades de aves fue mayor en la zona urbanizada libre de especies de aves explotadoras de ambientes perturbados. Dicho patrón mostró

estar cercanamente relacionado con la ausencia de especies de aves explotadoras de ambientes urbanos, subrayando el papel negativo que juegan estas especies cuando forman parte de comunidades de aves urbanas. Así, mientras que la urbanización mostró tener un efecto similar sobre las riqueza de especies en un asentamiento humano muy pequeño rodeado por bosques conservados y un asentamiento humano pequeño rodeado por bosques y campos de cultivo abandonados, la presencia de especies explotadoras de ambientes perturbados jugó un papel crucial en el aumento de la tasa de recambio de especies con respecto a las comunidades de aves de los bosques nativos, además de ser responsables del incremento significativo en la densidad de aves dentro de los sitios urbanos.

Estrechamente relacionado con lo anterior, los resultados referentes al estudio del gorrión casero (*Passer domesticus*), una especie explotadora de ambientes urbanos exótica, agresiva e invasiva (Capítulo IV), reforzaron las conclusiones del Capítulo III. Los resultados de esta sección muestran que, independientemente de la escala geográfica de análisis, sitios invadidos por el gorrión casero tienen comunidades de aves pobres y fuertemente dominadas, mientras que las comunidades no invadidas mostraron ser significativamente más ricas y equitativas. Además, la presencia del gorrión mostró tener un efecto importante sobre la distribución de las abundancias de las comunidades de aves, modificando el orden de abundancias de las especies más abundantes y reduciendo sus números. El análisis de recambio de especies entre zonas invadidas y no invadidas reveló que la disminución en la riqueza de especies de aves en zonas invadidas por el gorrión son debidas a la pérdida de especies, más que al cambio en la composición de especies. Finalmente, al analizar la naturaleza de las comunidades de aves en sitios naturales no invadidos, sitios perturbados no invadidos y sitios perturbados e invadidos, fue evidente la pérdida de especies debido a la perturbación de los hábitats, sin embargo la invasión del gorrión representa una fuerza negativa adicional que causa un efecto todavía más dramático.

Como parte de los mecanismos responsables de la diversidad de las comunidades de aves en zonas urbanas, el tamaño de los asentamientos humanos mostró tener efectos importantes sobre la riqueza y composición de las comunidades de aves. Los resultados de este análisis mostró que la riqueza de especies de aves está íntimamente relacionada con el tamaño de los asentamientos humanos. Dicha relación fue más pronunciada en asentamientos humanos que la relación que existente entre la riqueza de especies de aves en parches de matorrales de diferentes tamaños ubicados próximos los asentamientos humanos estudiados. Cabe resaltar que, en un análisis que contempla a los asentamientos humanos como unidades de estudio, el tamaño de los asentamientos humanos fue la

única variable relacionada con cambios en la riqueza de especies de aves, mientras que el porcentaje de construcción, la riqueza de especies de plantas, la cobertura arbórea y la densidad poblacional no mostraron ninguna relación significativa. Lo anterior parece estar relacionado con la escala de análisis, ya que estudios previos llevados a cabo en la ciudad de Morelia muestran que variables tales como la cobertura foliar juegan un papel crucial explicando la riqueza de aves urbanas a nivel puntual. Finalmente, la composición de especies varió en relación con el tamaño de los asentamientos. Los resultados de esta sección sugieren que los asentamientos humanos se comportan como islas ecológicas y que existen umbrales de tamaño de asentamientos humanos que determinan la riqueza de especies y composición de sus comunidades. Sin embargo, dichos umbrales parecen no ser comparables entre regiones ecológicas distintas. En el caso de los asentamientos humanos del centro-norte del estado de Michoacán, el umbral fue identificado en asentamientos mayores a 10.2 km^2, en el que la riqueza de especies dejó de aumentar y el grupo de especies que conformó a las comunidades de aves de asentamientos urbanos cambió drásticamente debido a un grupo de especies de aves que sólo fueron registradas en asentamientos grandes (Capítulo V).

Tomando datos puntuales independientes en las tres ciudades más grandes del estado de Michoacán (i.e., Morelia, Uruapan y Zamora), las características de hábitat moldearon la riqueza y abundancia de las especies de aves residentes (Capítulo VII). Cabe resaltar que esta sección de la tesis comprende el primer estudio que evalúa la importancia relativa de los diferentes componentes de los ambientes urbanos sobre comunidades de aves residentes, haciendo especial énfasis sobre los componentes urbanos que conforman parte de la estructura de hábitat dentro de asentamientos humanos. En particular, las especies de aves abundantes (para las que se registró más de un individuo promedio por punto de conteo) sólo fueron afectadas por elementos de la infraestructura urbana (i.e., número de cables, número de pararrayos, altura de las edificaciones), mientras que las especies medianamente comunes (para las que se registró entre 0.03 y un individuo promedio por punto de conteo) y raras (para las que se registró menos de 0.03 individuos por punto de conteo, representando menos de 10 individuos del total de muestreos) mostraron estar, en general, positivamente relacionadas con la estructura de la vegetación (e.g., cobertura arbórea, altura de plantas herbáceas) y negativamente relacionadas con las amenazas urbanas (e.g., número de perros, número de transeúntes). Aunque no encontramos relaciones significativas entre la riqueza de especies de aves y sus abundancias con nivel socioeconómico de los sitios muestreados, encontramos una tendencia positiva entre la riqueza de especies y la abundancia de especies medianamente en relación con el nivel socioeconómico. Lo anterior parece estar relacionado con algunas características que mostraron ser cruciales para este grupo de aves (e.g., alta cobertura arbórea y arbustiva, baja intensidad de

actividades humanas).

Los resultados presentados anteriormente permiten hacer recomendaciones que podrían mitigar el efecto negativo que tiene la urbanización, y sus procesos, sobre las comunidades de aves que habitan dentro de zonas urbanas neotropicales:

1. Implementar programas de educación ambiental que permitan utilizar a las aves como grupo carismático para generar un vínculo entre la gran cantidad de conocimiento que se tiene y los habitantes urbanos.

2. Tomar en cuenta el tamaño de los asentamientos humanos cuando se pretenda manejar a las comunidades de vida silvestre que habitan dentro de zonas urbanas.

3. Identificar los componentes de la vegetación que benefician a las especies raras de aves y usar la información para implementar acciones que incrementen sus poblaciones.

4. Controlar las poblaciones de especies explotadoras de ambientes urbanos (tanto exóticas como nativas), ya que sus elevadas abundancias afectan negativamente a diversas especies de aves nativas que podrían integrarse a las comunidades de aves urbanas en ausencia, o bajas poblaciones, de las especies explotadoras.

5. Controlar a las mascotas callejeras y/o ferales en zonas urbanas, ya que pueden representar una amenaza de depredación para las aves.

6. Concentrar los sitios de tráfico de personas y de vehículos en zonas altamente desarrolladas de las ciudades para concentrar sus efectos negativos en zonas particulares y permitir la existencia de zonas más seguras para las aves en otras áreas de las ciudades.

7. Incluir políticas de justicia ambiental, definida como con la finalidad de homogeneizar la calidad ecológica de los diferentes sectores de las ciudades.

Non-exotic invasion of Great-tailed Grackles
Quiscalus mexicanus in a tropical dry forest reserve

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We report two recordings of Great-tailed Grackles *Quiscalus mexicanus* in the Chamela Biosphere Reserve, which is an important conservation area for pristine tropical dry forests in West Mexico. These recordings are important for three main reasons: (1) they reveal the recent encroachment of the reserve by human-disturbed areas; (2) the recorded grackles fought with West Mexican Chachalacas *Ortalis poliocephala*, and won, underlining their possible negative effects towards other native bird species; and (3) if Great-tailed Grackles successfully invade the conservation area, it could turn into an unmanageable scenario with possible negative consequences within an important area for bird conservation in the dry tropics.

Key words: dispersal, Great-tailed Grackle, *Quiscalus mexicanus*, tropical dry forest, Chamela, Mexico

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Invasive species play a significant role in global change, representing a threat to biodiversity (Vitousek *et al.* 1997). Although a great proportion of invasive bird species are exotic (e.g. House Sparrow *Passer domesticus* in the Americas), some native bird species are also able to invade new areas by dispersing through matrixes of human-disturbed habitats (e.g. Canyon Towhee *Pipilo fuscus*, Great-tailed Grackle *Quiscalus mexicanus*). Successful native invasive bird species could have dramatic effects on local avifaunas, a process tended to be ignored because the invaders are native to the country where their invasions occur.

The Great-tailed Grackle is a large-sized icterid presently distributed from southern Canada to Peru (Stiles & Skutch 1989, Howell & Webb 1995, Sibley 2001). This grackle has broadened its distribution in the last 150 years, expanding from southern Mexico, to central-northern Mexico, most of the USA, and part of Canada. This expansion is closely related to landscape matrixes generated by agricultural and urban activities (Wehtje 2003). In Mexico, the Great-tailed Grackle is highly successful in urban areas, filling a niche similar to what Rock Pigeons *Columba livia* and European Starlings *Sturnus vulgaris* occupy in Europe (Christensen 2000).

Results and discussion
Although the Great-tailed Grackle is well distributed along human-disturbed landscapes in Mexico, it does not enter natural habitats. We were surprised to record this grackle within the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve. Our first sight-recording was in February 2008, when a male Great-tailed Grackle was recorded within the build-up area of

the Chamela biological station (19°29'52"N, 105°02'39"W, 90 m a.s.l.). Our second observation was conducted in early May 2009, when we sight-recorded four males and one female Great-tailed Grackles in the edge between the forest and the biological station, competing for food-leftovers (vegetables and fruit) besides the station's kitchen, where other wildlife species feed daily (e.g. West Mexican Chachalaca *Ortalis poliocephala*, San Blas Jay *Cyanocorax sanblasianus*, Yellow-winged Cacique *Cacicus melanicterus*, Back-streaked Oriole *Icterus pustulatus*, Collared Peccary *Tayassu tajacu*, White-nosed Coati *Nasua narica*).

The nearest areas from where the grackles could have dispersed to the biological station are a trash dumping site and a crop-field area, both located ~2.7 km away. Although several urban settlements, where the grackle is present and abundant, are quite close to the biological station (Careyes: 6.7 km; San Mateo: 9.4 km; Juan Gil: 11.4; Zapata/Villa: 14.9 km), this species has never been recorded in the station grounds since the reserve was established in 1971 (Hutto *et al.* 1985, Arizmendi *et al.* 1990, Ornelas *et al.* 1993). Furthermore, during intensive mist netting and point-counts from 1999 to 2001, and from 2004 to 2008, we did not capture or observe grackles within the Biosphere Reserve (Vega-Rivera, Schondube & MacGregor-Fors, unpubl. data).

We consider these recordings important for three reasons. First, finding the Great-tailed Grackle in the build-up area of the Chamela Biological Station suggests that human disturbance encroaches upon the reserve (Vega-Rivera *et al.* 2004). This could explain why the grackles were able to find a small patch of suitable habitat completely surrounded by pristine forest. Indeed, an analysis of regional landcover change using remote sensing shows a decrease in forest cover and an increase in fragmentation around the biosphere reserve in the last seven years (Sánchez-Azofeifa *et al.* 2009). Secondly, we recorded two male grackles fighting successfully for food with West Mexican Chachalacas, a species which is almost three times heavier. This pinpoints their possible effect towards local neotropical bird species. Finally, although we do not know the impact of Great-tailed Grackles on the bird community of the preserve, if this species settles in the area we expect a negative effect on the local avifauna. This is worrisome because the Chamela-Cuixmala biosphere reserve is a crucial area for bird conservation in the dry tropics (Arizmendi & Márquez-Valdelamar 2000, Arriaga *et al.* 2000, Stattersfield *et al.* 1998).

While we are starting to understand the effects that invasive bird species have on native avifaunas (Blackburn *et al.* 2009, MacGregor Fors *et al.* 2009), we know even less of the consequences that the invasion of new habitats by a native non-local species can have on bird communities. Usually this problem does not get public attention because it represents a conflict of native local vs. native non-local species. Due to the negative effects that human-commensal native non-local invasive bird species could have on native local communities, we suggest that Great-tailed Grackles should be removed from the area to avoid an unmanageable invasion scenario. However, given the present context of fragmentation and habitat modification by human activities that favour a few generalist human-commensal bird species, we can wonder whether the removal of Great-tailed Grackles from the Chamela Biological Station is going to be helpful. In other words, will we be able to safeguard specific native local bird communities in the light of the changing world? And at what cost?

References

Arizmendi M.C., Berlanga H., Márquez-Valdelamar L., Navarijo L & Ornelas, F. 1990. Avifauna de la región de Chamela, Jalisco. Instituto de Biología-UNAM, México.

Arriaga L., Espinoza J.M., Aguilar C., Martínez E., Gómez L. & Loa E. 2000. Regiones terrestres prioritarias de México. CONABIO, México.

Blackburn T.M., Lockwood J.L. & Cassey O.P. 2009. Avian invasions. The ecology and evolution of exotic birds. Oxford University Press, Oxford.

Christensen A.F. 2000. The fifteenth- and twentieth-century colonization of the Basin of Mexico by the Great-tailed Grackle (*Quiscalus mexicanus*). Global. Ecol. Biogeogr. 9: 415–420

Howell S.N.G. & Webb S. 1995. A guide to the birds of Mexico and Northern Central America. Oxford University Press, Oxford.

Hutto R.L., Hendrics P. & Pletschet S. 1985. Un censo invernal de las aves de la Estación de Biología Chamela, Jalisco, Mexico. Ann. Inst. Biol. UNAM 56: 945–954.

MacGregor-Fors I., Morales-Pérez L., Quesada J. & Schondube J.E. 2009. Relationship between the presence of House Sparrows (*Passer domesticus*) and Neotropical bird community structure and diversity. Biol. Invasions 11: doi:10.1007/s10530-009-9432-5.

Ornelas J.F., Arizmendi M.C., Marquez-Valdelamar L., Navarijo M.L. & Berlanga H.A. 1993. Variability profiles for line transect bird censuses in a tropical dry forest in Mexico. Condor 95: 422–441.

Sánchez-Azofeifa G.A., Quesada M., Cuevas-Reyes P., Castillo A. & Sánchez-Montoya G. 2009. Land cover and conservation in the area of influence of the Chamela-Cuixmala Biosphere Reserve, Mexico. Forest. Ecol. Manag. 258: 907–912.

Sibley D.A. 2001. The Sibley guide to birds. Alfred A. Knopf, New York.

Stattersfield A.J., Crosby M.J., Long A.J. & Wege D.C. 1998. Endemic bird areas of the World: priorities for biodiversity conservation. Birdlife Conservation Series No. 7. Birdlife International, Cambridge.

Stiles F. & Skutch A. 1989. A guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca.

Vega-Rivera J.H., Alvarado F., Valdivia T. & Rappole J. 2004. First report of cowbird parasitism on the Black-capped Gnatcatcher in western Mexico. Southwest. Nat. 49: 277–278.

Vitousek P.M., D'Antonio C.M., Loope L.L., Rejmánek M. & Westbrooks R. 1997. Introduced species: a significant component of human-caused global change. New. Zeal. J. Ecol. 21: 1–16

Wehtje W. 2003. The range expansion of the great-tailed grackle (*Quiscalus mexicanus* Gmelin) in North America since 1880. J. Biogeogr. 30: 1593–1607.

Samenvatting

In 2008 en 2009 werden in het droog- tropische bosreservaat Chamela-Cuixmala in het westen van Mexico twee waarnemingen van Langstaarttroepialen *Quiscalus mexicanus* gedaan. Deze soort komt van het zuiden van Canada tot in Peru voor. Het was een schok deze commensaal van mensen in een ongerept tropisch bos aan te treffen. Dat te meer daar een conflict om voedsel met de driemaal zo zware West-Mexicaanse Chachalaca *Ortalis poliocephala* door de Langstaarttroepiaal werd gewonnen. Bij de problematiek rond invasieve soorten wordt er gewoonlijk van uitgegaan dat de kolonisten exoten zijn. In dit geval, echter, gaat het om een inheemse soort die een kwetsbaar en ongerept habitat binnendringt, daartoe in staat gesteld door negatieve ontwikkelingen buiten het park (habitatversnippering en verstedelijking). De vraag is: wat te doen? Verwijdering van de binnendringers zal op den duur, bij voortschrijdende menselijke invloed rond het reservaat, steeds moeilijker en kostbaarder worden. Een niet ingrijpen zou echter grote consequenties kunnen hebben voor de kwetsbare lokale avifauna. (RGB)